The archaeology of chimpanzee technology:

Ecological perspectives on strategies of early hominin raw material acquisition and the formation of technological landscapes

Katarina Almeida-Warren

Magdalen College

University of Oxford

A thesis submitted for the degree of

Doctor of Philosophy

Hilary 2022

To Savais and Yo,

may your spirits live on amongst the sacred hills of Bossou

And to Sebastian (1991-2022)

Abstract

Since the discovery of the first Oldowan tools, the study of Plio-Pleistocene (~3.5 – 0.8 million-years ago) lithic assemblages has played an important part in discerning early hominin behaviour. However, despite the subsequent 80 years of research, the most fundamental questions of human evolution remain unanswered: What were the behavioural predecessors of stone tool use? How did our earliest technological ancestors live? And how did tool use, and the lithic assemblages produced, fit into the wider behavioural and ecological landscape? Using a primate archaeology approach, this thesis seeks to expand our understanding of how the environment may have shaped hominin behaviour by focusing on two main areas of enquiry: perishable technology and landscape use. It also aims to tackle some of the methodological challenges surrounding cross-comparison between hominin and chimpanzee archaeological records, such as the discrepancy in resolution and accuracy of spatial data collection methods. Chapter 1 provides an introduction and an overview of the historical backdrop and methodological developments to the entire thesis. Chapter 2 discusses the development of a new spatial mapping method which enables, for the first time, standardised spatial resolution across the primate order. This is followed by three core empirical chapters. Chapter 3 explores the archaeology of perishable technology by investigating the diversity and drivers of plant material procurement strategies in chimpanzee termite-fishing. The results indicate that some

differences between the three study sites could be attributed to ecological differences, while others suggested that cultural processes were at play. These findings reveal techno-cultural variation and flexible exploitation strategies that parallel the behaviours associated to the use of stone tools by our earliest ancestors, suggesting these behaviours have a much deeper origin than originally thought. Chapters 4 and 5 combine landscape archaeology with agent-based modelling to produce the first landscape-scale study of the ecological and behavioural correlates of chimpanzee stone tool-use. Analyses of the empirical data in Chapter 4 uncovered spatial relationships between nut-cracking sites, proximity to nest sites, and food availability, suggesting the presence of *activity hotspots* reminiscent of patterns of landscape-use that have been proposed for our earliest tool-using ancestors. Following from this, agent-based modelling results presented in Chapter 5 indicate that variations in the spatial distribution of resources did not produce variations in the spatial patterning of nut-cracking activity. This suggests that the dynamic relationship between the environment, behaviour and the spatial patterning of stone tool use may be even more complex than originally thought. Finally, Chapter 6 reports on the current conservation status of and major threats to the Diécké Forest — the second largest forest in Guinea and home to another population of nut-cracking chimpanzees. It was found that the chimpanzee presence in the area continues to decline with no recent evidence of nutcracking or other activities. Together with research conducted in Bossou, this research provides important insights into the fragility of West African chimpanzee populations and their cultural heritage.

Statement of Authorship

This thesis follows the integrated thesis format. All main body chapters (Chapters 2-6) are either published, submitted, or in preparation for submission in peer-reviewed journals. As such, these chapters are the product of collaborations with my supervisor and other researchers who supported their development in an advisory capacity, and, where relevant, provided data, resources, as well as analytical and computational support. I am responsible for the majority contribution of the work, including conceptualization, intellectual development, methodology, primary data collection, data curation, formal analysis, interpretation, visualization, and writing up. Exceptions include Chapter 3, first-authored by Dr. Alejandra Pascual-Garrido, for which I was responsible for data analysis and presentation, and contributed equally towards data collection, intellectual development, writing, and revisions; and Chapter 6, which benefited from contributions from Dr. Nicolas Payette regarding code revisions, model validation and analyses.

Note that these chapters are written in the first-person plural, to reflect their collaborative nature. Chapters that are published or in preparation for publication include an abstract and acknowledgements in line with the original manuscripts. The published versions including other co-authored articles published during the course of this DPhil are included at the end of the thesis (Appendix G).

Chapter 2 was originally published in:

Almeida-Warren, K., Braun, D. R., Carvalho, S. (2021) The DistoX2: A methodological solution to archaeological mapping in poorly accessible environments. *Journal of Archaeological Science*: Reports 35:102688. https://doi.org/10.1016/j.jasrep.2020.102688

Chapter 3 was originally published in:

Pascual-Garrido, A., **Almeida-Warren, K**. (2021) Archaeology of the perishable: Ecological constraints and cultural variants in chimpanzee termite-fishing. *Current Anthropology* 62(3): 333-362. https://doi.org/10.1086/713766

Chapter 4 is currently under consideration at the International Journal of Primatology:

Almeida-Warren, K., Matsuzawa, T., Carvalho, S. (Under Review) Landscaping the behavioural ecology of primate stone tool use. *International Journal of Primatology* [Preprint: BioRxiv, 2021.08.24.457369. https://doi.org/10.1101/2021.08.24.457369]

Publications

Published

Carvalho, S., Erin, W., Abwe, E. **Almeida-Warren, K.**, et al. (2022) Using non-human culture in conservation requires careful and concerted action. *Conservation Letters*: e12860. https://doi.org/10.1111/conl.12860

Pascual-Garrido, A., **Almeida-Warren, K.** (2021) Archaeology of the perishable: Ecological constraints and cultural variants in chimpanzee termite-fishing. *Current Anthropology* 62(3): 333-362. https://doi.org/10.1086/713766

Almeida-Warren, K., Braun, D. R., Carvalho, S. (2021) The DistoX2: A methodological solution to archaeological mapping in poorly accessible environments. *Journal of Archaeological Science: Reports* 35:102688. https://doi.org/10.1016/j.jasrep.2020.102688

Carvalho, S., **Almeida-Warren, K.** (2019) Primate Archaeology. Encyclopaedia of Animal Behaviour, 2nd Ed. Academic Press. https://doi.org/10.1016/B978-0-12-809633-8.90156-0

Almeida-Warren, K., Sommer, V., Piel, A. and Pascual-Garrido, A. (2017) Raw material procurement for termite fishing tools by wild chimpanzees in the Issa valley, western Tanzania. *American Journal of Physical Anthropology* 164:292-304. https://doi.org/10.1002/ajpa.23269

Submitted

Almeida-Warren, K., Matsuzawa, T., Carvalho, S. (Under Review) Landscaping the behavioural ecology of primate stone tool use. *International Journal of Primatology* [Preprint: BioRxiv, 2021.08.24.457369. https://doi.org/10.1101/2021.08.24.457369]

In preparation

Almeida-Warren, K., Fitzgerald, M., Carvalho, S. (manuscript in final draft stage; expected submission Apr/2022) Revisiting the second largest forest of Guinea a decade later: Chimpanzee presence, conservation status and threats in Diécké, Korohouan area. *Primates*

Pascual-Garrido, A., **Almeida-Warren, K.**, Carvalho, S. (manuscript in preparation; expected submission Jun/2022) Primate Archaeology 3.0. *Nature Human Behaviour*

Almeida-Warren, K., Carvalho, S, Payette, N. (manuscript in preparation; expected submission Jun/2022) Simulating the formation of chimpanzee nut-cracking sites: perspectives from agent-based modelling. *Nature Ecology & Evolution*

Acknowledgments

I am eternally grateful to my supervisor Prof. Susana Carvalho for her mentorship, friendship, and kindness throughout this journey. Thank you for this incredible opportunity and for always believing in my potential as a researcher. You encouraged me to rise to the challenge, grasp opportunities for growth, and, importantly, to slow down and take time when I most needed. I could not have wished for a better supervisor, and it is a great privilege to be your first DPhil student.

This thesis would not have been possible without the communities and research teams who supported my data collection while in the field – *Asante sana* and *Balika* (thank you). I am indebted to the inhabitants of Bossou and Korohouan for their hospitality and consent to pursue my research and for tolerating my poor attempts at speaking your beautiful Manon language. I owe most of my knowledge about the chimpanzee study populations and the forests they live in to all my research assistants across Tanzania and Guinea. I am especially grateful to Shedrack Lucas (Issa), Henry Didier Camara, and Jules Doré (Bossou) for sharing their invaluable knowledge and wisdom; and to Nasibu Zuberi Madumbi (Gombe), Patrick Hassan (Issa), Gouanou Zogbila, and Vincent Mamy (Bossou) for their comradeship and voracity.

My time at Bossou was infinitely enriched by Dagouka Sami, who took me under his wing and was a constant source of joy, reassurance, and comfort. *Merci de m'accueillir dans votre famille et de me faire sentir chez vous* (Thank you for welcoming me into your family and making me feel at home). I was also very lucky to have had such a wonderful research companion in Dr. Maegan Fitzgerald. I am grateful for her friendship, confidence, and encouragement. I also thank Bouna Zogbila for a seemingly unlimited supply of the most delicious pineapples.

At Oxford, special appreciation goes to my academic sibling, Dan Schofield, with whom I've shared the highs and lows of this long and winding journey; and my compatriot, João Coelho for being a sounding board to my statistical frustrations. I would like to thank my office companions over the years – Lucy Baehren, Josh Bamford, Megan Beardmore-Herd, Sophie Berdugo, Aaran Davis, Phillipa 'Fig' Hammond, Adam Kenny, Lynn Lewis-Bevan, Jana Muschinski, and Ilse Pitt – for their camaraderie and being all-round excellent people. My time at the Primate Models for Behavioural Evolution Lab has been a period of much personal and professional growth, and I am grateful to all my colleagues for making it a welcoming, inclusive, and collaborative environment. My most appreciative thanks go to Dr. Alejandra Pascual-Garrido for her mentorship, friendship, and trust and providing me with so many exciting research opportunities. Finally, I thank my dear friends Richard and Regine Davy for making Oxford feel like my home away from home and filling grey days with sunshine in the form of delightful conversations exchanged over "fizz and nibbles".

I would not be where I am today without my dad, who supported my dream to become an archaeologist despite the poor career prospects, while other parents were encouraging their children to pursue medicine and other more financially rewarding or prestigious careers. He

did, however, always urge me to be realistic and seek opportunities to explore my passion as much as possible. I am eternally grateful for his candour and unwavering encouragement. Special gratitude also extends to my mum for being on call day or night whenever I needed advice or simply a shoulder to cry on. Thank you for being my beacon of calm and comfort, especially during the most challenging moments. I would also like to thank my dear sister for all her love and the many happy moments we shared on weekends exploring our neighbourhoods together.

I owe a great part of this achievement to Matthew Bluteau, whose unwavering affection and companionship got me through these last two years. Thank you for sticking with me, and most of all, for being my reason for getting up in the morning on the bleakest of days. Finally, I would also like to thank David and Heather Bluteau for financing a much-needed getaway to recharge before the final push, and for indulging me with a Christmas I will never forget.

To say that my PhD journey did not have an impact on my mental health would be the understatement. In acknowledgement of and solidarity with the 27% students that are facing mental health problems, I hope this thesis can serve as a testament that it can be done. I am indebted to the people who showed me kindness and understanding and encouraged me to seek the help that I needed. Special thanks go to my mum, Nic, Lena, and Ce for sharing their own experiences and for listening without judgement. I also would like to thank Oxfordshire Talking Space, for all their support and guidance towards reaching emotional stability and finding joy in life again. If there is one non-academic lesson that I have learned from this experience is that it is important to live, and always find time to enjoy the little moments, no matter what life throws at you.

I was very fortunate to receive funding for graduate study from the Portuguese science foundation, Fundação pela Ciência e Tecnologia [grant number: SFRH/BD/115085/2016], supported by the Programa Operacional Capital Humano (POCH) and the European Union. I am also very thankful for the research grants awarded by the Boise Trust Fund and the National Geographic Society [grant number: EC-399R-18], which allowed me to conduct fieldwork in Guinea and Kenya. Magdalen College also generously assisted with travel grants and provided me with much needed financial support during the last year of the DPhil.

In Tanzania, I am grateful to the Tanzania National Parks (TANAPA), Tanzania Wildlife Research Institute (TAWIRI), and Tanzanian Commission for Science and Technology (COSTECH) for permission to conduct research in Gombe and Issa. I also thank the Jane Goodall Institute, the Greater Mahale Ecosystem Research and Conservation Project for logistical support while in the field. In the Republic of Guinea, I would like to thank the Direction Nationale de la Recherche Scientifique, the Institut de Recherche Environmentale de Bossou (IREB) under the direction of Dr. Ali Gaspard Soumah, the Kyoto University Primate Research Institute (KUPRI), particularly Prof. Tetsuro Matsuzawa and Dr. Naruki Morimura, for research permissions and for assistance and guidance throughout. I would also like to thank Dr. David Braun, the Koobi Fora Field School, and the National Museums of Kenya for supporting my fieldwork in Kenya.

Contents

List of Figures ..... **xvi**

List of Tables ..... **xvi**

Chapter 1: Introduction **1**

The archaeology of our technological origins: a methodological and theoretical history 1

Structure of Thesis Research 28

Chapter 2: The DistoX2 ..... **35**

Abstract 35

Introduction 36

Methods 45

Results 50

Discussion 57

Conclusions 64

Acknowledgements 66

Chapter 3: Archaeology of the perishable **68**

Abstract 68

Introduction 69

Background 74

Methods 77

Results 81

Discussion 91

Conclusion 99

Acknowledgments 101

Chapter 4: Landscaping the behavioural ecology of primate stone tool use 103

Abstract 103

Introduction 104

Methods 110

Results 121

Discussion 125

Conclusions 131

Acknowledgements 134

Chapter 5: Simulating the formation of chimpanzee technological landscapes 135

Introduction 135

Methods 142

Results 169

Discussion 178

Conclusion 184

Chapter 6: Revisiting the second largest forest of Guinea a decade later 186

Introduction 187

Diécké Forest 188

Chimpanzee Status and Tool Use 199

Korohouan: revisited a decade later 202

Discussion 208

Acknowledgments 212

Chapter 7: Conclusion 214

Summary 214

Challenges and limitations 219

Future directions 222

Bibliography 229

Appendix A: Supplementary information for Chapter 2 287

A1 - Custom-made tripod mount 287

A2 – Arrow Gold GNSS Receiver 289

Appendix B: Supplementary information for Chapter 3 290

B1 – Supplementary analyses: type of raw material selection 290

B2 – Supplementary analyses: species selection 293

B3 – Supplementary GLMM results 294

Appendix C: Supplementary information for Chapter 4 296

C1 – Description of response variables 297

C2 – Supplementary results for tool site selection 298

C3 – Supplementary results for tool site re-use 300

C4 – Supplementary results for tool site inactivity 301

Appendix D: Supplementary information for Chapter 5 303

D1 – Model Overview Design Details 303

D2 - GIS processing 342

D3 – Supplementary information for the experimental setup 346

D4 – Simulation outputs 347

Appendix E: Supplementary information for Chapter 6 356

Appendix F: Supplementary information for Chapter 7 360

F1 – Koobi Fora Field Reports 375

F2 – "Stones on the move" project report 380

E3 – Lithic analysis results 372

Appendix H: Publications 370

List of Figures

Figure 1.1. Hominin chronology and the timing of the emergence of major hominin industries.. 13

Figure 1.2. Location of chimpanzee study sites. 31

Figure 2.1. DistoX2 and accessories. 41

Figure 2.2. DistoX2 setup options. 42

Figure 2.3. DistoX2 precision. 51

Figure 2.4. Accuracy of the tested methods: a) DistoX2 at L2; b) DistoX2 at L3; c) Tape and compass method at L3. 52

Figure 2.5. 2D-plan of the test points at L2 mapped using the three different methods: total station, DistoX2, and tape and compass. 55

Figure 2.6. Linear distance error between each test method and the total station baseline relative to distance from datum. 56

Figure 3.1. Map of western Tanzania indicating the three study sites. NP: National Park. 75

Figure 3.2. Raw material sourcing for termite-fishing tools by wild chimpanzees. 82

Figure 3.3. Percentage of plants sourced for tools by species (sourced; grey), compared to the species general availability among exploited species (available; black). (a) Gombe, (b) Issa, (c) Mahale 86

Figure 3.4. Examples of source plant locations at Issa from where chimpanzees removed tool material, indicated by white arrows (a, b) or orange tape (c) 88

Figure 3.5. Comparison of number of removals per sourced plant by study site in response to distance to mound (a, c, e) and species abundance (b, d, f). At Gombe, (a, b); at Issa (c, d); at Mahale (e, f).. 90

Figure 4.1. Map of the Bossou Forest and surrounding area. 111

Figure 4.2. Map of the study area and surrounding area, highlighting the locations of recorded nut-cracking sites, quadrats, nests, and watercourses..... 112

Figure 4.3. Probability of tool site presence in response to: a) Raw materials of size class 3 – 5; b) Trees that are sourced by chimpanzees for food; c) Distance to the nearest nest cluster. 121

Figure 4.4. Frequency of tool site use relative to: a) Raw materials that have been used as tools; b) Distance to nearest nest cluster (km); c) Raw materials of size class 3 to 5; d) Wild trees that are sourced by chimpanzees for fruit; e) Mean availability of oil palm nuts; f) Distance to nearest river (km) 123

Figure 4.5. Probability of tool site inactivity in response to: a) Mean nut availability; b) Raw materials that have been used as tools. 124

Figure 5.1. NetLogo interface of the empirical model based on the Bossou landscape. 143

Figure 5.2. Overview of chimpanzee-agent procedures. 145

Figure 5.3. Results of the sensitivity analysis for daily caloric intake (kcal). 171

Figure 5.4. Results of the sensitivity analysis for daily distance travelled (km). 171

Figure 5.5. Results of the sensitivity analysis for the proportion of time the group remained as one single unit..... 172

Figure 5.6. Empirical data distributions compared to the corresponding simulated outputs: a) caloric intake per day (kcal); b) distance travelled per day (km). 174

Figure 5.7. Spatial distribution of nut-cracking activities..... 174

Figure 5.8. Empirical and simulated patterns of monthly food availability. 175

Figure 5.9. Daily caloric intake (forage_kcal) relative to the spatial clustering of food (smoothness), number of nest sites (rows), and water abundance (columns). 176

Figure 5.10. Distance travelled per day (km) relative to the spatial clustering of food (smoothness), number of nest sites (rows), and water abundance (columns). 177

Figure 5.11. Proportion of fusion relative to the spatial clustering of food (smoothness), number of nest sites (rows), and water abundance (columns). 178

Figure 5.12. Rasterized distribution of all Bossou nut-cracking sites (a); Rasterized simulation output of the distribution of nut-cracking activity (b). 180

Figure 6.1. Map of the national classified forests of Guinea and the locations of the Ziama, Diécké, Nimba, and Bossou forests. 189

Figure 6.2. Distribution of main commercial activities and tree cover loss in the Guinée Forestiére Region. 193

Figure 6.3. Map of the Diécké Forest highlighting the locations of known survey areas and nearby villages. 200

Figure 6.4. Material traces of human presence collected during surveys in the classified area: one shoe, a plastic bottle, dozens of wires used for snares, and >100 shotgun shells... 209

Figure A.1. Blueprint of DistoX2 custom-made tripod mount 288

Figure A.2. Accuracy of the Arrow Gold GNSS Receiver as reported by the device during field surveys under two canopy conditions 289

Figure D.1. Overview of chimpanzee-agent procedures. Dashed arrows and hashed boxes indicate steps that are only available under certain conditions 306

Figure D.2. Visualization of the diamond-square algorithm on a 5 × 5 array. 340

Figure D.3. Examples of artificially generated landscapes used in the experimental setup. 346

Figure F.1. XRD results of the Aluminium-rich samples. 368

Figure F.2. XRD results of the Amphibole-rich samples. 368

Figure F.3. XRD results of the Kaolinite-Iron-Oxide-rich samples. 369

Figure F.4. XRD results of the Quartz-rich samples. 369

List of Tables

Table 2.1. Practical details of common mapping methods compared to the DistoX2. 40

Table 2.2. Disto X2 technical specifications. 43

Table 2.3. Raw DistoX2 precision results in hand-held and tripod modes. 50

Table 2.4. DistoX2 precision results in hand-held and tripod modes converted into XYZ format. 51

Table 2.5. DistoX2 accuracy relative to the total station at the two different test locations: L2 (Koobi Fora, Kenya) and L3 (Oxford, UK). 53

Table 2.6. Tape and compass accuracy relative to the total station with and without major outliers. 54

Table 2.7. Raw measurement accuracy of the DistoX2 and tape and compass methods relative to the total station baseline. 56

Table 2.8. Summary of specifications and practical information of current and novel mapping methods. 64

Table 3.1. Abundance of raw material types for each site. 83

Table 3.2. Proportion of raw material types available versus proportion of tool materials. .. 84

Table 3.3. Family and species of plants sourced for tool material types at Gombe, Issa and Mahale. B = bark, T = twig, V = vine, G = grass.. 85

Table 3.4. Results from the final reduced model (GLMM; lacking the non-significant three-way and two-way interactions) investigating potential predictors influencing number of removals. 89

Table 4.1. Results of the final GLM investigating potential predictors influencing tool site selection. 122

Table 4.2. Results of the final GLM model investigating potential predictors influencing tool site abandonment. 125

Table 5.1 - Summary of food seasonality and energetic parameter values used in the model. 150

Table 5.2. Summary of physiological and biological parameter values of ape-agents used in the model. 151

Table 5.3. Fixed parameters used for empirical validation. 163

Table 5.4. Unknown parameters and ranges used for parameter calibration. 164

Table 5.5. Parameter settings used in the experimental setup. 168

Table 5.6. Parameter calibration results, including mean parameter values, estimation method used, and performance outputs. 170

Table 5.7. Summary of overall multiple regression results assessing the sensitivity of model outputs to parameter variations. 170

Table 5.8. Statistical results of the comparisons between empirical data and simulation outputs. 173

Table 6.1. Summary of the survey activities that have taken place in the Diécké Forest Reserve..... 201

Table 6.2. Chimpanzee traces documented in the Korohouan area during the 2006-2009 and the 2018 surveys. 205

Table 6.3. Data recorded for nut-cracking sites surveyed in 2006-2009 and 2018. 207

Table 6.4. Summary of mammalian traces documented in 2011 by the WCF (144.8 km), compared with traces encountered during the 2018 survey in the Korohouan core area (21.7 km)..... 207

Table 6.5. Summary of traces of anthropogenic origin collected in 2011 by the WCF (144.8 km), compared with traces collected during the 2018 survey in the Korohouan core area (21.7 km)..... 208

Table B.1. Pairwise results (P-values) comparing pairs of raw material types available for each site. 290

Table B.2. Comparison of abundance of raw material types between sites relative to total suitable. 291

Table B.3. Pairwise results (P-values) comparing pair of sites for each raw material type. .. 291

Table B.4. Comparison of proportions of sourced plants relative to total suitable plants between sites. 291

Table B.5. Pairwise results (p-values) comparing proportions of tool species relative to all suitable plants between paired sites. 292

Table B.6. Pairwise Wilcoxon test (P-values) comparing average number of parts removed per source plant between paired sites. 292

Table B.7. Proportion of source species abundance versus utilization at each site. 293

Table B.8. Results from the full model investigating potential predictors influencing number of removals 294

Table B.9. Results from the reduced model (GLMM; lacking the non-significant three-way interaction) investigating potential predictors influencing number of removals 295

Table C.1. Summary of the response variables used in this study and their descriptions. 297

Table C.2. Likelihood ratio test results of the Full-Null model comparisons of the site selection models. 298

Table C.3. Results of the AICc-Based Model Selection of the GLM for the predictors of tool site selection. 298

Table C.4. Results of the additional GLMs investigating potential predictors of tool site selection. 299

Table C.5. Descriptive statistics and test results of the comparison between tool sites with low frequency (N = 10) and high frequency (N = 7) of nut-cracking events. 300

Table C.6. Likelihood ratio test results of the Full-Null model comparisons of the site inactivity models. 301

Table C.7. Results of AICc-Based Model Selection of the GLM for the predictors of tool site inactivity 301

Table C.8. Results of the additional GLM models investigating potential predictors of tool site inactivity..... 302

Table D.1. Free parameters and values. 322

Table D.2. Summary of published information of frequency of water intake through drinking. 330

Table D.3. Intake rates (g/min) of common food items consumed by female chimpanzees in Kanyawara, Kibale NP 332

Table D.4. Caloric value (kcal/g) of different wild foods consumed by the chimpanzees of Bossou..... 334

Table D.5. Summary of parameter values used for simulating foraging intakes in the model. 335

Table D.6. Summary of parameter values associated to nut-cracking and kernel consumption. 336

Table D.7. Summary of parameter values associated to nesting. 339

Table D.8. Input parameters used in the 'Rasterize (Vector to Raster)' window to convert the outline of the Bossou forest into a gridded raster of the chimpanzee home-range. 343

Table D.9. Input parameters used in the 'inverse distance weighted interpolation' window to convert the quadrat data into a gridded raster. 344

Table D.10. Input parameters used in the 'Heatmap (Kernel Density Estimation)' window to convert the quadrat data into a gridded raster. 344

Table D.11. Reference table results for *exploration-probability*. 347

Table D.12. Reference table results for *max-food-density*..... 347

Table D.13. Reference table results for *min-party-size*. 347

Table D.14. Reference table results for *nest-count-coefficient*. 348

Table D.15. Reference table results for *nest-interaction-coefficient*. 348

Table D.16. Reference table results for *nest-suitability-coefficient*..... 348

Table D.17. Results from the multiple regression model investigating potential predictors of variation in daily caloric intake. 349

Table D.18. Results from the multiple regression model investigating potential predictors of caloric efficiency. 350

Table D.19. Results from the multiple regression model investigating potential predictors of variation in distance travelled per day. 351

Table D.20. Results from the multiple regression model investigating potential predictors of variation in rates of fusion. 352

Table D.21. Results from the multiple regression analysis of the experimental data investigating potential predictors of daily caloric intake. 353

Table D.22. Results from the multiple regression analysis of the experimental data investigating potential predictors of distance travelled per day. 353

Table D.23. Results from the multiple regression analysis of the experimental data investigating potential predictors of rates of fusion. 354

Table D.24. Results from the multiple regression analysis of the experimental data investigating potential predictors of overall nut-cracking frequency. 354

Table D.25. Results from the multiple regression analysis of the experimental data investigating potential predictors of spatial patterning of nut-cracking sites (Moran's I Index). 355

Table E.1. – List of animal species encountered indirectly during surveys in the Korohouan area of the Diécké Forest Reserve. 357

Table E.2. List of plant species recorded during surveys in the Korohouan area of the Diécké Forest Reserve. 357

Chapter 1

Introduction

The archaeology of our technological origins: a methodological and theoretical history

In the early 1930's, Mary and Louis Leakey made a discovery that would forever change the course of archaeological enquiry, methodology and exploration. The Oldowan tools found at Olduvai Gorge in Tanzania (M. D. Leakey, 1971), not only showed that the origin of technology was far more ancient that previously thought, but the novel large-scale excavation methods employed by Mary Leakey allowed archaeologists to tackle, for the first time, more refined questions about the lives of our earliest ancestors – who were they, how they lived, moved and interacted with their environment, and what were the conditions that led to the emergence of technology in our lineage (Plummer, 2004; Schick & Toth, 1993).

Until this point, conventional archaeology focused on digging deep, narrow trenches, through a column of sedimentary deposits, to analyse palaeontological and technological changes though time, often assuming a linear progression in behavioural complexity (Schick

& Toth, 1993). The practice of uncovering large, horizontal surfaces of discrete Palaeolithic deposits, pioneered by Mary Leakey (1971), spearheaded a theoretical shift from merely investigating the what, where and when, to the why and how (Schick & Toth, 1993). One crucial emerging area of research sought to understand the broader contexts of the lithic assemblages themselves – how they came to be and what they represented within the hominin behavioural landscape, with a particular focus on social organisation, subsistence strategies and landscape-use (Behrensmeyer, 2011; Plummer, 2004).

This new era of archaeological enquiry set the precedent for a wealth of new methodological approaches, many of which are still in practice today. While some looked for answers in modern human analogues, such as present-day hunter-gatherer societies (e.g. Binford, 1983, 1980; Lee and DeVore, 1976), others turned to non-human primates (e.g. baboons: Washburn and DeVore, 1961; chimpanzees: Goodall, 1963) and other animals (Brain, 1983).

In parallel, another branch of research began tackling the archaeological record through an experimental lens. Several actualistic studies were initiated to understand how tools were made and to gain further insights into their technological complexity and the associated motor and cognitive implications. Others focused on assessing the post-depositional effects of different taphonomic processes on the distribution, density, and size composition of experimental knapping assemblages (Isaac et al., 1997; Schick & Toth, 1993; Toth, 1983, 1985). Such studies began providing methodological protocols for diagnosing the degree of preservation of archaeological sites, which, in turn, translated into more detailed observations of depositional contexts, material composition, spatial distribution and orientation of assemblages (Plummer, 2004). This transition towards assessing the integrity of archaeological assemblages was a critical step in Oldowan research (Plummer, 2004).

Soon, it became clear that in order to fully understand hominin behaviour in context, it was no longer sufficient to merely focus on high-density assemblages as isolated units of human activity (Stern, 1991), but rather to take into account the whole landscape and all the archaeological information that it contained. From ethnographic studies of hunter-gatherer populations (e.g. Binford, 1980), it was becoming more and more apparent that their activities did not revolve around a single site but rather a network of sites that were visited with different frequencies based on their function and location. Additionally, actualistic experiments were providing increasing evidence that assemblages rarely remain static and truly immune to taphonomic action through time (Kaufulu, 1997; Schick, 1997; Schick & Toth, 1993).

As research became more focused on questions of land-use patterns, site activity differentiation, and socio-economic organization, another crucial paradigm shift emerged, calling for a landscape-wide approach to the study of Palaeolithic archaeology (Behrensmeyer, 2011). "*[L]ike modern hunter-gatherers, prehistoric human populations did not inhabit a site but rather a landscape, and their movement around the landscape was an essential part of their various adaptations to the surrounding conditions*" (Dibble et al., 2016, p. 22).

This concept was first explored by Cyril Fox (1932, 2010), who studied the archaeology of Cambridgeshire (England) through a broad geographic perspective, expanding from the traditional artefact or site-based approach. Fox (1932, 2010) set the foundations for what is now known as 'Landscape Archaeology' in Britain, which became integral to historical and prehistoric archaeology in Europe and North America from the 1970's onwards (Behrensmeyer, 2011). It was Glynn Isaac (1981a) who first introduced this approach to

Palaeolithic archaeology in East Africa during the 1970s, where he pioneered theoretical and methodological practices for examining artefacts and bone occurrences over large areas of the ancient hominin landscapes (Behrensmeyer, 2011).

From Olduvai Gorge, research expanded to Koobi Fora (East Turkana, Kenya), where Isaac launched an ambitious project involving extensive surface surveys of continuous isochronous outcrops, to determine differential artefact assemblages and their relationship with both current and ancient geographic features (Isaac & Harris, 1980). Termed "scatters-between-patches", this investigation revealed that 90% of the archaeological record was contained not in the dense patches, but in the scatters in between (Isaac et al., 1981), demonstrating that archaeologists had been overlooking a considerable portion of the hominin record.

In his seminal paper "Stone age visiting cards", Isaac (1981b) discussed the theoretical underpinnings of this approach, concluding that the spatial patterns of individual artefacts and skeletal remains over a palaeo-landscape would make more appropriate units of analysis for decoding the early archaeological record, rather than the sites as a whole.

These findings, combined with the evidence from actualistic experiments, justified more targeted sampling through excavation of multiple locations along a stratigraphic horizon. This strategy allowed for the identification of *in situ* material, the more precise recording of spatial data for each piece using a coordinate system, and the gathering important information on the degree of taphonomic and hydrological disturbance of archaeological deposits (Behrensmeyer, 2011).

East Turkana became a testing ground for many ideas about early hominin behaviour (Schick & Toth, 1993), including theories of hominin land-use, such as Isaac's (1976) "home-base-model", and the "central-places theory" (Isaac, 1983) that succeeded it (Plummer, 2004). Isaac was particularly interested in the possibility of identifying temporal shifts in behaviour from *ad hoc* resource exploitation dictated by environmental parameters, to more strategic exploitation strategies whereby hominins made calculated decisions about how they used the landscape (Behrensmeyer, 2011). Such changes could potentially be reflected in changes in artefact densities from sparsely distributed debris indicating a low degree of resource management, to dense accumulations attesting to greater ability to organize raw material and food acquisition, and the focal use of particular areas that were returned to on a regular basis (Behrensmeyer, 2011).

Isaac's legacy spurred his successors to investigate more deeply the different behavioural and natural processes that could shape archaeological signatures in different ecological contexts across both spatial and temporal landscapes (Behrensmeyer, 2011; Sept, 2011).

The subsequent 40 years have witnessed even further theoretical and methodological advances, technological developments and milestone discoveries, that have not only added more definition to our understanding of the early hominin record, but have also completely reshaped our perspective of human evolution (Carvalho & Beardmore-Herd, 2019; Domínguez-Rodrigo, 2012b). These paradigm shifts did not stem from archaeological research alone but were the product of contributions from several other fields, most notably primatology.

CONTRIBUTIONS FROM PRIMATOLOGY

The potential value of non-human primates in reconstructing early hominin socio-ecological behaviours has been explored since the 1960's, when Washburn and DeVore (1961) began studying the social behaviours of yellow baboons (*Papio cynocephalus*) in Kenya. While baboons are not our closest evolutionary relatives, they were considered good proxies because they demonstrated a number of traits that had been ascribed to early hominins, namely a high degree of terrestriality, and shared similar social systems and environments (Mitani, 2013). Therefore, it was posited that early hominins would have faced similar socio-ecological problems and would consequently have developed similar behavioural responses (Washburn & DeVore, 1961). These studies not only served to find commonalities between non-human primates and early hominins, but also to identify major differences between them, in the quest for defining human uniqueness.

Meanwhile, Jane Goodall embarked on a journey to Tanzania to study the chimpanzees of Gombe, where she observed termite fishing by wild chimpanzees for the first time (Morell, 1993). Goodall's (1963, 1964) descriptions challenged several previous assumptions about human behaviour, most notably, that technology was a uniquely human trait (Carvalho & Beardmore-Herd, 2019; Carvalho & McGrew, 2012). In a communication with her mentor, Louis Leakey, he famously stated: "Now we must redefine 'tool', redefine 'man', or accept chimpanzees as humans" (McGrew, 2010a: 579).

From termite-fishing, to nut-cracking, and leaf-sponging, the technological repertoire of chimpanzees is continuously expanding (McGrew, 2010a; Whiten et al., 1999). Tool use in the wild has also been documented in a number of other primate species such as orangutans (*Pongo sp.*) who use a variety of plant tools for insect harvesting and fruit processing (Van

Schaik et al., 1996); bearded capuchins (*Sapajus libidinosus*) who crack nuts with stones and employ stick probes to flush out small prey from rock cervices (Ottoni & Izar, 2008); and Burmese long-tailed macaques (*Macaca fascicularis aurea*) who use stones to extract marine invertebrates and have begun to crack nuts of recently introduced oil palms (Malaivijitnond et al., 2007; Proffitt, Luncz, et al., 2018). New reports are uncovering further tool-using primates, such as the Nicobar long-tailed macaque (Pal et al., 2018) and the white-faced capuchin (Barrett et al., 2018). Beyond primates, technological behaviours are extending to other animals, namely, cetaceans (e.g. *Tursiops* sp; Smolker et al., 1997; Patterson and Mann, 2011; Kopps and Sherwin, 2012) and corvids (e.g. *Corvus* sp.; Hunt, 1996; Bluff et al., 2010; Rutz et al., 2016). These studies have provided new frameworks for understanding the evolutionary contexts for the emergence of tool use, the mechanisms of cultural transmission and variation, as well as the cognitive and learning processes associated with technological behaviours.

At the turn of the millennium, the archaeological excavation of a chimpanzee nut-cracking site (Mercader et al., 2002), set the precedence for a new era of primatological and archaeological research (Carvalho & Almeida-Warren, 2019; Carvalho & Beardmore-Herd, 2019). The excavation recovered 4,300 year-old chimpanzee nut-cracking tools, revealing that, much like early hominins, chimpanzees were also capable of producing a recognisable and durable archaeological record (Mercader et al., 2007). The new research avenues that arose from this discovery resulted in the establishment of a new subfield – Primate Archaeology – with the goal of consolidating an interdisciplinary methodological framework at the intersection of primatology and archaeology that would enable greater understanding of the evolutionary foundations of hominin technology and behaviour (Haslam et al., 2009). The application of archaeological methods to traditional primatological approaches enabled

researchers for the first time, to study non-human primate technology with the same granularity as the human material record, uncovering previously unidentified behavioural, spatial and ecological patterns (Carvalho & Almeida-Warren, 2019; Carvalho & Beardmore-Herd, 2019). The wide array of methods now being employed by Primate Archaeology is summarised in Appendix E, originally published in the Encyclopaedia of Animal Behaviour and reprinted here with permission from Elsevier.

Chimpanzee research following this paradigm, is revealing population-level specialisation and regional variations (McGrew et al., 1979; Pascual-Garrido, 2019; Sanz & Morgan, 2011), as well as cognitive complexity in both tool manufacture and raw material selection and procurement strategies (Almeida-Warren et al., 2017; Carvalho et al., 2008; Sanz & Morgan, 2010). That chimpanzees, much like early hominins, are selective of the lithic and plant raw materials they use for tools, is demonstrating that they too have some level of understanding of the physical and mechanical properties of different materials (Almeida-Warren et al., 2017; Carvalho et al., 2008; Pascual-Garrido, 2019).

These approaches have also expanded to the study of other stone tool-using primates. Excavations of capuchin nut-cracking sites in Serra da Capivara, Brazil, have begun to tap into the capuchin archaeological record, revealing that this behaviour dates back to at least 600 years (Haslam, Luncz, Staff, et al., 2016). At macaque mollusc processing sites in Thailand, geological and sea-level reconstructions of excavated contexts are suggesting that these activity sites may have formed up to 1,000 years ago (Haslam, Luncz, Pascual-Garrido, et al., 2016). There is also evidence of raw material selection for tools in both species (Gumert et al., 2009; Visalberghi et al., 2009).

More recently, it has been found that capuchins are capable of producing stone flakes as unintentional by-products from stone on stone percussion (Proffitt et al., 2016). Unlike the lithic tool fragments generated through chimpanzee nut-cracking (Proffitt, Haslam, et al., 2018), these flakes exhibit the same conchoidal fracturing characteristic of Oldowan assemblages, challenging the long-standing assumption that Oldowan flakes could only be produced through intentional and calculated knapping. Together with research on the use of nut-cracking by-products by chimpanzees (e.g., Carvalho et al., 2009; Kaplan, 2012), these studies are not only shedding light on how intentional stone tool making may have emerged, but also raising the possibility that other primate species may have contributed towards the Plio-Pleistocene archaeological record.

The archaeological study of nest-building and termite fishing is also gaining momentum, and are providing a framework for reconstructing archaeologically invisible aspects of hominin behaviour (Almeida-Warren et al., 2017; Hernandez-Aguilar, 2009; Pascual-Garrido, 2018; Pascual-Garrido et al., 2012; Stewart et al., 2011). Such studies are gradually building a solid profile of primate technology and exploring its evolutionary implications (Carvalho & Almeida-Warren, 2019; Haslam, 2012; Haslam et al., 2017).

WHITHER THE EARLIEST TOOLMAKERS

The intersection of milestone developments in both primatological and archaeological research have almost entirely reshaped the early assumptions and interpretations that arose from Olduvai Gorge nearly a century ago. Discoveries from Gona (Semaw, 2000) and, more recently, Ledi Geraru (Braun et al., 2019) in Ethiopia have pushed back the chronological boundary of the Oldowan to over 2.58 Ma, far beyond the first Oldowan tools discovered at Olduvai Gorge (1.8 Ma; Leakey, 1971). We now know that the Oldowan in Africa spans at

least one-million-years from 2.6 to 1.6 Ma, and has also been documented throughout Eurasia between 2.0 to 0.6 Ma, totalling a two-million-year-old record worldwide (Barsky, 2009). Up until recently (i.e. McPherron et al., 2010; Harmand et al., 2015), the Oldowan industry was also the oldest known evidence of tool use (Braun, 2013; Toth & Schick, 2009). However, indirect evidence in the form of cut-marks on fossil bones, from Dikika (~3.4 Ma; McPherron et al., 2010), paired with studies comparing Oldowan and chimpanzee assemblages, both archaeological and experimental (de la Torre, 2004; Schick & Toth, 2006), suggested the existence of a much older, less complex technological industry akin to the pounding tools used for nut-cracking by chimpanzees (Panger et al., 2002). Concrete evidence for this has now been discovered at Lomekwi (3.3 Ma) in West Turkana, establishing a new pre-Oldowan industry – the Lomekwian (Harmand et al., 2015; Lewis & Harmand, 2016) (See Figure 1.1).

These developments provided the concrete evidence needed to refute the long-standing assumption that *Homo* was the only hominin genus to have become technological (Carvalho & Beardmore-Herd, 2019). The Oldowan now overlaps chronologically with several *Australopithecus* and *Paranthropus* taxa (Braun, 2013; Toth & Schick, 2009), and the variation in technological diversity and raw material acquisition that is emerging from Oldowan assemblages (e.g. Delagnes and Roche, 2005; Braun et al., 2008; Harmand, 2009) is providing increasing evidence that the Oldowan was likely a product of not one, but multiple species.

As pre-Oldowan technological industries emerge, our technological ancestors acquire a new face and new species, such as *Kenyanthropus platyops,* come to the forefront as possible candidates for the earliest hominin tool users (Harmand et al., 2015; Lewis & Harmand, 2016). Other hominin contemporaries include *Au. Afarensis* and *Au. Deyiremeda*, suggesting

that the earliest known industry emerged in a species with a brain-size barely larger than extant African apes (Lewis & Harmand, 2016). As our knowledge of tool use in non-human primates grows and recognises that the use and manufacture of tools is prevalent among our closest living relatives, we are again readdressing our technological timeline and considering the possibility that our technological origins may go back as far as our shared last common ancestor around 7-8 Ma (Langergraber et al., 2012; Panger et al., 2002; Rolian & Carvalho, 2017).

For a long time after the Olduvai Gorge discovery, it was assumed that Oldowan tools, particularly sharp flakes produced from knapping, were exclusively used for meat-processing, due to their association with animal bones; and that the Oldowan had emerged in response to a dietary shift towards greater meat consumption (Plummer, 2004). However, more refined analyses of hominin assemblages (e.g. Arroyo and de la Torre, 2016), show that Oldowan tools may have been used in a variety of contexts beyond knapping and butchering, such as plant processing (cutting and pounding), and crushing bones to access bone-marrow (Plummer, 2004; Toth, 1997). Targeted analyses of Oldowan pounding tools, has also revealed that these heavier-duty tools were frequently reused and often repurposed for different pounding activities, while also demonstrating variations in functionality between different sites (Arroyo et al., 2020).

In contrast, the Lomekwian (~3.3 Ma) assemblage is characterized by larger tools and a considerably lower proportion of flakes, which were produced using bipolar and passive percussion techniques (Lewis et al., 2016). These key features are hallmarks of chimpanzee stone tool use, such as nut-cracking (bipolar) and baobab pounding (passive), suggesting it is likely that the Lomekwian was predominantly used for processing plant foods (Lewis et al.,

2016). This evidence, combined with the recent discovery that flakes can be produced unintentionally as by-products of capuchin stone-on-stone pounding (Proffitt et al., 2016), suggests that early stone knapping may have developed naturally from pre-existing pounding behaviours, rather than as an intentional and systematic technology.

Broader landscape studies have also begun to provide small clues as to early hominin ranging patterns. Research comparing the compiled data of early hominin artefact assemblages from multiple sites throughout the Great African Rift Valley has highlighted that there is evidence of a distinct temporal shift in artefact distributions between 2.3 and 1.5 Ma, from small and sparse scatters of material, to larger and denser artefact accumulations (Rogers et al., 1994). There is also some evidence that ecological factors (e.g., proximity to water and raw material sources) may have dictated where tool discard took place. Between 2.3 and 1.8 Ma, most assemblages are sparse and appear to be tethered to alluvial floodplains, where raw materials are often deposited by fluvial action. It is only by 1.6 – 1.4 Ma, with the emergence of new technological industries (e.g. Acheulean; Figure 1), that lithic accumulations become associated to a range of different habitats (Braun, Rogers, et al., 2008; Rogers et al., 1994). This also coincides with a shift towards clear polarized patterning of artefact distributions, whereby dense concentrations of archaeological material are counteracted by low density inter-site scatters, with little variation in between (Braun, Rogers, et al., 2008; Rogers et al., 1994). Recent work in Koobi Fora has also found that in the latter part of the early record (1.6 – 1.4 Ma), different archaeological localities may have served different purposes, shaped by the palaeoenvironmental context (e.g. channel vs. floodplain) and the proximity to raw materials (Braun, Rogers, et al., 2008). These transitions coincide with the emergence of anatomical and dietary adaptations evident in the hominin fossil record (e.g., increased brain and body size, erect body posture, smaller

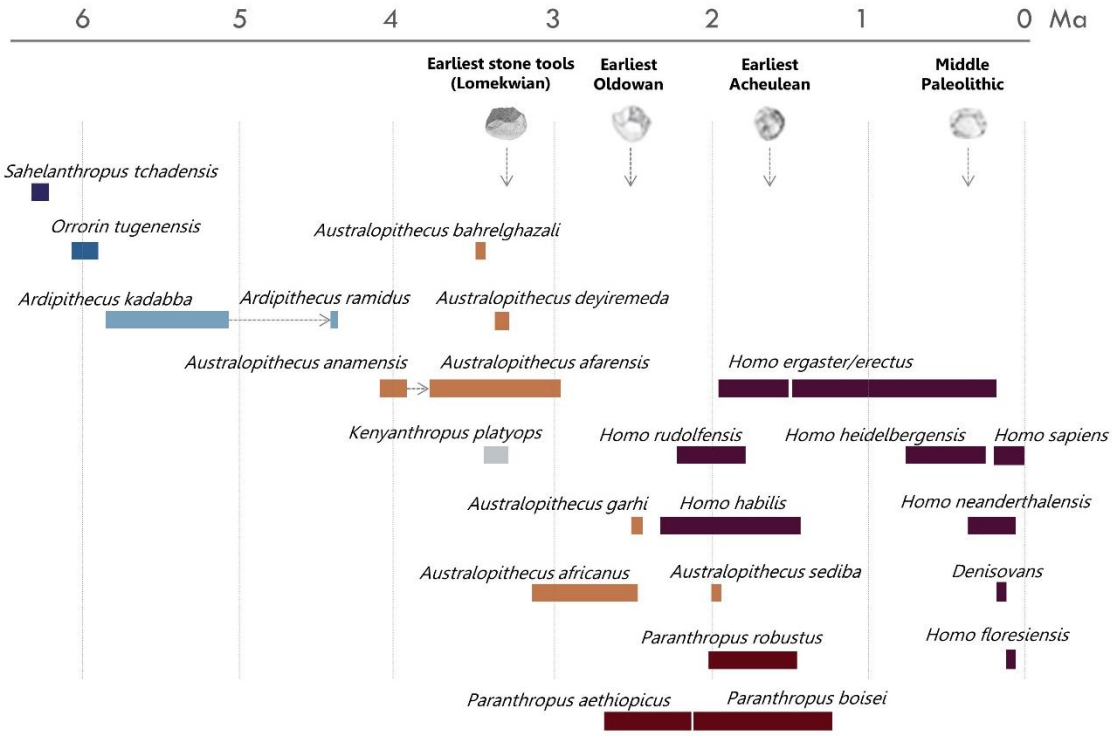


Figure 1.1. Hominin chronology and the timing of the emergence of major hominin industries. Colours indicate different genera. Original figure by René Bobe, with modification by Katarina Almeida-Warren.

dentition, use of fire), suggesting a potential correlation between these changes and an increase in complexity of foraging behaviours (Rogers et al., 1994).

This plethora of new discoveries is not only adding more definition to our understanding of the early hominin record and providing new tools to work towards a more accurate picture of the past, but is also changing the course of archaeological enquiry (Domínguez-Rodrigo, 2012b; Carvalho and Beardmore-Herd, 2019). Ever since Mary and Louis Leakey uncovered the first Oldowan tools, archaeologists have strived to understand the behaviours of the Oldowan tool-makers, in particular, how did our hominin ancestors navigate the landscape and interact with their environment. Almost a century later, archaeologists are now

redirecting these questions to a new time-period – a time before the Oldowan and the emergence of the *Homo* genus. Nevertheless, due to the sparse archaeological record before 2.6 Ma, we still know little about the technological and behavioural precursors of the Oldowan, including the use of perishable technologies, as well as patterns of landscape-use, resource exploitation.

PERISHABLE TECHNOLOGY

Perhaps unsurprisingly, research about early hominin technology has almost exclusively focused on stone tool use. Although the paleo-archaeological understanding of plant and bone use is gradually expanding – with milestone discoveries in the last two years including 200,000-year-old remains of grass bedding in South Africa (Wadley et al., 2020), the earliest evidence of fibre technology at 50 ka (Hardy et al., 2020), and a large assemblage of worked bone tools used for hide and fur processing dated between 90-120 ka (Hallett et al., 2021) – no direct record of plant or bone tools exists prior to 300 ka or 2 Ma, respectively (Backwell & D'Errico, 2001; Conard et al., 2015). Lithic artefacts remain the most conspicuous evidence of our ancestral material culture – their durability making them the most reliable archaeological indicator for inferring early human behaviour and cognition, and tracking changes over time (Hussain & Soressi, 2021).

Nevertheless, observations of the modern world suggest that plant technology pre-dates the earliest stone tools and may have even been more prevalent. Indeed, the technological repertoire of non-industrialized human societies, as well as that of our closest living relatives, is predominantly plant-based and constitutes some of the most complex and diverse forms of tool use (Carvalho & Almeida-Warren, 2019; Hoffecker & Hoffecker, 2018). It has even been suggested that the use of wooden implements may have driven changes in stone tool

use and manufacture for the production of specialized wooden tools (Gürbüz & Lycett, 2021). As a likely precedent to stone tool use (Panger et al., 2002), **investigating the processes involved in the sourcing, selection, and manufacture of plant tools can provide vital insights into the suite of behaviours and cognitive abilities that formed the foundations of stone tool use** (Carvalho & Almeida-Warren, 2019). Crucially, advancing this research in tandem with lithic studies will ultimately provide a more complete picture about our technological past.

MODELLING EARLY HOMININ SITE FORMATION AND PATTERNS OF LANDSCAPE-USE

Beyond finding the earliest, largest or most unique evidence of ancient human existence, it is perhaps what these material remains represent in terms of our ancestral lifeways that has been the most compelling yet challenging endeavour (Cegielski & Rogers, 2016). Archaeologists have been developing interpretative models of hominin land-use patterns since the discovery of the first Oldowan tools (Plummer, 2004; Schick & Toth, 1993). It has been a subject of great interest not only because of the reconstructions of foraging and ranging strategies they provide, but also because of the various underlying cognitive and social behaviours they imply (e.g. forward planning, spatial navigation, food transport, food sharing, sexual division of labour). From an evolutionary perspective, these models can serve to hypothesise aspects of biological evolution pertaining to dietary shifts, and potential associations with environmental change and the timing of anatomical adaptations such as dental reduction and increase in brain size.

Early interpretations of Oldowan behaviour relied heavily on analogies with modern hunter-gatherer populations, such as the Kalahari San (e.g. Leakey, 1971), often suggesting

similarities in the spatial and social organization, complex living structures, division of labour and food sharing (Braun, 2013; Plummer, 2004; Schick & Toth, 1993). Leakey (1971) classified the assemblages uncovered from excavations of the Olduvai Beds I and II into four categories. Large high-density accumulations of fossils and artefacts with very little vertical distribution were described as living floors akin to modern hunter-gatherer campsites, while smaller accumulations were characterised as butchery kill sites.. Small accumulations located in fluvial deposits were termed stream channel sites, and finally lithic assemblages with high vertical dispersion were classified as sites with diffuse material. Influenced by Lee and DeVore's (1976) work on the Kalahari San, she depicted a landscape in which small groups of hominins living in habitational structures would send out males to hunt, scavenge for carnivore kills, and protect dependent group members from predators and other hominin groups.

In a similar vein, Isaac (1976) proposed a 'home base model' which viewed archaeological sites as ancient hominin campsites – home bases that served as daily meeting points for socializing and food sharing. Through this model, Isaac (1976) sought to isolate features that distinguished hunter-gatherer from primate adaptations, attributing hominins with sexual division of labour, whereby females gathered plant foods and males hunted or scavenged for meat which they would bring back to a central meeting place, or 'home base'. Greatest emphasis was placed on the more social aspects of behaviour, namely food sharing between group members, and associated underlying behaviours such as delayed consumption and transport of food items. Within this behavioural complex, Isaac (1976) speculated that this would have provided the social backdrop for developed cognitive skills, emergence of language, and cultural manifestations such as marriage systems (Plummer, 2004; Schick & Toth, 1993; Stern, 1991).

However, after the "scatters-between-patches" investigations and critiques from Binford (1980, 1981), the 'home base model' was replaced by the 'central place foraging model' (Isaac, 1983). This version discarded the more contentious assumptions of the 'home bases' such as the sexual division of labour and residential base camps, while maintaining the premise that lithic and faunal accumulations represented favoured localities that acted as a hub for radiative foraging routes (Blumenschine & Masao, 1991; Sept, 2011; Stern, 1991).

In contrast, Binford (1981) viewed archaeological assemblages as a result of frequent tool discard at locations where carnivores frequently abandoned carcasses. Rather than focal areas of hominin activity, these locations would have been part of a foraging route ('routed foraging model') intersecting fixed critical resources (e.g., shelter, water, and raw materials for tools). The 'stone cache model' (Potts, 1984) suggested instead that assemblages represented an energy saving strategy where hominins cached raw materials near carcass acquisition hotspots. These "caches", whether established deliberately or as a by-product of successive episodes of unrelated discard behaviour (e.g., raw materials and tools left by the scavenged or butchered remains of a carcass; or under a frequently visited shade-giving tree), would, over time, have become artificial islands of raw material on the ancient landscape (Schick and Toth, 1993; Plummer, 2004).

Adopting some elements of the 'stone-cache-model', the 'favoured places' hypothesis (Schick, 1987), posits that the occasional discard of stones tools and raw materials at 'favoured places' over time would have generated *de facto* caches. These favoured places would represent locations that offered some degree of protection, shade, and, potentially, vantage points for identifying potential prey, dangerous predators or conspecific

competitors, where hominins could process food, rest and socialize (Schick & Toth, 1993, 2006).

Over the years, many more models have been proposed, but there is still little consensus as to which model provides the most plausible scenario of hominin landscape-use (Braun, 2013; Hernandez-Aguilar, 2009; Plummer, 2004; Schick & Toth, 2006). On the one hand, this is because they emphasize different aspects of hominin behaviour and do not consider many other social, ecological, and biological variables (e.g., group size, time-budgets, body size). On the other hand, while landscape-scale studies of hominin assemblages are helping to identify some potential patterns driving artefact distributions (e.g. Rogers et al., 1994; Braun et al., 2008b; Blumenschine et al., 2012), research has largely remained site-focused (Behrensmeyer, 2011). Consequently, this has limited the recovery of supporting large-scale archaeological evidence that could help disentangle this debate, particularly with regard to early chronologies in which high-density sites are rare (Dibble et al., 2016). Without being able to reproduce the exact conditions (whether biological, behavioural, or ecological) that formed the archaeological record in the real world, this task becomes inherently more challenging.

It is important to also note that all models emerge from an era of archaeological research before the discovery of the Lomekwian and the foundation of Primate Archaeology. Many of the assumptions on which they were built are no longer justified – for example, that lithic assemblages are exclusively related to hunting or carcass processing activities (e.g. Blumenschine, 1987; O'Connell et al., 1988). In light of recent discoveries and paradigm shifts, it is becoming increasingly paramount to revisit this question and devise new and testable models that better fit current knowledge of the hominin record and take into

account the yet unexplored pre-Oldowan technological period. The first step in this endeavour is to expand our understanding of the relationships between ecology, behaviour, and the formation of archaeological assemblages.

NEW PERSPECTIVES

In the absence of a sizeable archaeological record prior to 2.6 Ma, recent developments in primatology and computational modelling are uncovering promising new avenues of enquiry for expanding our understanding of the nature of early and pre-Oldowan assemblages and the behaviours they portray. This thesis harnesses the combined potential of these two disciplines to pioneer research into the ecology of chimpanzee technology as a comparative analogue for advancing two key areas of archaeological enquiry: 1) the selection and procurement of raw material for plant tools as a behavioural precursor of lithic technology; 2) the ecology of stone technology and the formation of technological landscapes.

Chimpanzees are one of our closest living relatives (Langergraber et al., 2014) and present the largest and most diverse technological repertoire compared to any other non-human species (Carvalho et al., 2013). Populations throughout Africa use a variety of stone and plant materials for extractive foraging, social interactions and self-maintenance (Carvalho & Almeida-Warren, 2019; McGrew, 1992, 2010a). They use stone cobbles and hardwoods as hammers and anvils to crack open nuts (Boesch & Boesch, 1990; Sugiyama & Koman, 1979); twigs, vines, grass, leaf petioles, and strips of bark to harvest social insects (e.g. ants, termites, bees) and honey (Boesch et al., 2009; McGrew & Collins, 1985; Pascual-Garrido et al., 2012; Sanz et al., 2010; Sanz & Morgan, 2009); palm petioles as pestles to pound and extract the soft core of the palm crown (Ohashi, 2015; Yamakoshi & Sugiyama, 1995); and wads of

chewed leaves or moss as sponges to soak up drinking water (Lapuente et al., 2017; Tonooka, 2001). Furthermore, many forms of plant tool use involve tool manufacture, i.e., the modification of plant materials prior to use. Examples include, but are not restricted to, the stripping of leaves and bark from twig tools for harvesting insects, the fabrication of brush tips on twigs used for termite-fishing (Sanz et al., 2009; Takemoto et al., 2005), and the folding of leaves to gather drinking water (Tonooka, 2001). Chimpanzees have also been observed to sharpen sticks for capturing bush babies (*Galago senegalensis*) sleeping in tree hollows (Pruetz & Bertolani, 2007).

Anatomically, they are the extant primate species that most closely matches our earliest ancestors in terms of body size, bone morphology, and brain size (K. D. Hunt, 1994; Russak, 2013). It is also likely, therefore, that they also have similar life histories, nutritional requirements, and metabolism, important for reconstructing long-term activity patterns and associated landscape-use. Ecologically, their range covers a suite of mosaic habitats, from high-canopy forests, to open woodlands and dry savannas, that match some of the palaeolandscapes that have been reconstructed for our earliest ancestors (e.g. Reed, 1997a). Research has also proposed that they would have had similar diets to chimpanzees, rich in fruit, nuts, insects and the occasional meat (Copeland, 2007; McGrew, 2014; Panger et al., 2002).

Studies of chimpanzee foraging adaptations have provided parallels for exploring the emergence of certain aspects of human behaviour (Mitani, 2013). For example, the apparent female sex-bias in tool use among some chimpanzee communities has been investigated in connection to the development of sexual division of labour in the hominin lineage (Boesch & Boesch, 1984b; McGrew, 1979). Meat acquisition and the social contexts of meat sharing

amongst chimpanzees has also been used to determine the possible mechanisms that drove meat procurement and food sharing in early hominins (Mitani, 2013).

Nevertheless, it is the study of chimpanzee technology that offers the most valuable sources of information for deciphering early hominin archaeological assemblages and uncovering the behavioural precursors of stone tool use. When chimpanzees source tool materials from plants, a scar is left at the point of extraction (Pascual-Garrido, 2018). These 'tool negatives' can remain identifiable for several months, providing a unique framework for studying the mechanisms of plant material selection and acquisition, key to understanding underlying cognitive processes such as foresight, planning, and ecological knowledge (e.g., of the mechanical properties of different materials).

Chimpanzee plant tool use has been studied extensively since the 1960's to investigate topics such as typological variation, technical complexity, and learning (e.g., McGrew et al., 1979; Collins and McGrew, 1987; Bermejo and Illera, 1999; Sanz et al., 2009; Musgrave et al., 2021). However, comparatively little is known about raw material procurement strategies. At the outset of the present research, raw material studies were limited to a handful of publications (Almeida-Warren et al., 2017; Mcbeath & McGrew, 1982; Pascual-Garrido et al., 2012). Thus, expanding these studies is an important step in gaining a better understanding of how these strategies vary between communities, what might cause such variations, and how they compare with chimpanzee and hominin stone tool use.

However, given the prevalence of stone tools in the hominin archaeological record, it is chimpanzee nut-cracking technology that has received the greatest attention. Studies of chimpanzee nut-cracking tools in juxtaposition with Oldowan lithics have been instrumental

for investigating the cognitive pre-requisites for stone tool use and the adaptive role of technology (Boesch & Boesch-Achermann, 2000; Wynn et al., 2011; Wynn & McGrew, 1989). More recently, research within the primate archaeology paradigm, has also revealed that chimpanzee nut-cracking assemblages have artefact densities and distributions that are comparable to the low-density 'scatters' that dominate the early hominin record as described by Isaac (Carvalho & McGrew, 2012). Thus, studying the contexts of chimpanzee nut-cracking technology at a landscape-scale can provide a unique modern analogue for understanding the formation of ancient archaeological landscapes.

While the chimpanzee technological landscape does not mirror the exact conditions (whether biological, behavioural, or ecological) that formed the hominin archaeological record, this can be adapted to the current empirical knowledge of hominin behaviour and palaeoecology through simulation.

Simulation is a powerful tool for formulating testable predictions about empirical observations, as it provides a controlled environment where different scenarios can be explored (Faith et al., 2021). Importantly, it also allows us to examine processes that cannot be observed over the temporal or spatial scales of typical field studies or laboratory experiments, such as the formation of time-averaged hominin assemblages (Faith et al., 2021; Holdaway & Davies, 2020; Premo, 2006).

Archaeologists began experimenting with computer simulations in the 1970's (cf. Hodder, 1978) to test the effect of different socio-economic parameters, often determined from studies of hunter-gatherer populations, that were thought to have influenced the location and formation of archaeological assemblages (Stern, 1991). In the development of the 'stone

cache model' of hominin site formation (R. Potts, 1984), computer simulations were used to demonstrate that the use of multiple locations for 'caching' lithic raw materials, was a more energetically efficient strategy than the use of a single location for technological activities as had been described in the 'home base model' proposed by Isaac (Isaac, 1976). However, due to scepticism about modelling fidelity combined with poor results, limited computational power, and high investment costs both in terms of time and money, this approach was largely abandoned (Barceló & Del Castillo, 2016; Wurzer et al., 2015).

Today, nevertheless, with greater computational capacity and the advancement of improved methods resulting from 40 years of testing, generative modelling has regained its place in archaeological inference (Wurzer et al., 2015). An increasingly popular method which has been employed by scientists in an array of research areas (e.g. biology, social sciences, physics, chemistry) is *agent-based modelling* (ABM), which takes a bottom-up approach to simulate interactions of individual agents with each-other and their environment to understand emerging global patterns (Lake, 2015; Samuelson & Macal, 2006). Although this method is most often used to make predictions, it has become a powerful tool for guiding data collection, designing experiments, explaining patterns, and developing testable hypotheses (Gilbert, 2019; Romanowska et al., 2019). In recent years, agent-based models have been used by archaeologists to predict how dietary adaptations (e.g., tuber consumption) may lead to different hominin ranging patterns (Griffith et al., 2010), simulate how environmental change during the Holocene affected resource availability and hominin survival (Wren et al., 2020), and explore the potential drivers of Pleistocene dispersals (Vahdati et al., 2019). Conceptual exercises have also begun to explore the relationships between strategies of stone tool acquisition, the distribution of raw materials, and the formation of lithic assemblages (Brantingham, 2003; Reeves, Proffitt, et al., 2021). The

versatility of ABM and its capacity for integrating spatial information (B. Davies et al., 2019), make it a robust approach for reconstructing patterns of behaviour within virtual representations of real-world, spatially-explicit landscapes, while also facilitating the artificial enhancement of these empirical systems to explore a variety of alternative ecological scenarios through controlled experimentation.

ECOLOGY OF TECHNOLOGY

The occurrence of technological behaviours and the ways in which they are manifested in non-human primate populations presents a considerable amount of both inter- and intra-specific variation (Haslam, 2012; Koops et al., 2013). For example, only two out of 12 currently recognized capuchin species (Martins-Junior et al., 2018) – *S. libidinosus* and, more recently, *C. capucinus* – are known to habitually use stone tools for extractive foraging in the wild (Barrett et al., 2018; Ottoni & Izar, 2008). In chimpanzees, although tool use is widespread throughout Africa, nut-cracking is exclusive to West African (*Pan troglodytes verus*) and Cameroonian (*P. t. ellioti*) populations (Abwe & Morgan, 2008; Haslam, 2012; B. J. Morgan & Abwe, 2006). Conversely, bonobos (*Pan paniscus*), the sister species of the chimpanzee, use few tools in the wild, and no tools for extractive foraging, despite the existence of raw materials and suitable prey species (McGrew et al., 2007).

Moreover, there is considerable variation in the tool sets and tool types used to exploit the same resources (Carvalho & McGrew, 2012; Sanz & Morgan, 2011; Whiten et al., 2001). Most chimpanzee termite-fishing populations only use one typological tool form – a fishing probe – made out of bark, grass or twig. However, chimpanzee populations in central Africa use composite tool sets made up of multiple tool types – a perforating stick, a puncturing stick, and a fishing probe with a modified brush-tip (Sanz et al., 2009; Sanz & Morgan, 2011).

Additionally, while at Gombe (Tanzania; McGrew et al., 1979; Pascual-Garrido, 2019), chimpanzees have been found to use bark, grass, vine, twigs, and palm fronds as tools for extracting termites, no bark or palm frond tools were recorded at Mt. Assirik (Senegal; McGrew et al., 1979), and only bark materials at Issa (Tanzania; Almeida-Warren *et al.*, 2017). Similar patterns emerge in chimpanzee nut-cracking. For example, chimpanzees in the Taï Forest (Côte d'Ivoire) and Tiwai Island (Sierra Leone) are the only populations known to use both wood and stone hammers to crack nuts, while those in Bossou (Guinea) and Kpayee-Lepula Forest (Liberia) are the only ones known to use portable stone anvils (Carvalho & McGrew, 2012).

Research seeking explanations of these variations have typically employed the method of exclusion, whereby behaviours that cannot be explained by ecological or genetic factors are attributed to culture (Koops et al., 2014; Whiten et al., 2001). While this is important for identifying culture or cultural behaviours in non-human animals, as opposed to behaviours that are common to the whole species or unique to specific ecological niches, it does not help understand the mechanisms that drove the emergence and development of these traits in the first place (Koops et al., 2013, 2014). This also applies to technological behaviours. Tool use can be viewed as a problem solving task aimed to mitigate challenges set by a given ecological niche and, therefore, techno-cultural behaviours are intrinsically connected to ecological affordances, and cannot be studied in isolation (Koops et al., 2014; S. McPherron, 2013). Recent findings have highlighted that ecology plays a major role in the development, transmission, innovation, and perpetuity of tool use (Grund et al., 2019; Humle et al., 2009; Humle & Matsuzawa, 2002; Koops et al., 2013, 2014). This can be broadly divided into two, not mutually exclusive, ecological hypotheses – *opportunity* and *necessity* (Koops et al., 2013, 2014). Opportunity refers to a population's rate of encounter with tool materials

and food resources that either require, or are most effectively exploited with aid of tools (Koops et al., 2014). Necessity refers to the emergence of tool use in response to scarcity of foods that do not require extractive foraging (Grund et al., 2019).

In a study comparing these two hypotheses (Koops et al., 2013, 2014), ecological opportunity appeared to be the main driver of tool use in chimpanzees, orangutans and capuchins. Chimpanzees in Seringbara (Guinea) use tools to exploit the more prevalent army ant nests, but not to harvest termites from rarer *Macrotermes* mounds (Koops et al., 2013). Moreover, in chimpanzee communities where exploitable nut species were available, nut-cracking behaviours only occurred in those where the density of nut-trees was greater (> 10 trees/ha; Koops et al., 2014). Similarly, orangutans where more likely to use tools to obtain *Neesia* seeds at sites that offered greater rate encounters. In this study, no evidence was found in support of ecological necessity, as there were no correlations between tool use and seasonal food scarcity (Koops et al., 2014).

However, recent studies are adding more complexity to this picture. Field experiments are revealing that both ecological necessity and opportunity may be equally important in the development, diffusion and maintenance of technology in a population, whereby necessity may motivate greater engagement with ecological opportunities (Grund et al., 2019). Alternative hypotheses are also emerging from studies of non-primate technological species. The "relative profitability hypothesis", developed to explain differences in tool use among corvids, suggests that technology arises if it provides a relatively greater energetic gain than alternative non-extractive foraging strategies (Rutz & St Clair, 2012).

Whether through opportunity, necessity, or another mechanism, it is becoming increasingly clear that ecology plays a crucial role in the development of tool use in non-human species, including primates. Ecological variables have also been found to have a potential effect on the technological behaviours themselves (Carvalho & McGrew, 2012). Previous research on chimpanzee nut-cracking has established that the availability and location of nut-trees and raw materials for tools seem to dictate site location and re-use, as well as the frequency and carrying distances of raw material and tool transport (Carvalho et al., 2011). The proximity to hydrological features, such as streams and rivers, may also correlate with the location of nut-cracking sites(Carvalho et al., 2007). Such ecological variables have also been associated to early hominin assemblages between 2.3 and 1.8 Ma as described by Rogers (1994), and have featured in numerous hypotheses surrounding early hominin resource exploitation strategies and the distribution of archaeological assemblages (Isaac, 1981a; Rose & Marshall, 1996; Sept, 2011).

Nevertheless, primate technology is yet to be explored in its full ecological context at a broad landscape-scale. In order to fully understand the behavioural ecology of technology it is necessary to study a species as part of its ecosystem, which includes the physical environment as well as its interactions with other plants and animals, whether as food sources, competition, or predators (Dibble et al., 2016; Rogers et al., 1994). This requires the study of tool sites in relation to other activity areas (e.g. feeding trees, sleeping sites) and broader environmental factors (e.g. vegetation composition, distribution, climate and geology). Given that hominin technology would have been subject to similar selective pressures (Carvalho & Beardmore-Herd, 2019; Panger et al., 2002), establishing these ecological relationships in non-human primates is crucial for elucidating the contexts for

archaeological accumulations, reconstructing patterns of landscape-use, and determining how these may have changed through time.

Structure of thesis research

Previous research in both Palaeolithic archaeology and primatology outlined above has provided key elements for the theoretical backdrop of this thesis:

I. Plant-based technology pre-dated the Oldowan, and that it was likely more prevalent and diversified than stone technology;

II. Hominin assemblages between 2.6 – 1.6 Ma (Oldowan) are diverse, and where likely the product of different hominin species who used stone tools for a wide variety of tasks, including plant processing;

III. 90% of the early archaeological record is characterised by sparsely distributed scatters of lithic material across the landscape, rather than hotspots of densely concentrated assemblages;

IV. A hominin lithic industry prior to the Oldowan exists at 3.3 Ma (Lomekwian), showing a reliance on percussive bipolar and passive-hammer techniques, distinct from the flake-dominated technology of the Oldowan;

V. The spatial patterning of archaeological assemblages, and therefore, hominin landscape use, may be dictated by certain ecological variables (e.g., proximity to water and raw material sources).

Despite this knowledge, we still know very little about hominin perishable technology or their patterns of land-use, particularly prior to 2.6 Ma. This is in part, due to a sparse record almost entirely dominated by stone artefacts, with a research bias towards the

study of high-density sites, but also due to a dearth of transferable data from modern analogues. Chimpanzees, as our closest living relatives, provide the comparative tools for such an investigation, especially regarding the earliest technological occurrences:

I. Chimpanzees have one of the most extensive and diverse technological repertoire of all non-human species, which includes stone tool use and a variety of plant-based technologies;

II. Chimpanzee technology produces an archaeological record;

III. Chimpanzee nut-cracking technology is similar to that of the Lomekwian and some elements of the Oldowan;

IV. Chimpanzee nut-cracking sites have artefact densities akin to the low-density assemblages that characterize the Plio-Pleistocene archaeological record;

V. Ecological variables have been found to drive the location and re-use of nut-cracking sites as well as the frequency and distance of tool transport.

Within the paradigm of Primate Archaeology, the current research aims to:

1) Examine the diversity and drivers of plant material procurement strategies in chimpanzee perishable tool use;

2) Investigate the ecological parameters shaping the selection, re-use and abandonment of locations for stone tool use by chimpanzees across their home range;

3) Explore, through agent-based modelling, how different environmental characteristics may shape landscape-scale patterns of chimpanzee stone tool use.

In doing so, this thesis sheds new light on some of the most fundamental, yet enigmatic, questions in human origins research: **What were the behavioural predecessors of stone tool use? How did our earliest technological ancestors live? And how did tool use, and the lithic assemblages produced, fit into the wider behavioural and ecological landscape?**

To ensure data would be comparable to hominin datasets, it was crucial to develop a standardized method of data collection that could be implemented in both hominin and non-human primate records, particularly in terms of mapping archaeological information. A major obstacle for conducting wide-ranging landscape studies is the cumbersome nature of the survey equipment (e.g., Total Station) and the considerable time required for setting up and recording data at every new location. This is particularly problematic in chimpanzee habitats where such heavy equipment often needs be transported on foot over uneven terrain through densely vegetated forests. As a result, primate archaeological research has largely relied on traditional approaches (e.g., the tape and compass method), which are more time consuming and less accurate than modern, more technologically advanced, archaeological practices.

To overcome these methodological limitations, a new method for archaeological mapping is proposed in Chapter 2. The DistoX2 is a highly portable hand-held laser distance measurer with an integrated compass and clinometer, which can be paired with an android or windows device as a fully digital data collection system. It was originally developed for mapping cave systems to replace the traditional time-consuming and labour-intensive method of manual measurements and paper sketches (Heeb, 2008, 2014). Although research for this project was not conducted in cave environments, the portability of the system makes it an excellent

solution for taking quick and precise relative measurements in forested environments. This project tests this new methodology for the first time in both chimpanzee and early hominin archaeological contexts.

The chimpanzee termite-fishing component of the project (Chapter 3) provides the first cross-cultural comparison of the environmental and cultural determinants of raw material procurement for termite-fishing tools. This work builds on my MSc research (see Appendix E; Almeida-Warren et al., 2017), which focused on a community of wild chimpanzees living in Issa (Tanzania), and spans two additional wild chimpanzee field sites in Tanzania: Gombe and Mahale (Figure 1.2). Termite-fishing using plant tools is habitual among all three study groups (Gombe-Kasekela; Mahale-Bilenge; Issa), predominantly occurring during the rainy season (October-December; Uehara, 1982; McGrew and Collins, 1985; Stewart and Piel, 2014). While all three field sites are spatially discrete, genetic assessments revealed that the three populations are related and were likely connected by a continuous forest ecosystem

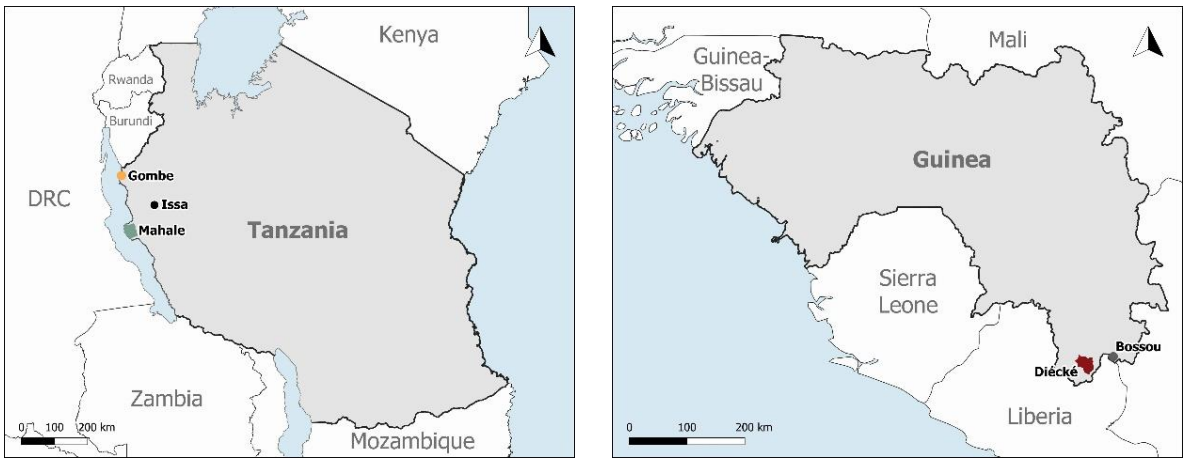


Figure 1.2. Location of chimpanzee study sites. Left: Tanzanian sites where data was collected on chimpanzee termite-fishing (Gombe, Issa, and Mahale). Right: Guinean sites where data was collected on chimpanzee nut-cracking (Bossou), and surveys were conducted to evaluate chimpanzee presence (Diécké).

or forest corridors in the past (Inoue et al., 2013). Thus, they formed the ideal study subjects for examining inter-community differences, while minimizing the potential effects of genetic divergence.

The study presented in Chapter 3 analysed archaeological data collected between 2014-2016 (inclusive), and sought to address three main questions*:* **How are chimpanzees procuring sources of raw material for the manufacture of termite-fishing tools? What differences exist between the termite-fishing communities of Gombe, Issa, and Mahale? Are these differences a reflection of the local environment?** Finally, the results are examined in the context of procurement strategies associated to chimpanzee and hominin stone tool use with a discussion on the implications for the origins of human technology.

The nut-cracking component of the project (Chapter 4) is the first to examine the broader ecological and behavioural landscapes of chimpanzee technology as well as the first to apply landscape archaeology methods in a non-human primate setting. For this study, fieldwork was conducted at the wild chimpanzee site of Bossou, Guinea (Figure 2). The chimpanzee community has been studied continuously since 1976, and is currently the only long-term study site where chimpanzees are known to habitually use portable stone hammers and anvils to crack nuts (Carvalho et al., 2007, 2013).

Here, the research tackles**: What are the ecological determinants of chimpanzee nut-cracking technology? Specifically, what drives the selection, re-use and inactivity of locations for nut-cracking activity?** Particular focus is given to the potential role of food, water, and sleeping sites, as these resources are critical for survival. Tool site selection

explores the ecological conditions that may determine where nut-cracking sites are established within the chimpanzee home-range. Tool site re-use (and use) focuses on the ecological factors that influence the frequency with which established sites attract nut-cracking activity. Lastly, tool site inactivity investigates the ecological conditions that may cause the cessation of nut-cracking activity at an established tool site. Together, these three points of enquiry constitute a comprehensive analysis of the conditions required for nut-cracking to occur and persist over time in discrete locations, key for discerning how technological behaviours map onto the broader contexts of landscape-use and activity patterns.

Using agent-based modelling, the data collected in Bossou is translated into a virtual environment to test how different ecological scenarios shape the spatial patterning of nut-cracking activity across the landscape (Chapter 5). In combining living chimpanzee archaeology (Chapter 4) with modern computational methods, this approach provides the first large-scale perspective of the relationship between behaviour, ecology, and the formation of archaeological sites. Crucially, this will enable development of more accurate interpretations of the early hominin technological record, as well as provide the first glimpse of the yet unexplored pre-Oldowan behavioural landscape.

This research also has important applications in the preservation of non-human material culture. With a rapidly decreasing population, our closest relative, the chimpanzee, has been classified as an endangered species and is estimated to become extinct within the next 50 years (Oates et al., 2015). The subspecies *P. t. verus*, known as the Western chimpanzee of which the Bossou community is part, is now critically endangered (Humle, Boesch, et al.,

2016). With an ageing and declining population of seven individuals, this may be one of the last projects to document the rich and unique cultural heritage of the Bossou chimpanzees.

During fieldwork in Bossou, a short expedition was organised to the nearby forest of Diécké to conduct a reconnaissance survey on the presence of chimpanzees in the Korohouan area and to examine the feasibility of expanding research efforts to that location. Diécké is the second largest forest in Guinea, and was first surveyed for chimpanzee presence in 1998 (Ham, 1998). The chimpanzees were found to crack different nut species to Bossou and use wooden tools (Carvalho et al., 2007; Humle & Matsuzawa, 2001), making Diécké a promising site for a comparative ecological study. The survey revealed, however, that the Korohouan area of the forest and its wildlife has suffered from considerable anthropogenic activity, rendering it unsuitable for the original research objectives. Instead, the survey findings are presented in Chapter 6, and discussed in the wider context of the historical, socio-political, environmental, and scientific developments that have occurred around the Diécké forest reserve over the last decades.

This thesis has been structured to provide an overview of the research context and theoretical backdrop (Chapter 1), followed by testing the performance of the novel method (Chapter 2). This is proceeded by the three key stages of the empirical work: the archaeology of perishable technology (Chapter 3), the ecology of chimpanzee nut-cracking (Chapter 4), and reconstructing primate technological landscapes using agent-based modelling (Chapter 5). The empirical component of the thesis is followed by a report on the presence and conservation status of the nut-cracking chimpanzees of Korohouan (Chapter 6), and a final chapter with the overall conclusions, challenges, and future areas of exploration (Chapter 7).

Chapter 2

The DistoX2

A methodological solution to archaeological mapping in poorly accessible environments

The content of this section was originally published in (Almeida-Warren, Braun, et al., 2021)**. This is an open access article distributed under the terms of the Creative Commons CC BY license**: **http://creativecommons.org/licenses/by-nc-nd/4.0**

Abstract

Spatial information is crucial to archaeological field research. From the plane-table to the total station, recent technological advances have enabled data collection to become fully digital and highly accurate. Nevertheless, the recent expansion of archaeological expeditions to novel environments often incompatible with modern mapping equipment, e.g. tropical forests or ephemeral shorelines, calls for further methodological innovations. Such projects,

as well as those under logistic or financial limitations, are still largely reliant on more time consuming, less accurate, traditional approaches, e.g. offset or tape and compass methods. The DistoX2 is a digital, highly portable, and versatile hand-held instrument originally developed for speleological surveys where total stations and DGPSs are not feasible. But, the potential of the DistoX2 system as a spatial mapping tool in above-ground contexts has been surprisingly overlooked. Here, we present a first assessment of the applicability of the DistoX2 for archaeological mapping in non-speleological environments. We investigate precision and accuracy in controlled above-ground settings relative to two common methods of data collection – total station, and tape and compass. We test the relative precision of the DistoX2 when mounted on a tripod or operated in hand-held mode and discuss its applicability, and potential combined used, in the context of other increasingly popular methods – GNSS and SfM photogrammetry. With a mean error of ≈ 5.00 cm for horizontal readings and ≈ 2.00 cm for vertical readings, the DistoX2 is considerably more accurate than the tape and compass method (μ ≈ 67.00 cm horizontal; μ ≈ 3.00 cm vertical). While the DistoX2 exceeds the error thresholds of projects that require high spatial sensitivity (e.g. Palaeolithic excavations), it provides a reliable, low-cost and more accurate alternative to many projects that resort to more traditional methods. This fills an existent methodological and financial gap amongst the growing diversity of archaeological expeditions.

Introduction

Spatial mapping has been a key component of archaeological research and documentation for over 100 years (Wheatley & Gillings, 2002). It helps determine the spatial relationships between archaeological objects and features, and the stratigraphic contexts in which they

are found, crucial for the interpretation of an archaeological site or assemblage and its possible relationship to others (S. J. P. McPherron, 2005).

While mapping techniques in accessible urban or open environments are well established, it is not standardized throughout all archaeological settings – ranging from highly accurate total station systems, to analogue tape and compass methods. The pursuit of a universal methodology, compatible with all archaeological environments, has become more urgent in the last decades, as archaeological research expands to the exploration of cave sites, tropical forests and non-human primate records (Carvalho & Almeida-Warren, 2019; Haslam et al., 2009; Mercader, 2002; Mercader et al., 2002, 2007; Trimmis, 2015, 2018). The challenges of these new environments, particularly in terms of accessibility, have made the implementation of many modern archaeological mapping methods unfeasible, thus limiting the potential of comparison across different datasets.

Mapping in the pre-digital era was achieved using a variety of methods and tools such as the plane table, the manual theodolite, or varying combinations of measuring tapes, levelling aids, and a compass (Dibble, 1987; Historic England, 2017; Wheatley & Gillings, 2002). While some of these methods are still used today, technological developments in engineering and Global Navigation Satellite Systems (GNSS) in the last decades have revolutionized the speed, accuracy and automation of mapping techniques, evolving from simple analogue approaches, to fully digital total station theodolite (TST) systems, and, more recently, to Real-Time Kinematic (RTK) GNSS, terrestrial laser scanning (TLS), and photography-based surveys, such as Structure from Motion (SfM) photogrammetry (Dibble, 1987; Jo & Hong, 2019; Kjellman, 2012; Martínez-Fernández et al., 2020; S. J. P. McPherron, 2005; Pearson et al., 2015; Roosevelt, 2014; Willis et al., 2016).

However, archaeology in extreme or poorly accessible environments, such as cave systems with restrictive access and densely forested landscapes with uneven terrain, has until recently been largely limited to the tape and compass method (Almeida-Warren et al., 2018; Trimmis, 2018). Also known as the distance-azimuth method, it typically involves the use of one measuring tape to measure the horizontal distance between a fixed reference point (datum) and the object of interest, a second tape to measure the vertical distance between the first tape and the object, and a compass to determine the direction of the object from the datum relative to North (Carvalho & Almeida-Warren, 2019). An alternative method (tape-compass-clinometer) measures the direct distance between the datum and the object, replacing the second tape with a clinometer to determine the inclination of the first tape (Ballesteros et al., 2013; Redovniković et al., 2014). While highly portable and effective, these methods lack the precision of more contemporary archaeological methods and are more time consuming both at the data collection level, recorded by hand, as well as data entry from paper to a digital format.

The limitations of such methods are particularly acute in primate archaeological research where standardized methods are needed to make meaningful comparisons between human and non-human primate records within an evolutionary context. Primate archaeologists study living non-human primates often in remote environments, such as densely vegetated high-canopy forests requiring daily travel of several kilometres on foot, and ephemeral shorelines where data collection is conditioned by the tides (Carvalho et al., 2008; Carvalho & Almeida-Warren, 2019; Haslam, Luncz, Pascual-Garrido, et al., 2016). They also face the additional challenge of working at 'living sites', which are still visited by the study species, often requiring minimal disturbance and rapid removal of equipment when subjects appear (Carvalho, 2011).

While a critical part of primate archaeology research deals with extant technological behaviour, the research questions mirror many of the spatial queries of traditional archaeology: How are archaeological objects spatially related to each other? How does the spatial distribution of assemblages change over time? Is there inter and intra-site variation? (Carvalho et al., 2008; Carvalho & Almeida-Warren, 2019; Falótico et al., 2019). Thus, as with traditional archaeology, precision in these contexts is essential for accurate mapping of archaeological objects and features.

The DistoX is a customized hand-held electronic laser distance measurer (e.g. Leica Disto A3; Leica Disto X310) retrofitted with a compass and clinometer. It was developed for mapping cave systems to replace the traditional time-consuming and labour-intensive method of manual measurements and paper sketches (Heeb, 2008). It is a compact (55 x 31 x 122 mm), light-weight instrument (150 g), which can be paired with and Android or Windows device, making it a highly versatile fully digital system for spatial data collection (Heeb, 2014). Further technical information including assembly instructions can be found here: https://paperless.bheeb.ch/.

Performance tests in cave settings have revealed that the DistoX system (X1 model) is considerably more accurate than the tape and compass method, and presents readings more comparable to total station measurements (Ballesteros et al., 2013; Redovniković et al., 2014). More recently, the DistoX1 has successfully been used to document archaeological remains found in caves on Kithera Island and Kastoria in Greece (Trimmis, 2015, 2018).

Nevertheless, while the DistoX has been adopted as one of the main speleological tools for mapping cave systems (see Trimmis, 2018), its potential in archaeological settings has yet to

be fully explored. The portable and relatively affordable nature of the DistoX system make it a suitable candidate to replace the tape and compass method, with the potential to bring archaeological data collection in challenging environments to a similar level and quality as that seen in major archaeological research projects around the world. The DistoX system could also benefit those archaeological projects with a limited budget, where a total station or other modern alternative equipment, although viable in practice, may be too costly financially (Table 2.1).

Table 2.1. Practical details of common mapping methods compared to the DistoX2.

Method	Weight	North	Functionality	Cost
Tape and compass	1 - 3 Kg	Magnetic North	Analogue or Semi-digital	$20 – 200[a]
Total station	4 - 10 Kg	Programmed by user	Fully digital	$4,000 - 10,000
GNSS/RTK GNSS	2 - 10 Kg	True North	Fully digital	$1,500 - 20,000
Photogrammetry	1 - 8 Kg	Programmed by user	Fully digital	$200 - 1,500
DistoX2	0.5 – 3[b] Kg	Magnetic North	Fully digital	$280 - 500[2]

[a]if using a digital compass
[b]depending on digital accessories chosen (e.g. mobile or tablet device), and whether tripod is included

To date, very little empirical literature exists on the performance of the DistoX method for capturing spatial provenience information. All equipment tests have, so far, been restricted to cave settings, and have provided limited statistical assessments (see Ballesteros *et al.*, 2013; Redovniković *et al.*, 2014; Redovniković, Stančić and Cetl, 2016). Here we test the latest model of the DistoX – DistoX2 – in controlled open-air settings. We assess performance in terms of precision, as well as accuracy relative to two common methods of spatial data collection – total station, and tape and compass.

The DistoX2

TECHNICAL SUMMARY

The DistoX2 is the latest model of the DistoX system (Figure 2.1a). It is a hand-held electronic measuring device composed by a Leica DistoX310 laser distance meter retrofitted with a tilt-compensated (3D) digital compass, clinometer, and a Bluetooth module for wireless data transfer (Heeb, 2014). It was originally developed in 2008 as a paperless alternative to mapping the internal structures of caves, where more typical digital spatial mapping instruments, such as GPS/GNSS modules and total stations, are not viable (Heeb, 2008;

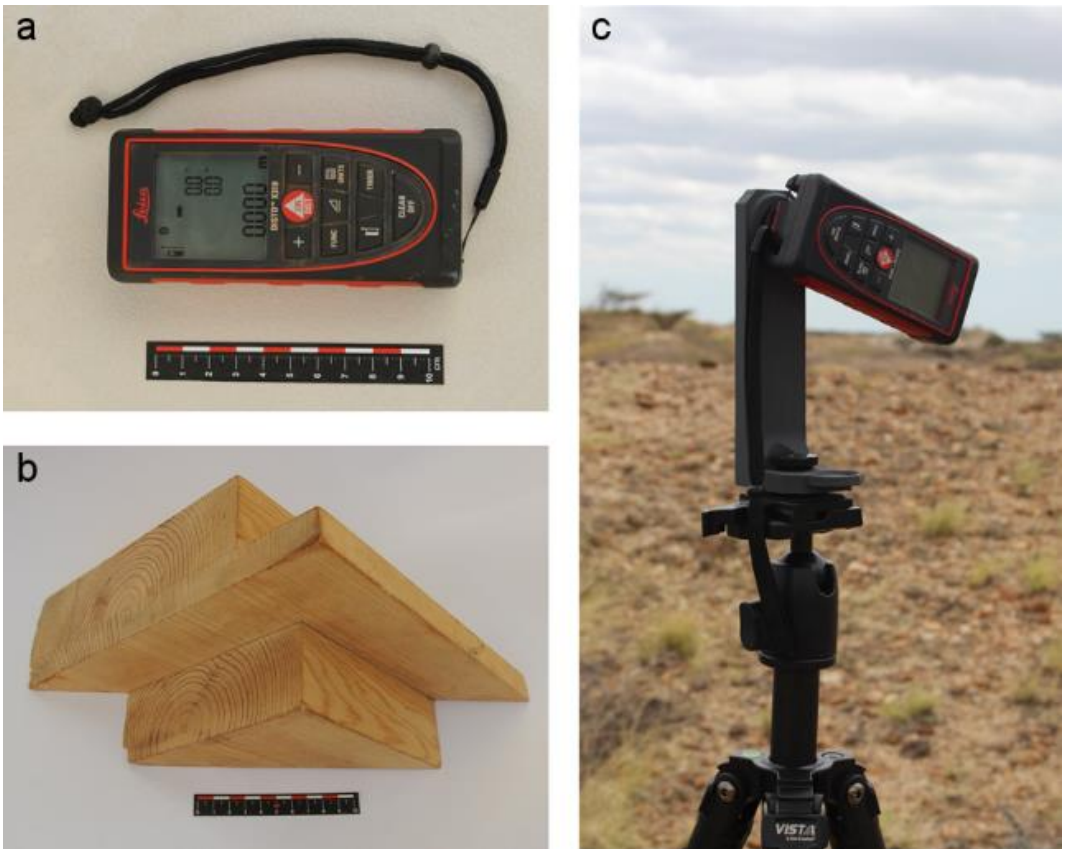


Figure 2.1. DistoX2 and accessories: a) DistoX2 instrument (Photo: F. T. Regala); b) Disto calibration block (Photo: F. T. Regala); c) Custom-made tripod adapter (Photo: K. Almeida-Warren).

Redovniković et al., 2014; Trimmis, 2018). Spatial mapping in forested environments, presents similar challenges to the cave settings – total stations are too heavy and bulky to carry manually in dense vegetation over large distances, and canopy cover is often too dense to achieve GPS readings at a sufficiently low resolution for accurate spatial mapping.

The DistoX2 provides instantaneous distance, inclination and azimuth readings. It can be used as a hand-held device without other supporting accessories or mounted on a tripod for additional stability; and measurements can be taken directly towards the target object or aimed at a reflector of fixed height placed on the target location (Figure 2.2). It can function as a stand-alone instrument, but its performance is most optimal when used in tandem with an external mobile device such as a phone or tablet (Redovniković et al., 2016). Data can be uploaded via Bluetooth connection onto a compatible data management application (Heeb, 2014). The currently available applications, both open-access, are PocketTopo for Windows OS (Heeb, 2008), and TopoDroid for Android OS (Corvi, 2016), which allow data management and organisation by project, data visualisation, and export in a variety of formats including .csv and .klm. These applications were designed for mapping

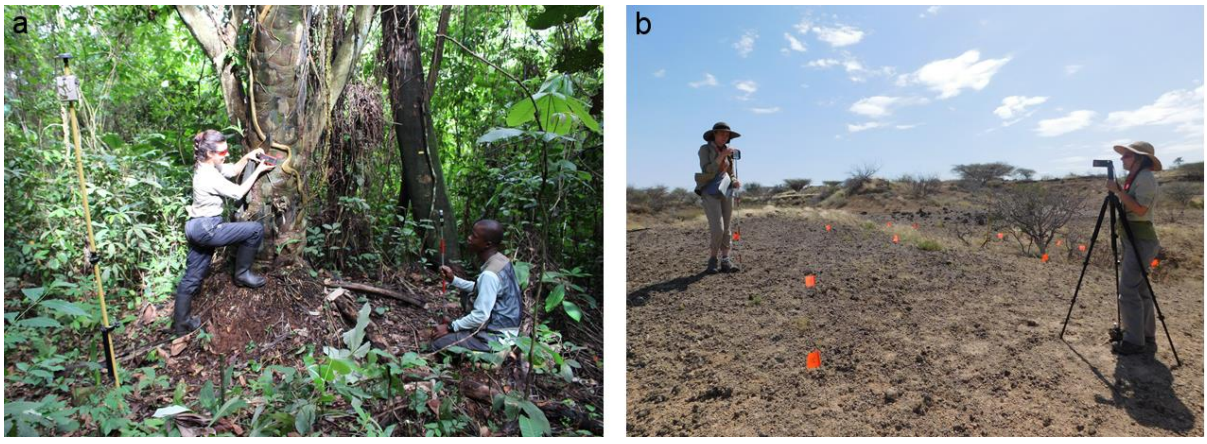


Figure 2.2. DistoX2 setup options: a) Hand-held mode (Photo: V. Mamy); b) Tripod mode (Photo: C. Daniel).

speleological contexts, but can be adapted to archaeological settings (e.g. Trimmis, 2015, 2018), although a tailor-made application that integrates common archaeological data collection specifications (e.g. grid systems, digital finds/feature forms, conversion between angle readings and XYZ measurements) would help make the data collection process more streamline. General DistoX2 technical specifications according to Heeb (2014) are presented in Table 2.2.

Table 2.2. Disto X2 technical specifications.

	Range	Resolution	Precision
Distance	0.05 - >100m	Magnetic North	0.2 cm[a]
Azimuth	0 - 360°[b]	0.1°	0.5° RMS[c]
Inclination	±90°	0.1°	0.5° RMS[c]

[a] up to 10 metres
[b] relative to magnetic North
[c] after successful calibration. RMS = root mean square

In order to achieve the best results, regular calibration of the DistoX2 is essential to correct for spatial and temporal magnetic shifts, particularly when starting a project in a different geographic location or after long periods of inactivity (Heeb, 2013). Calibration is possible free-hand or with a calibration block (Figure 2.1b) and the calibration function available on the Android or Windows software interface (Heeb, 2013; Regala, 2015; Tátá Regala, 2016).

It is important to note that azimuth readings are always relative to magnetic North and need to be corrected for magnetic declination (deviation from true North) (Redovniković et al., 2014). Magnetic declination fluctuates over time and is different depending on geographic location. Historic and current magnetic declination data can be consulted by coordinate location on the National Centers for Environmental Information website (https://www.ngdc.noaa.gov/geomag-web/).

PREVIOUS TESTS

Performance tests of the DistoX1 system in cave settings relative to the tape, compass and clinometer (TCC) method, and the total station revealed that, although less accurate than the total station, the DistoX1 is considerably more accurate than the TCC method (Ballesteros et al., 2013; Redovniković et al., 2014). Tests in El Pindal Cave (Spain), demonstrated that the DistoX1 measurements deviated from the total station readings by 0.72 m ± 0.04 %, while the TCC measurements deviated by 9.18 m ± 11.64 % (Ballesteros et al., 2013). Tests in cave Veternica (Croatia) mapping out a series of points along a 565.44 m traverse showed TCC deviations of up to 2.06 m in vertical distance from the total station baseline, while the DistoX1 only diverged by a maximum of 0.56 m (Redovniković et al., 2014). Horizontal distance error presented more exaggerated results, with TCC error ranging 0 – 30 m, and the DistoX1 error remaining consistently under 0.5 m. While not specified in the paper, the wide range for TCC error is likely due to the fact that the effect of angle measurement error and resolution (i.e. from compass and clinometer) is exacerbated as the distance from the measuring station increases, whereby at 0 m angle error would be negligible, but at 500 m the divergence from the true position would be considerable. One would expect a similar effect on the DistoX1, albeit to a lesser degree due to greater instrument accuracy and precision. However, data of these measurements were not provided in the publication.

Only one article has been published so far on the performance of the latest model of the DistoX – DistoX2 – where it was compared to the total station using two different post-processing applications (Redovniković et al., 2016). Both tests revealed similar results, with DistoX2 error ranging 0.07 – 0.24 m for horizontal measurements, and 0.00 – 0.03 m for vertical measurements. However, the test was only conducted on 14 physical control points,

8 of which were included in the study. The remainder of the publication focuses on comparing point clouds generated from photogrammetry using the 8 control points taken with the DistoX2, with points clouds produced from the equivalent total station data. In this case, for the 900,000 common generated points, measurement deviation between the DistoX2 and the total station point clouds was found to be largely under 0.04 m (Redovniković et al., 2016).

While previous empirical work has gone some way in testing the DistoX performance and providing evidence supporting the DistoX as a better system than the tape and compass method for spatial mapping in cave settings, it has relied on small sample sizes (between 2 and 38 test points) and all have used different methodological protocols, which limits the potential/feasibility of collating and homogenizing the various results. Given the potential of the DistoX system as a spatial mapping method in above-ground scenarios we conduct a series of tests in controlled outdoor settings to assess the DistoX2 performance relative to the total station and tape and compass methods. We also test the relative precision of the DistoX2 when mounted on a tripod, as compared to when operated in hand-held mode. This data will not only complement the current literature on the performance of the DistoX system but will also assess its capacity for spatial data collection across all non-aquatic environments, and for bridging the gap in methodological discrepancies between the optimal and the most challenging archaeological settings.

Methods

We tested the DistoX2 at two main levels: precision in both hand-held and tripod modes; and accuracy relative to the total station and to the tape and compass method. Tests were

conducted in three geographically distinct open-air settings: Bossou, Republic of Guinea (L1); Koobi Fora Base camp, East Turkana, Kenya (L2); and University Parks, Oxford, United Kingdom (L3). L1 and L2 are field sites where the DistoX2 has been used for recording modern wild chimpanzee tool-use sites and Plio-Pleistocene archaeological surface assemblages, respectively. All DistoX2 measurements were taken with the aid of a reflector to avoid interference caused by low-lying vegetation or other foreground objects obstructing line of sight. Test points were allocated to cover a range of distances and location within a 15-metre radius of the DistoX2 position and were marked with numbered pin-flags. The DistoX2 was calibrated with a calibration block at each measurement location prior to tests. Data were imported and processed on a Samsung Android tablet using the TopoDroid application (Corvi, 2016).

Precision

The precision test served to determine variation between successive measurements taken of the same point. This helps establish the level of relative error a single measurement might have. While the technical specifications of the DistoX2 provide information regarding instrument precision, we sought to verify this data in a real-world scenario, and to compare results between the two different device setups. Test data were collected from a total of 100 points – 50 points were documented in L1 using hand-held setup whereby the researcher was manually holding the DistoX2 positioned on the established datum; the other 50 points were documented in L3 using the tripod setup whereby the DistoX2 mounted on a tripod and set on a 5 second timer so the researcher could release their hands from the device before the measurement was taken. Each of the 100 points was recorded successively 5 times to determine device precision.

We designed a custom-made tripod mount with the help of Science Oxford, composed of 3D-printed piece and non-magnetic bolts for fixing (Figure 2.1c). See Appendix A for details on the design and a link to the 3D-model where downloads for printing are freely available.

Accuracy

Accuracy tests served to assess the performance and measurement errors of the DistoX2. In this case we use the total station measurements as a baseline and statistically compared the deviation in measurements (absolute error) of the DistoX2 with that of the tape and compass method in relation to a total station system. The DistoX2 accuracy relative to the total station was tested at L2 and L3. At L2 we collected 50 test points using a Leica Builder 505 (angular accuracy = 5"; distance accuracy = 2.0 mm) with a CPR111 True-Zero prism (constant = 0.0 mm; centring accuracy: 2.0 mm). At L3 we collected another 50 test points using a Leica TS06 (angular accuracy = 2"; distance accuracy = 1.5 mm), paired with a GPR111 prism (constant = 0.0 mm; centring accuracy: 2.0 mm). All total station points were recorded using the prism except for the datum and Disto position which were recorded by direct laser. Because control points with precise coordinate data were unavailable at either of the locations, the total station North was set to the magnetic North readings of the DistoX2, to avoid introducing further error from an additional measuring device. For this reason, we did not have to correct the DistoX2 readings for magnetic declination.

Tape and compass data were only collected for the 50 test points established at L3. We used a standard 30 m tape (resolution = 0.2 cm) to measure horizontal distance, a 5 m retractable tape (resolution = 0.1 cm) to measure vertical distance, and the in-built 3D digital compass of a Garmin Oregon 700 (resolution = 1.0°; reported accuracy = 2.0°, calibrated before use) to measure azimuth. The north reference was set to the default – true north – and azimuth

readings were converted to a magnetic north reference based on declination information for the date of recording (Magnetic Model EEM2017 version 0.914, Declination = -0.752 decimal degrees). A string, plumb-bob and spirit level were used to keep the horizontal tape level to the datum. Although we recognize that using a digital compass with greater resolution and accuracy would directly improve the accuracy of this method, we wanted to reproduce a realistic scenario, using the equipment that is typically employed.

Statistical analyses

All statistical analyses were calculated in RStudio Version 1.1.383 (R Studio Team, 2016). We employed non-parametric tests as most data distributions were returned as not normal following a Shapiro-Wilk tests in R ('shapiro.test()' function). For the precision tests we calculate the average deviation from the mean for each set of five measurements taken for each test point. Comparisons of average deviation between the two methods were computed using a two-sample Wilcoxon signed-rank test (non-parametric equivalent to the two-sample t-test). For accuracy tests, comparison of errors between the different methods was computed with paired Wilcoxon tests. Errors were calculated as the absolute difference ($|\Delta|$) between each pair of measurements being compared. 3D error values were calculated as the Euclidean distance between test and reference XYZ coordinates for each test point.

Raw angular and distance errors between methods were also compared using paired Wilcoxon tests. Here, total station XYZ coordinate outputs were converted to angular and distance measurements to serve as a baseline for the comparison of raw errors (angles and distances) between the two methods; and inclination values from the DistoX2 were converted to vertical distance (Z) to enable direct comparison with the tape and compass method.

Angular and distance measurements recorded by the DistoX2 were converted into XYZ coordinates in R using the following trigonometric equations:

$$\boldsymbol{X = \sin\alpha \times (\cos\beta \times d)}$$

$$\boldsymbol{Y = \cos\alpha \times (\cos\beta \times d)}$$

$$\boldsymbol{Z = \sin\beta \times d}$$

, where $\boldsymbol{\alpha = azimuth}$, $\boldsymbol{\beta = inclination}$ and $\boldsymbol{d = distance}$

Angular and distance measurements recorded using the tape and compass method were converted into XYZ coordinates using the following trigonometric equations:

$$\boldsymbol{X = \sin\alpha \times d}$$

$$\boldsymbol{Y = \cos\alpha \times d}$$

$$\boldsymbol{Z = h}$$

, where $\boldsymbol{\alpha = azimuth}$, $\boldsymbol{d = distance}$ and $\boldsymbol{h = height}$

For the conversion of total station XYZ coordinates to angular and distance measurements, azimuths were calculated in R. Unsigned angles between the vectorized coordinates and a fixed point (x = 0, y = 1) representing North, were computed using the 'angle.calc' function of the Morpho package (version 2.8; Schlager et al., 2020), then converted from radians to degrees using the 'rad2deg' function of the REdaS package (version 0.9.3; Maier, 2015). Finally, angles were converted to a 360 degree format by subtracting the output from 360 where the original X coordinate was negative. Horizontal distance between the datum and each test point was calculated in QGIS (version 2.18.4) using the inbuilt Distance Matrix tool.

Major outliers for all data were defined as outliers that fell below the first quartile (Q1) subtracted by three times the interquartile range (IQR) or above three times the IQR added to the third quartile (Q3). Level of significance was set at $p < 0.05$.

Results

Precision

Overall, the precision test of the DistoX2 using the raw data output (angles and distance) yielded, on average, sub-degree and sub-centimetre precision for both hand-held and tripod modes (Table 2.3). Nevertheless, comparison between modes revealed that the average deviation values of the tripod mode were significantly lower than the reported values for the hand-held mode, demonstrating that the tripod mode yields greater precision (Wilcoxon signed-rank test, Az: $z = 4.63$, $w = 1905.5$, $p < 0.01$; Dist: $z = 5.84$, $w = 2078.5$, $p < 0.01$; Inc: $z = 3.36$, $w = 1678.5$, $p < 0.01$).

Table 2.3. Raw DistoX2 precision results in hand-held and tripod modes. Values calculated from the average deviation.

	Hand-held mode				Tripod mode			
	mean	median	IQR	95% CI	mean	median	IQR	95% CI
Azimuth (°)	0.069	0.048	0.046	0 - 0.284	0.023	0.032	0.032	0 - 0.048
Distance (m)	0.006	0.005	0.003	0 - 0.014	0.002	0.003	0.003	0 - 0.005
Inclination (°)	0.023	0.032	0.048	0 - 0.048	0.009	0.000	0.000	0 - 0.048

For ease of interpretation we also converted the data into linear XYZ measurements, where the DistoX2 in tripod mode was found to be two-times more precise than the hand-held

alternative with an average deviation of < 0.75 cm (95% CI) for all axes (Wilcoxon signed-rank test, X: z = 4.78, w = 1943.5, p < 0.01; Y: z = 5.30, w = 2019.0, p < 0.01; Z: z = 4.19, w = 1854.0, p < 0.01) (Table 2.4; Figure 2.3).

Table 2.4. DistoX2 precision results in hand-held and tripod modes converted into XYZ format. Values in metres, calculated from the average deviation.

	Hand-held mode				Tripod mode			
Axes	mean	median	IQR	95% CI	mean	median	IQR	95% CI
X	0.005	0.005	0.005	0 - 0.011	0.002	0.003	0.002	0 - 0.005
Y	0.006	0.005	0.004	0 - 0.016	0.002	0.003	0.002	0 - 0.006
Z	0.002	0.001	0.003	0 - 0.007	0.001	0.000	0.000	0 - 0.007

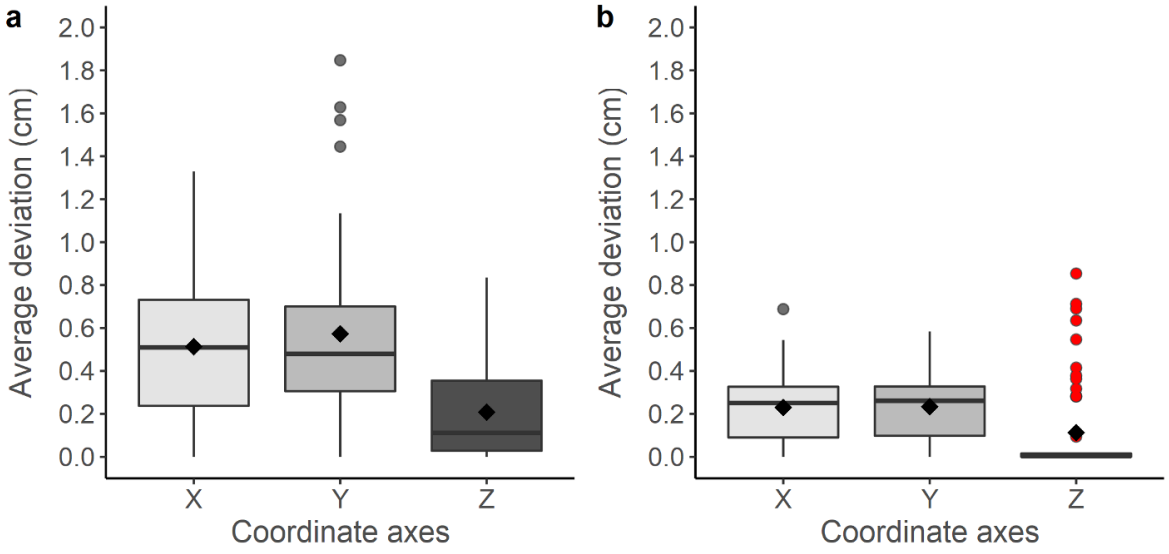


Figure 2.3. DistoX2 precision: a) Hand-held mode; b) Tripod mode. Boxes indicate the Interquartile range (IQR) and whiskers indicate values within 1.5 * IQR from their respective box. Circles represent outliers with major outliers indicated in red. Mean values are represented by the diamond symbol, and medians by the horizontal lines.

Accuracy

The accuracy tests of the DistoX2 relative to the total station system were performed at two different locations. At L2 the DistoX2 errors ranged 0-0.10 metres for all axes (Table 2.5, Figure 2.4a). At L3 the DistoX2 presented somewhat higher errors, ranging 0-0.20 metres for the X and Y axes, 0-0.10 for the Z axis, and 0.02-0.20 for the overall 3D error (Table 2.5;

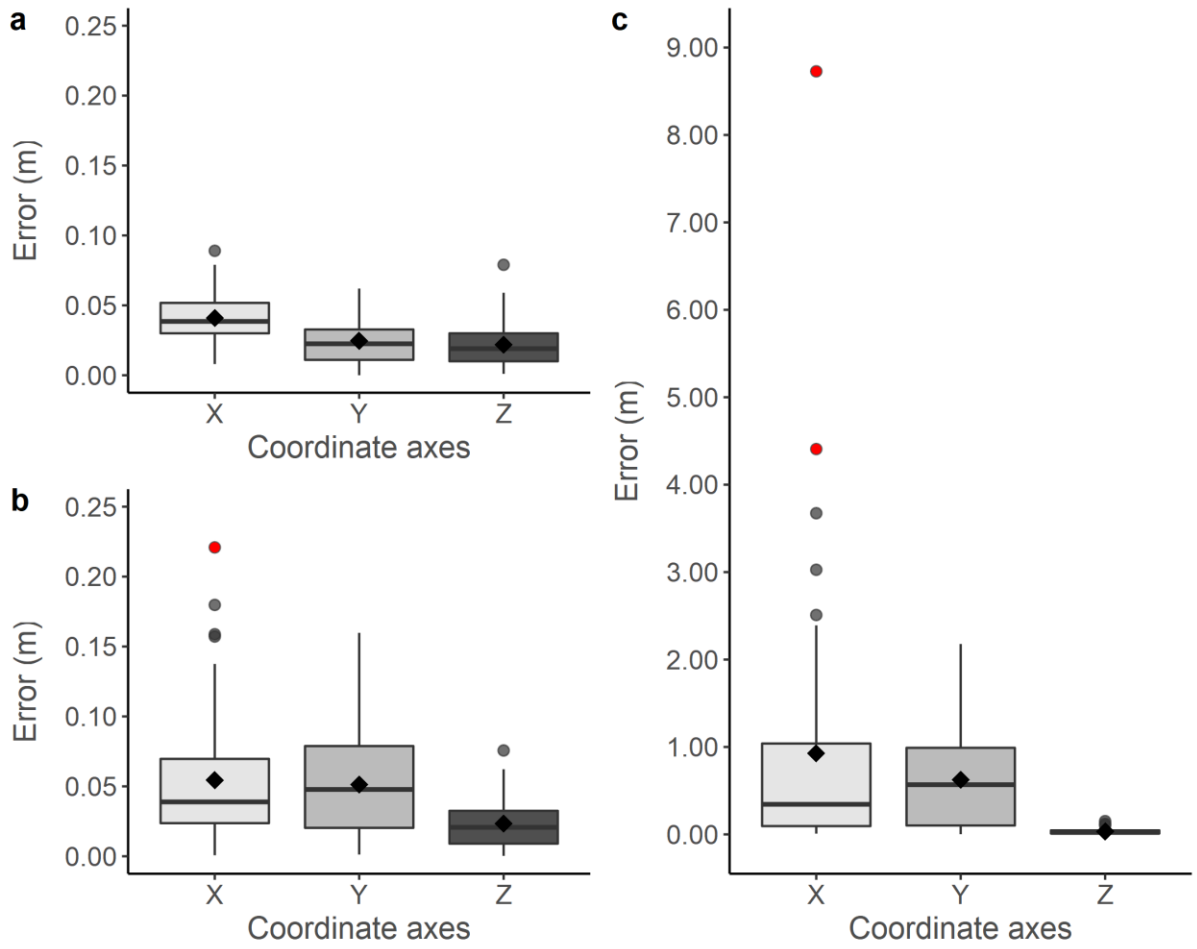


Figure 2.4. Accuracy of the tested methods: a) DistoX2 at L2; b) DistoX2 at L3; c) Tape and compass method at L3. Values reported as absolute errors. Boxes indicate the Interquartile range (IQR) and whiskers indicate values within 1.5 * IQR from their respective box. Circles represent outliers with major outliers indicated in red. Mean values are represented by the diamond symbol, and medians by the horizontal lines.

Figure 2.4b). However, these results were only significantly different for the Y axis and the composite 3D error (Wilcoxon signed-rank test, X: z = -0.32, w = 1203, p = 0.75; Y: z = -3.37, w = 760, p <0.01; Z: z = -0.46, w = 1183, p = 0.64; 3D: z = -3.28, w = 773, p < 0.01).

Table 2.5. DistoX2 accuracy relative to the total station at the two different test locations: L2 (Koobi Fora, Kenya) and L3 (Oxford, UK). Values in metres, calculated from the absolute error; 3D error calculated as Euclidean distance.

				Disto X2 – L2				Disto X2 – L3
Axes	mean	median	IQR	95% CI	mean	median	IQR	95% CI
X	0.041	0.038	0.022	0.011 - 0.078	0.054	0.039	0.046	0.001 - 0.175
Y	0.025	0.022	0.022	0.001 - 0.061	0.051	0.048	0.059	0.002 - 0.130
Z	0.022	0.019	0.020	0.001 - 0.059	0.023	0.021	0.023	0.001 - 0.061
3D	0.057	0.055	0.024	0.028 - 0.093	0.089	0.073	0.064	0.018 - 0.184

Accuracy tests of the tape and compass relative to the total station conducted at L3 produced sub-metre average errors for the X and Y axes, with several points exceeding the one-metre error threshold, while error values for the Z axis were largely within the 0-0.1 metre range (Table 2.6). Paired comparisons between the error values of the two methods tested at L3, demonstrated that the DistoX2 is significantly more accurate than the tape and compass method (Paired Wilcoxon test, X: z = -5.96, v = 20, p < 0.01; Y: z = -5.88, v = 28, p <0.01; Z: z = -2.52, v = 376, p <0.01; 3D: z = -6.06, v = 9, p <0.01). The level of significance was maintained even when the most extreme outliers were removed (Paired Wilcoxon test, X: z = -5.82, v = 20, p < 0.01; Y: z =-5.74, v = 28, p <0.01; Z: z = -2.63, v = 331, p <0.01; 3D: z = -5.93, v = 9, p <0.01; Table 2.6, Figure 4c). Figure 2.5 shows a map of the coordinate positions of each test point taken with the three different methods.

Table 2.6. Tape and compass accuracy relative to the total station with and without major outliers. Values in metres, calculated from the absolute error; 3D error calculated as Euclidean distance.

				TC – all data				TC – excluding major outliers
Axes	mean	median	IQR	95% CI	mean	median	IQR	95% CI
X	0.928	0.344	0.945	0.012 - 4.242	0.693	0.332	0.795	0.011 - 2.936
Y	0.626	0.568	0.888	0.003 - 1.837	0.637	0.602	0.908	0.003 - 1.852
Z	0.034	0.023	0.036	0.001 - 0.117	0.034	0.022	0.034	0.001 - 0.118
3D	1.277	0.834	1.367	0.032 - 4.287	1.056	0.799	1.100	0.032 - 3.07

Comparison of raw angle and distance errors between the DistoX2 and the tape and compass methods provides some insight into the nature of the stark discrepancy in accuracy (Table 2.7). While statistical significant differences were apparent for all measurement (Paired Wilcoxon test, Az: $z = -6.06$, $v = 9$, $p < 0.01$; Dist: $z = -5.75$, $v = 41$, $p < 0.01$; Z: $z = -3.53$, $v = 271$, $p < 0.01$), it is clear that the higher values and variance of the azimuth error of the tape an compass method is the principal contributor, suggesting that the compass used is a driving cause of the lower accuracy of this approach. While resolution and reported accuracy of the compass accounts for this in part, additional random error was likely introduced by the general imprecision of the whole system – compass orientation is done by hand and relies on the visual aptitude of the human eye for alignment with the measuring tape, with the compass changing location between each measurement. By comparison, the DistoX2 and total station are in fixed positions and use exact guides (e.g. reflector, prism) and visual aids (e.g. laser, magnifier) to record orientation. Thus, even with the highest attention to detail, the tape and compass method is more prone to extrinsic errors that could result in a higher incidence and range of erroneous measurements.

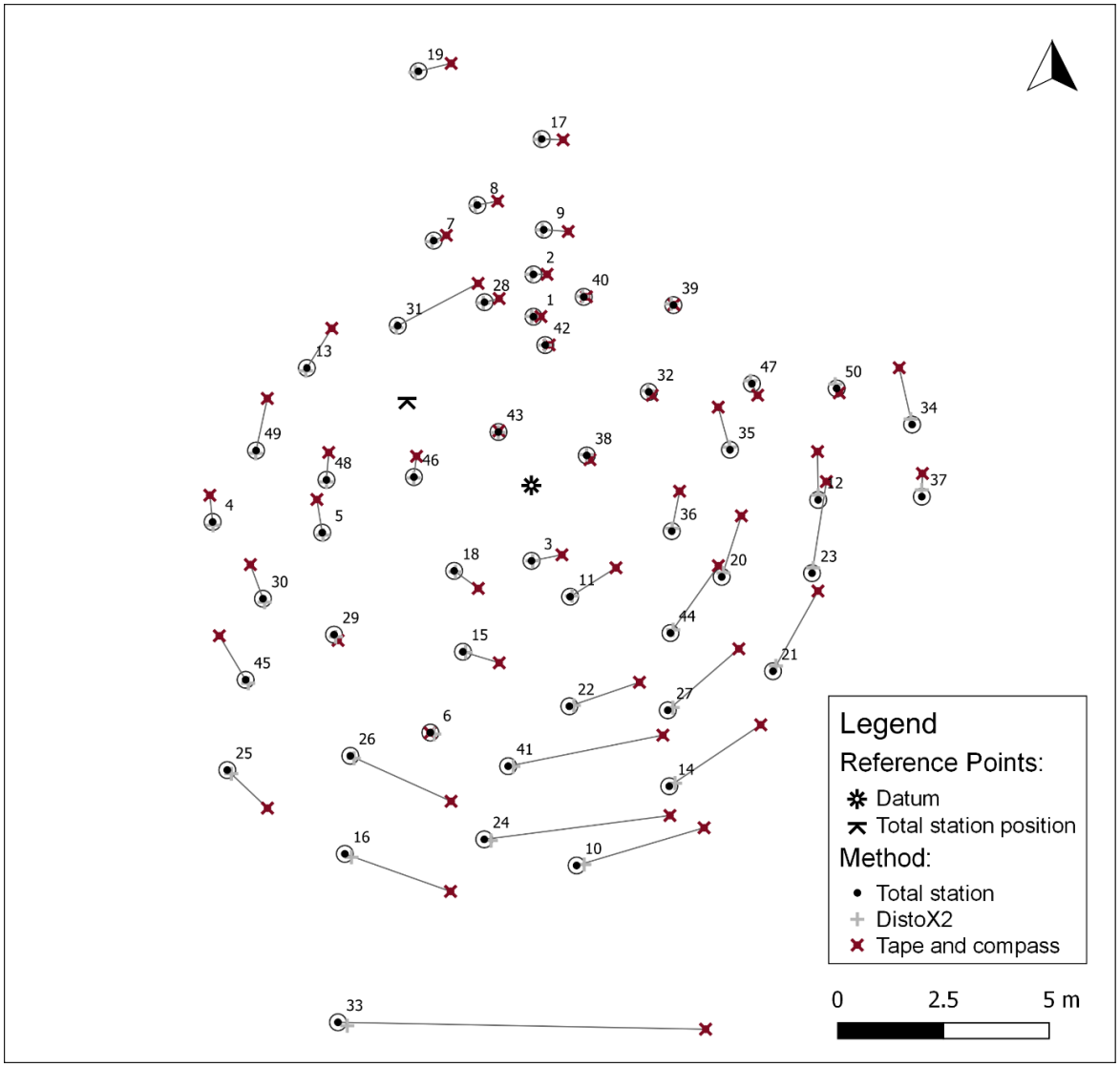


Figure 2.5. 2D-plan of the test points at L2 mapped using the three different methods: total station, DistoX2, and tape and compass. Numbers denote individual survey points. Open circles represent a 20-cm buffer around the total station measurements. Lines illustrate the linear error between the tape and compass and total station methods where error is greater than 20 cm.

Angular errors translate into linear errors that increase with distance. This effect is particularly apparent for the tape and compass method, which also demonstrates high variance in error values reflecting the inconsistent nature of this method (Figure 2.6). While

the DistoX2 measurements were also affected by this trend, the effect is far less extreme due to its higher precision, accuracy, and corresponding lower error dispersal.

Table 2.7. Raw measurement accuracy of the DistoX2 and tape and compass methods relative to the total station baseline. Values calculated from the absolute errors.

	DistoX2				Tape and Compass			
	mean	median	IQR	95% CI	mean	median	IQR	95% CI
Azimuth (°)	0.769	0.761	0.364	0.386 - 1.146	11.323	8.824	14.389	0.21 - 31.989
Horizontal distance (m)	0.007	0.006	0.008	0 - 0.017	0.015	0.015	0.005	0.008 - 0.024
Vertical distance (m)	0.016	0.014	0.014	0.001 - 0.045	0.034	0.022	0.036	0.001 - 0.117

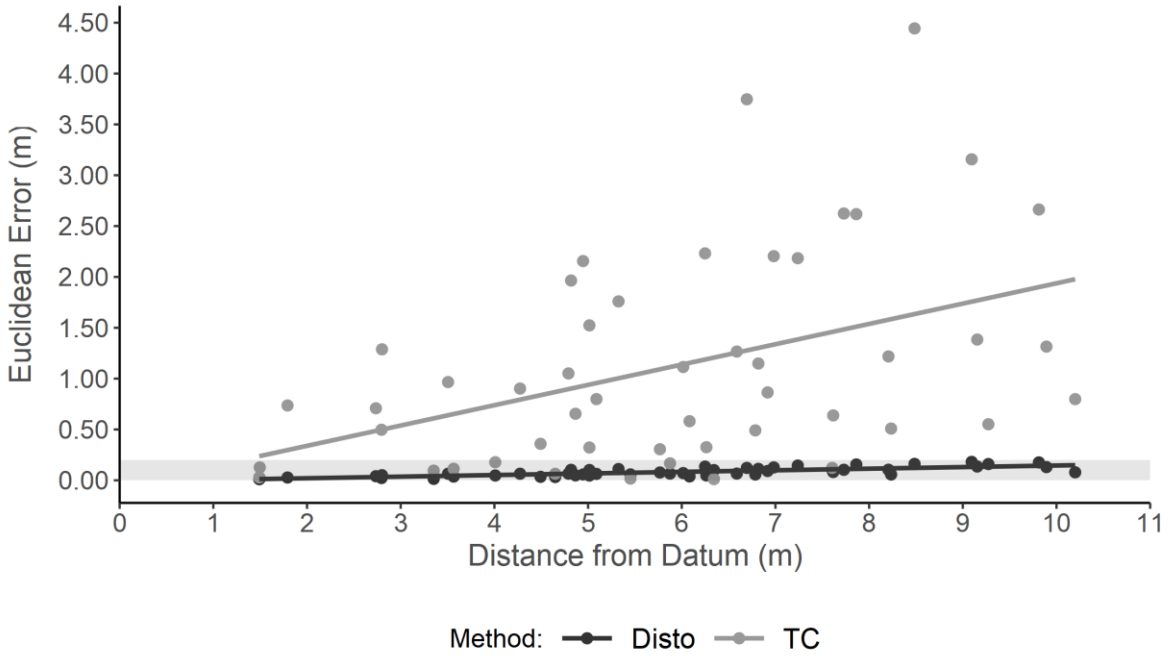


Figure 2.6. Linear distance error between each test method and the total station baseline relative to distance from datum. Disto = DistoX2; TC = tape and compass. Grey bar indicates the 0.0 – 0.2 metre error range.

Discussion

Observations on overall performance

In addition to the current study, the authors have had extensive experience in using all three survey methods in a range of real-world archaeological settings. KAW and SC have previously used the tape and compass method during primate archaeological fieldwork at wild chimpanzee sites in Tanzania and Guinea. SC also used the total station to record several chimpanzee nut-cracking sites in Guinea, and DRB uses it extensively for documenting Plio-Pleistocene excavations throughout Africa. More recently, KAW has used the DistoX2 to map chimpanzee tool sites in Guinea, as well as document surface material from Plio-Pleistocene deposits in Kenya. The following observations are a reflection on our collective experiences.

The DistoX2 system proved to be an easy to use, highly versatile instrument. While initial calibration required time and often several attempts before reaching acceptable calibration levels, the spatial data collection itself was fast and extremely efficient, and to a similar degree to the total station. It was only less so, in bright sunlight conditions when it was difficult to see the laser beam for targets beyond ~ 10 metres, although laser enhancement glasses help mitigate this. The fact that data were recorded automatically in digital format and could be viewed in real time on a tablet was another major advantage of this system. Exporting and loading the data to a computer was also easy and intuitive.

Another major advantage of the DistoX2 was that it uses magnetic north as point of reference, and, once calibrated, it is ready to use anywhere within an approximately 100 km radius. This, combined with its small size and portability, enables mapping of several sites

consecutively and instantaneously in a short period of time. In contrast, a total station generally needs to be "told" where North is, usually with the aid of a minimum of two fixed geo-referenced points. This means every site needs at least two geo-reference points, and every mapping session requires the total station to be setup and referenced relative to the known points. For multi-site projects covering large areas, the whole process from setup to completion of data collection can take up a considerable amount of research time (Fitts, 2005), although the use of a self-tracking (robotic) total station can help overcome the more nuanced logistical challenges of large-scale surveys (Holdaway and Fanning, 2008). While we did not document the exact recording times for each of the discussed methods, previous tests in cave settings have reported that a survey with the total station took a total of 48 hours and three people, while the same survey was achieved with the DistoX in five hours by two people (Redovniković et al., 2014). Lastly, learning to use the DistoX2 system was relatively easy and took less than a day of training. In contrast, the total station often requires extensive training and a high level of expertise, which may pose additional limitations for archaeological projects with logistic and financial constraints.

Spatial mapping using the tape and compass method was the most time consuming, often requiring readjustments of the tape and levelling string. Between two people measuring and recording, where each person was handling multiple objects at the same time, it was also necessary to confer and redo measurements on several occasions to ensure accurate recording. The compass was also highly sensitive to movement and could display divergent readings for any given target point, providing greater potential for erroneous measurements. These factors combined with the high range of error uncovered during data analysis, indicate that the tape and compass method is the least reliable and most prone to random human and instrument errors. While the addition of a third person dedicated solely

to recording the measurements, the application of tension, sag and temperature corrections to distance measurements, and the use of a more accurate digital compass would have improved data quality and collection efficiency, this would not have been a realistic representation of most archaeological operations that use this method.

Total station real-world accuracy under field conditions is estimated at around ±0.05 – 0.10 cm (Sapirstein, 2016). This not only allows for highly accurate provenience data, but also enables the detailed recording of object orientation and slope required for high-profile excavations, such as those in Palaeolithic contexts (McPherron, 2005; Peng et al., 2017). While the DistoX2 observes a much higher error threshold (around ±0.10 – 15.00 cm), it can be considered a suitable method for archaeological projects that do not demand sub-cm accuracy – e.g. surface surveys, recovery excavations, community projects. It could also complement the total station and other current methods in large-scale projects where both excavations and surface surveys are taking place over a large geographic area.

Nevertheless, the DistoX2 would be of most benefit to projects for which modern mapping techniques are incompatible, whether due to site characteristics, or logistical and budgetary limitations. Worldwide, there are many expeditions that, due to such conditions, still rely on older provenience techniques (Peng et al., 2017), including the tape and compass method tested here. The DistoX2 presents an affordable and versatile alternative to such methods while providing a tenfold improvement in accuracy as well as other benefits such as digital recording, speed and consistency. Thus, the DistoX2 narrows the error thresholds between the diverse range of archaeological projects, bringing those that would typically rely on traditional methods closer to the total station standard.

Other methods

While the focus of the present research was to test the performance of the DistoX2, we also consider two of the latest methods that are becoming increasing commonplace in archaeological research – photogrammetry, and high-accuracy GNSS. Extensive literature now exists on the performance of these approaches in open archaeological settings, many reporting high levels of accuracy and precision comparable to the total station (Fitts, 2005; Hill et al., 2019; Peng et al., 2017; Roosevelt, 2014; Sapirstein, 2016; Tripcevich and Wernke, 2010; Willis et al., 2016). Conditions permitting, at least one of these methods may be feasible for archaeological mapping in poorly accessible environments. Close-range photogrammetry, for example, has been successful in both underground and underwater settings, albeit to varying degrees (Chang et al., 2019; Jordan, 2017; Lee, 2018; Yamafune et al., 2017); and has been implemented for generating 3D-models of both natural and archaeological features in these environments (Dabove et al., 2019; Figueira et al., 2015; Perfetti et al., 2020; Unhammer, 2016; Yamafune et al., 2017). One of the great advantages of photogrammetry is that the core equipment required – a digital camera – is already part of the archaeologist's toolkit. Additional elements, such as tripods, access to SfM software, as well as material for identifying ground control points, can be acquired at relatively low cost. It is a great visual tool for complementing traditional excavation recording methods, reconstructing archaeological objects, and providing immersive 3D-visualisation for preservation and dissemination of cultural heritage. It can be implemented in almost all archaeological settings, except for forested environments (Willis et al., 2016), where low-lying vegetation and many vertical obstacles (trees) could greatly impact the feasibility of this method unless it is possible to clear large areas of vegetation.

Archaeological studies investigating accuracy of SfM photogrammetry have reported errors as low as 0.20 cm, ranging ~0.0 - 5.0 cm (Peng et al., 2017; Sapirstein, 2016; Willis et al., 2016). However, we highlight that most of these studies have scaled their SfM models with ground control points that were georeferenced using a total station or real-world coordinates, and very few tested the accuracy of point provenience data directly (i.e. compared the total station coordinates of pre-defined points with those yielded from photogrammetric data). Nevertheless, accuracy and precision of photogrammetry-generated models can be extremely variable as it is dependent on a variety of factors, including: the scale and texture of the subject, the image quality and degree of overlap among photos, the number of ground control points, the camera used, the accuracy of the scaling method (e.g. georeferenced control points, measurements between known points, object of known scale), and whether coded targets are included (Peng et al., 2017; Sapirstein, 2016). Thus, in order to achieve reliably consistent results requires expertise and strict protocols (Sapirstein and Murray, 2017). This is even more crucial when no other methods of spatial data collection are being used. In most fieldwork scenarios, SfM composites cannot be generated in situ in real-time, consequently failure to take sufficient overlapping photos covering the whole area of interest could result in complete loss of valuable data if the area is under active excavation or a site of modern activity (e.g. an active chimpanzee nut-cracking site).

At a practical level, extracting spatial provenance of archaeological artefacts and features using SfM photogrammetry without the aid of a total station or a GNSS device, requires precise measurements of the distances between multiple ground control points or the inclusion of an object of known dimensions. It may also require the use of a camera boom to enable greater surface coverage and a shade to diffuse strong sunlight and reduce

shadows. While the whole process, from taking the photographs, to generating the 3D-models, to extrapolating the desired spatial data, can be time-consuming and labour-intensive (Sapirstein and Murray, 2017), SfM photogrammetry may be a good alternative to the total station in archaeological projects that implement photogrammetry as part of the recording practices whether for digital archives or public outreach.

High-accuracy GNSSs technology is rapidly advancing, and such devices may well replace the total station in open-air settings in the coming decades, if not years. Currently, most RTK GNSSs range from sub-cm to 2 cm horizontal accuracy in optimal conditions (e.g. good satellite coverage, clear sky) (EOS Positioning Systems Inc., 2017; Hill et al., 2019; Pearson et al., 2015). However, this system requires connection to an RTK network (via cell signal) or nearby base station (Pearson et al., 2015), which are not always available or feasible in remote field sites. As an alternative, some GNSS companies offer subscription access to differential correction services (e.g. AtlasTM; CenterPointTM RTX) that can provide base-station free corrections at accuracies as low as two centimetres (Ames et al., 2020; EOS Positioning Systems Inc., 2017). Nevertheless, the accuracy of such systems is still heavily conditioned by access to open sky and clear satellite geometry. One of the authors (KAW), who used an EOS Arrow Gold with Atlas H10 correction extensively during fieldwork in the Bossou (Guinea), found that the system performed very poorly under forested conditions. Often the device struggled to reach a reliable measurement (Fix solution frequency = 2.5%, n = 1324), with data outputs returning error values of ≈ 2.13 m HRMS and ≈ 4.00 m VRMS (Appendix B), despite observing each point for several minutes to half an hour. Battery life may also be a limitation if there is no daily access to a power source. In the case of the Emlid Reach RTK, battery autonomy is approximately 30 hours (Hill et al., 2019), while for the EOS Arrow Gold it caps at around 8 hours (EOS Positioning Systems Inc., 2017). In contrast, the

DistoX2 can last 2-3 days of intensive data collection to approximately two weeks of low to moderate usage. While the cost of commercially available GNSS instruments is becoming more and more affordable, a complete survey kit even at the lower end of the spectrum will range between $1,500 – $2,500. In projects with a limited budget, a GNSS device especially if requiring the added cost of periodic subscriptions to correction services may not be economically feasible (Ames et al., 2020).

Ultimately, the method used for collecting spatial provenience data is a decision that depends on the nature of the project – from the characteristics of the site (location, environment, scale, accessibility), archaeological significance/importance, funding available, and project duration, to the team size and the amount of logistical support. In some cases, the total station will be the only compatible option, while for others, practical or budgetary limitations will require the use of alternative methods. For ease of comparison, we provide a summary of key information as well as some practical limitations regarding each of the survey methods discussed in this study (Table 2.8).

While the current research has mainly focused on assessing the DistoX2 as a stand-alone data collection method, we would like to highlight that the DistoX2 could equally be used in tandem with other methods. Currently several archaeological projects employ a combination of total station, GNSS and/or photogrammetry, including expeditions directed by one of the authors – DRB – in Koobi Fora, Kenya. The DistoX2 system constitutes a new addition to the archaeologist's toolkit that can complement and facilitate the tailoring of spatial mapping strategies to the specific goals of an archaeological project.

Table 2.8. Summary of specifications and practical information of current and novel mapping methods.

	Tape and compass	Total station	RTK GNSS	Ground-based photogrammetry	DistoX2
Accuracy[a]	0 - 300 cm	< 0.5 cm	0 - 2 cm	0 - 5 cm	0 - 15 cm
Distance range	~ 20 m	~ 4 km	~ 15 km (Base and Rover RTK) ~ 100 km (RTK network)	~ 300 m	~ 100 m[b]
Weight	1-3 Kg	4-10 Kg	2-10 Kg	1-8 Kg	0.5-3[c] Kg
Speed	Slow	Moderate	Moderate	Slow	Fast
Operating time	10-26 hrs[d]	8-30 hrs	8-30 hrs	4-15 hrs	2-3 days[e]
Expertise required	Low	High	Moderate-High	Moderate-High	Moderate
Optimal conditions	Any	Open spaces	Overground with open sky	Any	Overground, underground
Practical limitations	Not suitable in locations with steep terrain unless used with a clinometer	Not suitable in locations with restrictive access	Performs poorly in forested conditions without a Base and Rover system or access to an RTK network	Not suitable in locations with many vertical obstacles, dense vegetation or contrasting light conditions	Unsuitable in locations with very strong sunlight or high magnetic interference
Cost ($)	20-200[f]	4,000-10,000	1,500-20,000[g]	200-1,500[g]	280-500[c]

[a] Reported as absolute error
[b] Up to 10-15 m in bright sunlight
[c] Depending on digital accessories chosen (e.g. mobile or tablet device), and whether tripod is included
[d] Unlimited if using a fully analogue system
[e] Up to two weeks for low to moderate usage
[f] If using a digital compass
[g] Depending on additional accessories, and whether a subscription to software and/or correction service is needed

Conclusions

Today, archaeological expeditions are becoming increasingly diverse, and the data collection methods used will depend on the requirements and limitations of the project at hand. While the total station should be the primary choice in most instances, especially when

very high accuracy is required, many projects may not meet the conditions or means required to implement such a method, or other current alternatives. Yet, other projects may also seek to combine several mapping methods to fit their needs. The DistoX2 provides a methodological solution to those projects that would still typically resort to more traditional, analogue methods, but also constitutes a novel system that complements other commonly used methods in projects that benefit multiple approaches.

The DistoX2 presents a good level of precision both in hand-held and tripod modes. However, it is most precise when mounted on a tripod, where the mean precision is ≈ 2.00 cm for the X and Y axes and ≈ 1.00 cm for Z.

The conservative estimate for DistoX2 accuracy relative to the total station is ≈ 5.00 cm for 2D dimensions and ≈ 2.00 cm for the Z axis (≈ 6.00 cm for 3D composite). These values are better than the previously published results, although the errors fall under the same upper boundary (see Redovniković et al., 2016).

In contrast, the tape and compass method, with a mean error of ≈ 69.00 cm for the X axis, ≈ 64.00 cm for the Y axis, and ≈ 3.00 cm for the Z axis, is considerably less accurate than the DistoX2, particularly with respect to the X and Y axes. The fact that the analogue or digital compass used in the tape and compass method cannot be calibrated to the same rigour nor have the same resolution as the DistoX2, is a major disadvantage to this approach. Furthermore, unlike the DistoX2, data collection using this method is not an automated process, and therefore has greater propensity for human transcription errors at the reading, recording, and data-entry levels. Despite being the most affordable, its high level of

measurement error makes this method a poor option for spatial data collection and should only be used when alternative methods (including the DistoX2) are not viable options.

In sum, the DistoX2 presents several features that make it a suitable and affordable alternative to the more commonly used digital spatial mapping methods in archaeology, and to the tape and compass method: 1) small, light-weight and highly-portable device; 2) can be calibrated, ensuring more accurate readings than standard analogue or digital compasses; 3) more accurate and more efficient than the tape and compass method; 4) records measurements instantaneously onto a digital interface, that can be exported and uploaded to a laptop for analysis.

The DistoX2 combines the portability and affordability of the tape and compass method with the speed, accuracy and digital features of the total station. Its applicability in poorly accessible field-sites fills a critical gap in archaeological mapping methods, and enables greater standardization of spatial data collection across all human and non-human archaeological records.

Acknowledgements

We are grateful to V. Mamy, L. Goigbe, B. Zogbila, G. Zogbila, A. Curley, C. Costa, C. Daniel, N. Mann, N. Gitaw, K. O'Brien, Dr. J. Reeves and Dr. M. Bluteau for support during the data collection process, and F. T. Regala at AESDA (Associação de Estudos Subterrâneos e Defesa do Ambiente) for DistoX2 training, suggestions and technical support. We thank P. Riggs at Science Oxford for producing a custom-made tripod adaptor; Dr. L. Luncz and the Institute of Archaeology (University of Oxford) for kindly loaning their survey equipment during

testing in Oxford. We also thank the Direction Nationale de la Recherche Scientifique, the Institut de Recherche Environmentale de Bossou (Guinea), Kyoto University Primate Research Institute, National Museums of Kenya, and the National Commission for Science, Technology and Innovation (Kenya), and the Koobi Fora Field School for research permissions and logistical support overseas.

This work was funded by the Fundação para a Ciência e Tecnologia (FCT) [grant number: SFRH/BD/115085/2016] to KAW, with support from the Programa Operacional Capital Humano (POCH) and the European Union; ICArEHB with support from FCT [grant number: UIDB/04211/2020]; the Boise Trust Fund (University of Oxford) to KAW; the National Geographic Society [grant number: EC-399R-18] to KAW; and a Philip Leverhulme Prize to SC.

Chapter 3

Archaeology of the perishable

Ecological constraints and cultural variants in chimpanzee termite fishing

The content of this section was originally published in (Pascual-Garrido & Almeida-Warren, 2021)**. © 2021 by The Wenner-Gren Foundation for Anthropological Research. All rights reserved.**

Abstract

Selection and transport of materials for tools is ubiquitous throughout our species' evolutionary history. Yet, our understanding of early human material culture is heavily skewed towards lithic technology. This poses challenges when reconstructing our technical origins, as organic raw materials, especially plants, likely played a significant role despite their absence from the record until 300 Ka. Studies of plant-tool use by living apes can serve as a proxy to reconstruct such aspects of human behaviour. Employing archaeological

methods, we investigated raw material procurement for termite-fishing tools by three chimpanzee (*Pan troglodytes schweinfurthii*) populations in Tanzania: Gombe, Issa and Mahale. All communities exploited plant sources from the immediate vicinity of termite mounds, as well as further away, and re-used them. However, at Issa, more parts were sourced per plant, with the number of removals decreasing as distance from the mound increased. These disparities are likely caused by environmental differences. Issa apes might try to minimize transport costs in what is a comparably more open and drier habitat, with fewer suitable sources available near mounds. Despite similar raw material types being available, Issa and Mahale chimpanzees exclusively used bark for tool manufacture, while at Gombe various materials were employed; these differences may reflect cultural variants. Our study highlights how environmental and cultural factors shape chimpanzee technology, and identifies similarities with raw material selection processes inferred for Oldowan tool users. The archaeology of the perishable, even if at its infancy, is providing a new framework for reconstructing archaeologically invisible aspects of early human behaviour and our own technological origins.

Introduction

The selection of raw materials for tool manufacture is ubiquitous throughout our evolutionary history, stretching back to the earliest stages of stone technology (Braun et al. 2008, 2009; Goldman-Neuman and Hovers 2012). This included the use of flexible procurement strategies, involving the targeting of locally-available material to keep the energy costs low (Kimura, 1999), but which may also have encompassed extensive energy investment, with long-distance transport, as a result of selective raw material sourcing (Braun et al. 2008). Such strategies are considered key aspects of Plio-Pleistocene hominin

adaptations and reflect the awareness of technically-desirable material, bipedal carrying abilities, and techno-cultural traditions of the tool users (Kimura, 1999; Schick, 1987; Stout et al., 2005, 2010). Furthermore, their long-distance raw material transport indicates foresight, planning and other cognitive abilities unseen in any technological non-human primate (de la Torre et al., 2003; Delagnes & Roche, 2005; Schick, 1987; Shea, 2017; Stout et al., 2010). Yet, it is possible that some of the characteristics attributed to the Oldowan were in place long before. All modern non-industrialized human societies as well as non-human primate species use plant materials for implements far more often than bones or stone (Carvalho & Almeida-Warren, 2019; González-Ruibal et al., 2011; Hoffecker & Hoffecker, 2018). Thus, while plant-based artefacts are completely absent from the early archaeological record until 300 kya (Conard et al. 2015; Richter and Krbetschek 2015; Thieme 1997), it is unlikely that our early ancestors overlooked the potential value of this material as a tool (Conard et al., 2015; Domínguez-Rodrigo et al., 2001; Wynn & McGrew, 1989). This suggests that current archaeological data are missing a substantial component of ancient technology (Panger et al., 2002).

The emerging discipline of primate archaeology compares material records across monkeys and apes and is enriching our understanding of human evolution (Carvalho & Almeida-Warren, 2019; Carvalho & Beardmore-Herd, 2019; Haslam et al., 2009, 2017; McGrew et al., 2019). For example, we now know that stone tool use and transport by monkeys and chimpanzees generate landscape-patterns of raw material acquisition and artefact deposition similar to inferred (archaeologically invisible) aspects of early human behaviour (Boesch & Boesch, 1984b; Carvalho et al., 2008; Luncz et al., 2016; McGrew et al., 2019; Mercader et al., 2002, 2007; Proffitt et al., 2016), including affinities to the Oldowan (Carvalho et al., 2008; McGrew et al., 2019; Toth & Schick, 2009). Furthermore, as described for Oldowan

technological behaviours (Braun et al. 2008, 2009; Kimura 1999; Goldman-Neuman and Hovers 2012; Stout et al. 2005, 2010), those of non-human primates are not only influenced by the local environment but also by their techno-cultural traditions (Carvalho et al. 2008; Luncz, Mundry, and Boesch 2012; Luncz, Wittig, and Boesch 2015, Luncz et al. 2016; Koops, McGrew, and Matsusawa 2013; McGrew et al. 2019; van Schaik et al. 2003).

But, perhaps as expected, primate archaeology has largely focused on lithic technology, even when plant-based technology is the most common, and arguably, the most diverse and complex form of primate tool use, as well as the only form involving manufacture (Whiten et al., 1999; Wynn et al., 2011). The opportunity to focus on ephemeral records remains another important asset of studying primate technology, providing a unique framework for reconstructing invisible aspects of hominin behaviour (Hernandez-Aguilar, 2009; Mcbeath & McGrew, 1982; Sanz et al., 2014; Sept, 1992; Stewart et al., 2011). These studies hold the key for obtaining a comprehensive understanding of primate technology as a whole (Carvalho & Almeida-Warren, 2019).

Studies of chimpanzees (*Pan troglodytes*) with whom humans shared a last common ancestor 8-7 mya (Langergraber et al., 2012) are particularly promising. Their prolific use and manufacture of various types of tools (McGrew, 1992; Whiten et al., 1999), make chimpanzees key living models to understand the emergence of technology in our own lineage (Carvalho and Beardmore-Herd 2019; McGrew 1992, 2004; Rolian and Carvalho 2017; Teleki 1974; Toth and Schick 2009; Wynn and McGrew 1989; Wynn et al. 2011).

The first scientifically-described mode of chimpanzee tool use was 'termite fishing', a skilful technique that makes use of slim and pliable plant probes to extract the nutritious insects

from their mounds (Goodall, 1964). This technology has gained considerable attention from the palaeoanthropology community (Lesnik, 2011, 2014) since Backwell and d'Errico (2001) published their paper suggesting the use of bone tools for termite foraging by *Paranthropus* (*Australopithecus*) *robustus*; followed by the discovery of 3.7 mya *Macrotermes* termite mounds at Laetoli in Tanzania (Darlington, 2005), roughly synchronous in time and space with *Australopitecus afarensis* (M. D. Leakey et al., 1976; M. D. Leakey & Hay, 1979). That the consumption of termites by chimpanzees and present-day modern humans is a well-documented phenomenon, poses the hypothesis that early humans also made use of this resource (Lesnik, 2018; Nonaka, 1996; O'Malley & McGrew, 2014).

The manufacture of termite-fishing tools by wild chimpanzees includes the use of a variety of plant parts and materials such as bark, grass, leaves, twigs, vines, petioles and palm fronds (Fay & Carroll, 1994; McGrew et al., 1979; McGrew & Collins, 1985; Sanz et al., 2004). Materials are usually obtained from near the termite mounds but also from further away when locally unavailable. Distances of transport vary between a few meters to more than a kilometre (McGrew, Tutin, and Baldwin 1979; Sanz, Morgan, and Gulick 2004; Teleki 1974), and recovered assemblages indicate a preference for materials and plant species employed (Bermejo and Illera 1999; Fay and Carroll 1994; Sanz, Morgan, and Gulick 2004; Sanz et al. 2014; Stewart and Piel 2014). However, without a detailed record of the raw material available it is difficult to assert through artefacts alone if plant species or materials were used due to their physical characteristics (and thus selected) or simply used because they were more abundant in the environment (Mcbeath & McGrew, 1982). Recent research has made a start in this respect, providing unequivocal evidence of tool material transport and selection for termite-fishing tools, including cultural preferences for material types used across groups (Almeida-Warren et al., 2017; Pascual-Garrido, 2018, 2019; Sanz et al., 2004;

Sanz & Morgan, 2007). However, while a combination of ecological and social factors is known to shape primate material culture (Carvalho et al., 2008; Gruber et al., 2012; Grund et al., 2019; Hobaiter et al., 2014; Humle & Matsuzawa, 2009; Koops et al., 2014; McGrew et al., 2019; Sanz & Morgan, 2013; Schuppli & van Schaik, 2019) including hominins (Andrefsky 1994; Braun et al. 2008, 2009; Goldman-Neurman and Hovers 2012; Harmand et al. 2009; Kimura 1999; Stout et al. 2005, 2010, 2019), the extent to which these factors dictate raw material use for termite-fishing tools by our closest living relatives still remains largely unexplored (Almeida-Warren et al. 2017; Koops, McGrew, and Matsuzawa 2013; McBeath and McGrew 1982; Musgrave et al. 2016, 2020; Sanz and Morgan 2007; Sanz et al. 2014).

Chimpanzee termite fishing offers a unique opportunity to investigate raw material procurement for tools: First, unlike the nomadic characteristic of other social insects habitually harvested with implements by these apes (Pascual-Garrido et al., 2013), *Macrotermes* termites reside in the same conspicuous mounds for decades (Sanz & Morgan, 2013), and possibly for much longer (Darlington 2005). This allows not only the easy recovery of artefacts at their place of discard (termite mounds) (Jones and Sabater Pi 1969; McGrew and Collins 1985; Suzuki 1966), but also the systematic study of raw material availability and use near tool-use sites (Almeida-Warren et al., 2017; Mcbeath & McGrew, 1982; Pascual-Garrido, 2019).

With the aim of more precisely defining the determinants that may influence raw material use for termite-fishing tools by wild chimpanzees (Mcbeath & McGrew, 1982; Sanz et al., 2014), we extended and compared our study conducted at the Issa valley (Almeida-Warren et al., 2017) to two other genetically related termite-fishing communities living in different habitats in western Tanzania: Gombe and Mahale (Inoue et al., 2013; Piel et al., 2013).

Previous studies indicate differences in raw material use and transport between these sites (Almeida-Warren et al., 2017; Pascual-Garrido, 2018). In this etho-archaeological study, we evaluate the influence of environmental and cultural factors on raw material procurement for termite-fishing tools by chimpanzees by addressing the following questions: How are chimpanzees using sources of raw material for the manufacture of termite-fishing tools? Are sources used once or multiple times? If so, how does this compare with the general abundance of the source species and its location (distance) in relation to the targeted mound?

Given that raw material availability and type, distance to the source, and cultural processes influence stone technology in chimpanzees (Carvalho et al. 2008; Luncz, Mundry, and Boesch 2012; Luncz, Wittig, and Boesch 2015, Luncz et al. 2016) and early humans (Andrefsky 1994; Braun et al. 2008, 2009; Kimura 1999; Stout et al. 2005, 2010), we also expect these variables to be determinants of chimpanzee termite-fishing technology. We also discuss implications for the understanding of the origins of human technology.

Background

Our study took place in three populations of *P. t. schweinfurthii* living in different habitats in western Tanzania (Figure 3.1). Study sites include: 1) *Gombe Stream National Park* (-4° 40' S, 29° 38' E; 772-1,500 m altitude) set in the eastern shore of Lake Tanganyika (Figure 3.1). The 35 km^2 national park is characterized by thicket woodland and vine tangle, interspersed by small patches of open woodland, and deep valleys falling from the rift escarpment to the lake. A wet season (November-April) is followed by a dry one (May-October), with an average annual rainfall of 1,495 mm (Collins & McGrew, 1988); 2) *Issa valley* (5° 30 S, 30° 33' E; 900-

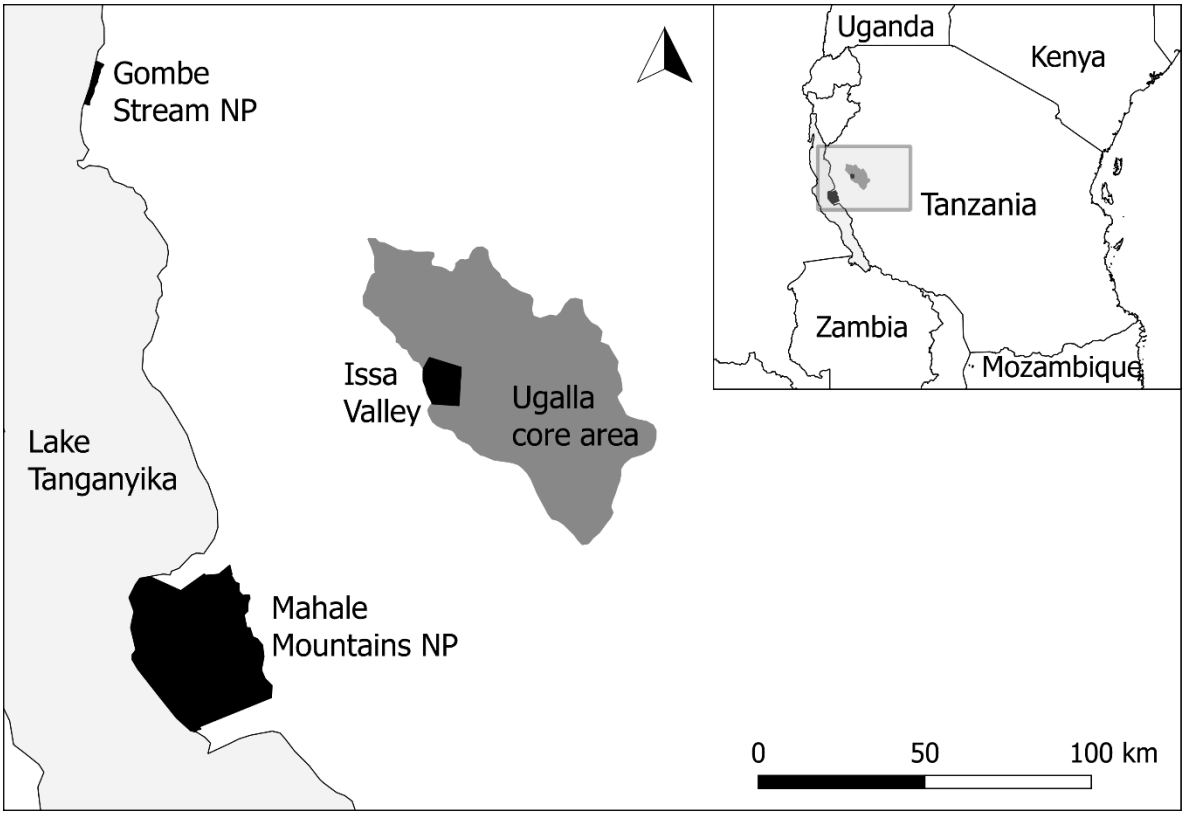


Figure 3.1. Map of western Tanzania indicating the three study sites. NP: National Park. Map credit: Katarina Almeida-Warren.

1,800 m altitude) is one of the driest, most open and seasonal habitats where chimpanzees reside. It is located 81 km inland and east of Lake Tanganyika (Figure 3.1) and its vegetation is mainly *miombo* woodland, dominated by *Brachystegia* and *Julbernardia* (Fabaceae), interspersed with swamp, dry grassland, wooded grassland, woodland, gallery forest, thicket forest, and hill forest (Hernandez-Aguilar 2006, 2009). As in Gombe, a wet season (November-April) is followed by a dry one (May-October), with an average annual rainfall of 1,200 mm (Stewart & Piel, 2014); 3) *Mahale Mountains National Park* (6° 1' S, 29° 26' E; 772-2,462 m altitude) is located on the eastern shore of Lake Tanganyika (Figure 3.1).

Our study took place in Bilenge (Collins & McGrew, 1987), located approximately 9 km to the north from the long-term Japanese research camp (Nakamura et al., 2013; Nishida &

Uehara, 1980). The terrain is mostly rugged and hilly, dominated by the Mahale mountain chain that runs from the northwest to southeast across the western part of the park. Bilenge is largely an open grassy forest and *miombo* woodland of *Brachystegia*, with narrow strips of vine tangle and forest along the valley. As at Gombe and Issa, a wet season (November-April) is followed by a dry period (May-October), with an average annual rainfall of 1,400 mm (Collins & McGrew, 1988).

Study communities

Study communities included the habituated community of Kasekela of Gombe Stream National Park (Goodall, 1986), the partly habituated community of the Issa valley (Stewart & Piel, 2014), and the unhabituated Bilenge (B) group of the Mahale Mountains National Park (McGrew and Collins 1985; Nishida and Uehara 1980; Uehara 1982). While these three populations are currently, but possibly not entirely, isolated from each other due to habitat fragmentation, genetic evidence suggests a history of gene flow between Issa and Mahale populations, and possibly also with Gombe (Inoue et al., 2013; Piel et al., 2013).

Chimpanzees at the three sites habitually termite fish at *Macrotermes* mounds. While apes at Gombe and Mahale are known to employ a wide variety of materials obtained from different plant species to manufacture their implements (McGrew 1992; McGrew and Collins 1985; Nishida and Uehara 1980; Uehara 1982), Issa chimpanzees specialize only in bark (Stewart & Piel, 2014). Chimpanzees at Gombe termite fish year-round, though efforts are most frequent at the start of the rainy season from October to December (Goodall, 1986). At Issa and Mahale, termite fishing is limited to the rainy months, with the most productive period being at the onset of the first rains (October-November) (McGrew and Collins 1985; Stewart and Piel 2014; Uehara 1982). While direct observation of the behaviour was possible

only at Gombe (Lonsdorf, 2005), at all study sites research focused on the recovery of artefacts and other remnants left by chimpanzees as result of their termite-fishing activities. This ensured a better standardization of the data collected and an unbiased cross-site comparison.

Methods

Data collection

Data were collected by APG and KAW assisted by experienced Tanzanian research assistants over 285 days from 2014 to 2016. This included a total of 117 days at Gombe (APG: 12Oct-12Nov2014; 14Nov-14Dec2015; 13Oct-12Nov2016; KAW: 16Apr-12May2015), 53 days at Mahale (APG: 25Nov-14Dec2014; 20Oct-08Nov2015; 21Nov-08Dec2016) and 115 days at Issa (APG: 09Jan-09Feb2015; KAW: 17May-27Jun2015; 02Nov-15Dec2015).

Research focused on 29 *Macrotermes* termite mounds that had been targeted by chimpanzees for termite fishing: seven at Gombe, eight at Issa, and 14 at Mahale. Due to time constraints and the need to collect sufficient data for each mound, chosen mounds constitute a subset of mounds at which termite fishing occurred. A mound was considered to have been targeted if one or more of the following criteria applied: (a) apes were seen fishing; (b) artefacts, fragments, debris or raw materials modified as a result of the manufacture process were present; (c) plants from which raw material was sourced were detected (source plants) (Almeida-Warren et al., 2017; Pascual-Garrido, 2018). At each of these mounds, a site datum was assigned to a nail placed on a tree near the centre of the mound to allow measurements in a standardized coordinate system to map the relative

positions of sources and to measure their distances to the targeted mound (Almeida-Warren et al., 2017; Carvalho et al., 2008). Mounds were visited every 1-3 days to record abandoned artefacts and sources.

RAW MATERIAL AVAILABILITY

The availability of raw material for termite-fishing tools (i.e., living plants) was recorded once for each targeted mound (n = 29). Employing cardinal orientations (N-S, E-W), we divided the mound vicinity into 4 quadrants and arbitrarily selected the northwest 90° quadrant of a 5-m circle around the mound for scrutiny (Almeida-Warren et al., 2017; Koops et al., 2013; Mcbeath & McGrew, 1982). For each surveyed quadrant, we counted the number of plants suitable for tool making by species and material class (bark, twig, vine, grass). Material types were determined based on previous research (McGrew et al., 1979; McGrew & Collins, 1985; Stewart & Piel, 2014)S. Suitable sources were defined as plants that could provide long, thin, flexible pieces from which a functional termite-fishing implement could be made (Almeida-Warren et al., 2017).

SOURCE PLANTS

Previous research at these sites indicates that chimpanzees obtain their tool material from plants close to targeted termite mounds but also from meters away (Almeida-Warren et al., 2017; Pascual-Garrido, 2018). Thus, we surveyed for vegetation that chimpanzees had utilised for tool making (source plants) within a 20-metre radius of the mound. Some materials may have been occasionally obtained from further away (Pascual-Garrido, 2018), but implementing a standardized search field allowed cross-site comparison and ensured data collection within a limited time-frame.

We followed the criteria established by Pascual-Garrido (2018) for the identification of sources discernible by at least one of the following: (a) presence of one or multiple removals (*scars*) as result of apes removing material; (b) *scars* were located in specific parts of the specimen; (c) only a selected number of species showed signs of being sourced; (d) they were normally concentrated within the mound periphery; (e) they included species represented in the tool assemblage; (f) chimpanzees were directly observed detaching the material. For each source identified, we measured the distance to the targeted mound, the species, the type of material procured (i.e., twigs, bark), and the number of *scars* – the latter as an indicator of the intensity of use. Each source was marked and assigned a number to avoid recording it twice during repeated visits to the mounds.

Samples from all plants recorded were collected and curated in camp with a dryer for future identification by Frank Mbago, Botany Department, University of Dar es Salaam, Tanzania.

Statistical analyses

Given that all data in this study had a non-normal distribution ($P < 0.05$), non-parametric statistics were implemented. To investigate potential differences among materials used, their availability, and the differences between them (i.e., raw material classes; species), both within and between sites, we conducted tests for equality of proportions using the prop.test function in R with Yates' continuity correction. To test if pairs of proportions were different within and between sites, we calculated individual *P* values of paired groups via pairwise post-hoc proportion tests with the "Bonferroni" correction method. Kruskal-Wallis tests were employed as a non-parametric version of one-way ANOVA to compare continuous variables (i.e., number of *scars* per individual source) between sites. To assess differences between pairs of sites we employed post-hoc pairwise Wilcoxon rank-sum tests.

To examine whether the distance of a source to the targeted mound and relative species abundance in the vicinity of the mound influenced the number of times a plant was procured and whether there were site-specific differences, we applied Generalized Linear Mixed Models (GLMM; Zuur et al. 2009) with the number of parts removed per individual plant (*scars*) as the response variable. As predictor variables with fixed effects, we included the site, distance of source to target mound, and mound-specific sourced species abundance relative to known sourced species, as well as their possible interactions (three-way and two-way). To control for possible between-mound variation we included mound ID as a random effect. Additionally, prior to fitting the model, we z-transformed distance to mound (mean = 6.57 metres, sd = 5.42) and species abundance (mean = 0.40, sd = 0.32). Because the response variable was zero-truncated (minimum value = 1) and there was evidence of moderate overdispersion (dispersion ratio = 3.2, P <0.01) we applied a zero-truncated Poisson-lognormal model with the addition of plant ID as an observation level random effect (OLRE; Harrison 2014). This was achieved using the 'glmmTMB' (ver 0.2.3) package in R. To test whether the predictors had a collective effect on the number of removals we first conducted full null model comparison using a likelihood ratio test (R function anova), where the null model excluded all fixed effects but was otherwise identical to the full model (Dobson, 2002; Schielzeth & Forstmeier, 2009). We tested the significance of three-way and two-way interactions by systematically dropping them from the model one at a time, and comparing the resulting reduced models with the respective full model using the drop1 function in R. P-values for the individual effects were based on the likelihood ratio test results from the drop1 function (Dobson, 2002). Collinearity between predictor variables, calculated by applying the vif function of the R package 'car' (J. Fox & Weisberg, 2011) to a linear model lacking the random effects and interactions, was not an issue (maximum VIF =

1.36). All analyses were performed in R (R Core Team, 2017). All tests were two-tailed and level of significance for all statistical analyses was set at $P < 0.05$.

Ethical Note

No data were collected from chimpanzee individuals for the purpose of this study. Data were recorded when chimpanzees were absent from the study mounds, with no direct contact with any of the individuals. Research was conducted under the permits of Tanzania National Parks (TANAPA), Tanzania Wildlife Research Institute (TAWIRI), and Tanzanian Commission for Science and Technology (COSTECH).

Results

Chimpanzees at Gombe, Issa and Mahale behaved similarly in that they sourced raw material from the immediate vicinity of termite mounds and also from further away, selected materials and plant species to make their implements (Pascual-Garrido, 2018), and re-used sources (Figure 3.2). However, chimpanzees in Issa exploited sources more intensively (i.e., more plant parts were extracted per individual), possibly to save transport-distance costs in what is a comparably more open and drier habitat, with less available raw material nearby. Despite the prevalence of twig raw materials at all sites, Issa and Mahale chimpanzees exclusively used bark for tool manufacture, while at Gombe various materials were employed – differences that potentially reflect cultural variants (i.e., behaviours present in at least one site and absent elsewhere without clear ecological differences; van Schaik et al. 2003; Whiten et al. 1999, 2001).

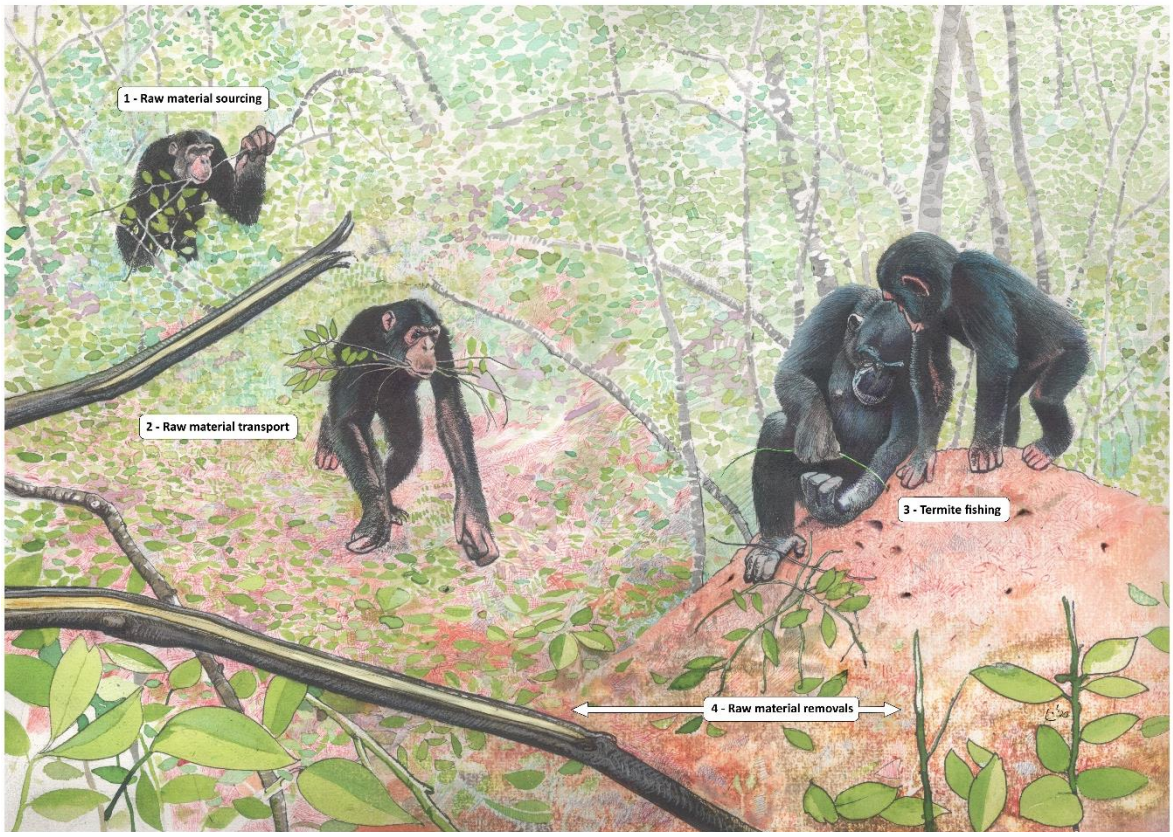


Figure 3.2. Raw material sourcing for termite-fishing tools by wild chimpanzees. 1. Tool material sourcing from the source plant; 2. Raw material transport to the tool-use site (termite mound); 3. Tool manufacture and use; 4. Physical traces left on source plants as result of chimpanzee tool material extraction (left: bark removal; right: twig removal).

Abundance of raw material versus use

Regarding the abundance of suitable sources per mound (plants that could provide at least one type of raw material), Gombe had the highest followed by Mahale and Issa (Table 3.1). At all sites, there was a significant difference between the proportion of raw material classes available near mounds, with twigs being the most abundant, followed by bark. Grass was rare at all sites, while vines were present only at Gombe (Table 3.1). Significant differences were maintained when comparing pairs of material types for each site except between vines

and grasses at Issa where they were equally rare (Table B.1). There were also significant differences between sites regarding abundance by material type (Table B.2). These differences were maintained when comparing pairs of sites except between Issa and Mahale where grasses and vines were equally available or absent, respectively (Table B.3).

Table 3.1. Abundance of raw material types for each site. Total was calculated based on the plants that could provide suitable raw material. χ^2 and *P* values are a result of an equality of proportions test between the number of plants that could provide each raw material type relative to the site total. Note that some plants could provide more than one type of raw material.

Site	Total	Mean per mound	Bark	Twig	Vine	Grass	χ^2	p
Gombe	457	65.3	0.486	0.871	0.013	0.116	892.925	< 0.001
Issa	264	33	0.182	0.936	0	0.023	756.47	< 0.001
Mahale	639	45.6	0.801	0.983	0	0.017	2057.557	< 0.001

However, despite availability of various materials at all sites, only Gombe chimpanzees procured different materials to make their implements (Table 3.2). While Gombe chimpanzees used twig (44.0%) and bark (48.7%) in almost equal proportions, they manufactured only a small percentage of their utensils from vine (6.1%), while grass was utilised only rarely (1.2%). Only artefacts made from bark were recovered at Issa and Mahale (Pascual-Garrido 2018).

Suitable versus sourced plants

In order to test for species selection, we compared the proportion of plants from suitable versus sourced species. Results showed that chimpanzees at Gombe utilised 85.3% of the total suitable species available, while at Issa and Mahale chimpanzees exploited only 12%

(Appendix B, Table B.4). Pairwise tests between sites revealed significant differences in the proportion of plants of known source species used between Gombe and all sites (P <0.001). This indicates that chimpanzees at Mahale and Issa were more selective regarding their tool species. There was no significant difference in proportions between Mahale and Issa (P = 1; Appendix B, Table B.5).

Table 3.2. Proportion of raw material types available versus proportion of tool materials. Adapted from Pascual-Garrido (2018).

Site	Type	Raw material[a]	Tools	χ^2	p
Gombe	Bark	0.486	0.487	0	1
	Grass	0.116	0.012	35.75	<0.001
	Twig	0.871	.44	178.644	<0.001
	Vine	0.013	.061	12.944	<0.001
	TOTAL (n)	457	411		
Issa	Bark	0.182	1	242.873	<0.001
	Grass	0.023	0	1.863	0.172
	Twig	0.936	0	333.13	<0.001
	Vine	0	0		
	TOTAL (n)	264	140		
Mahale	Bark	0.801	1	4.926	0.026
	Grass	0.017	0	0	1
	Twig	0.983	0	434.21	<0.001
	Vine	0	0		
	TOTAL (n)	639	25		

[a] Calculated based on the number of plants that could provide suitable raw material

Table 3.3. Family and species of plants sourced for tool material types at Gombe, Issa and Mahale. B = bark, T = twig, V = vine, G = grass. Adapted from Pascual-Garrido (2018).

Family	Species	Gombe	Issa	Mahale
Annonaceae	*Artabotrys collinus*		B	
	Artabotrys monteiroae		B	
	Annona senegalensis	B	B	
	Monanthotaxis buchananii		B	B
	Monanthotaxis poggei	B, T		
	Uvaria angolensis	B, T	B	B
	Uvaria sp. A of FTEA[a]		B	B
	Uvaria welwetschii		B	
Apocynaceae	*Dicyophlena lucida*	B, T		
	Diplorhynchus condylocarpon	B, T		
Asclepiadaceae	*Gymnema sylvestre*	T		
Capparidaceae	*Maerua holstii*			B
Combretaceae	*Combretum zeyheri*	T		
Connaraceae	*Byrsocarpus orientalis*	T		
Euphorbiaceae	*Cleistanthus polystachyus*		B	
Gramineae	Grass	G		
Guttiferae	*Garcinia buchananii*			B
Malvaceae	*Azanza garckeana*		B	
Rubiaceae	*Rothmannia urcelliformis*		B	
	Sabicea orientalis	V		
Sapindaceae	*Allophylus congolanus*	B, T		B
	Paullinia pinnata			B
Sapotaceae	*Mimusops kummel*			B
Sterculiaceae	*Dombeya burgessiae*		B	
Tiliaceae	*Grewia* sp.		B	
	Grewia forbesii	B, T		
	Grewia platyclada	B		
	Grewia mollis	B		
	Grewia rugosifolia		B	
	Grewia stolzii			B

[a] FTEA = Flora of Tropical East Africa

Source Taxa

Species exploited for implements during this study included a total of 31 species from 15 families, with six species yielding more than one tool material type. Annonaceae and Tiliaceae were the families most prevalent, the latter represented exclusively by one genus: *Grewia* (Table 3.3). In order to test if chimpanzees preferred some species over others, we compared for each source species the number of individuals exploited relative to their

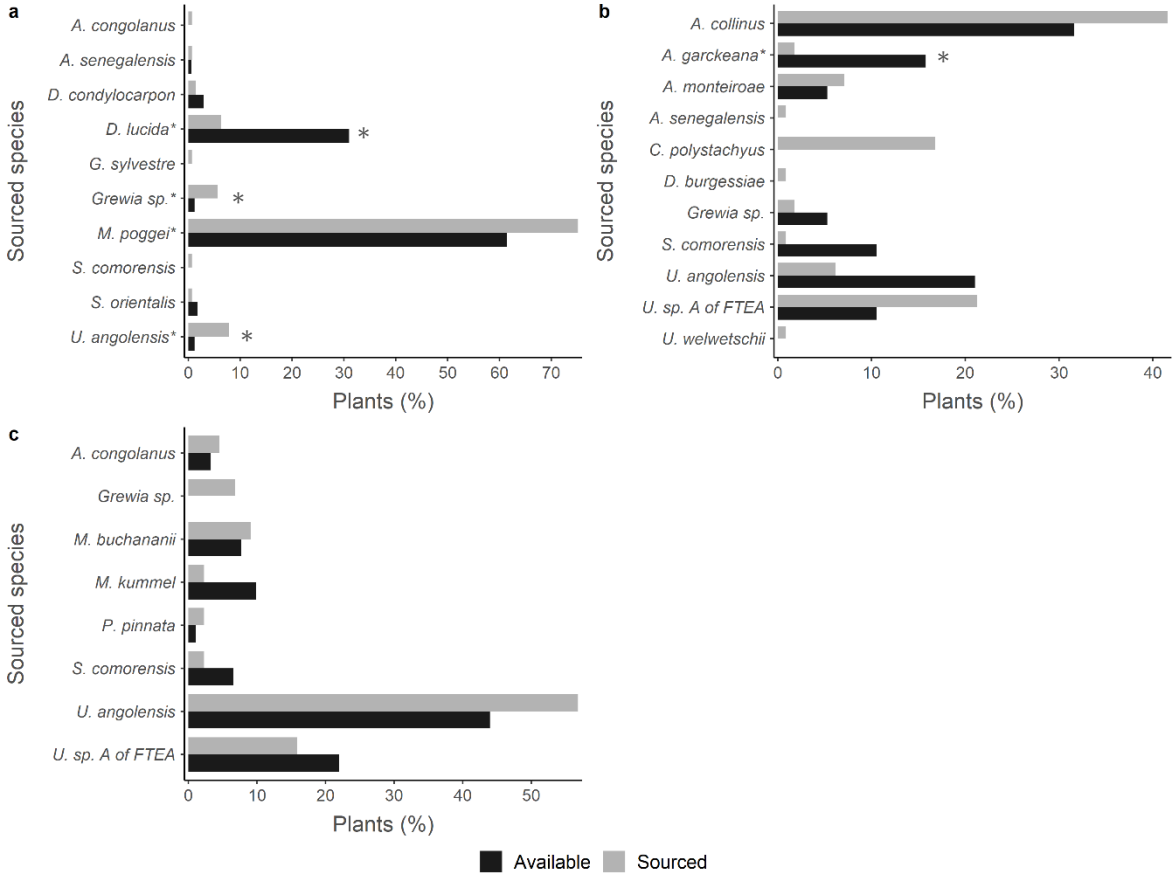


Figure 3.3. Percentage of plants sourced for tools by species (sourced; grey), compared to the species general availability among exploited species (available; black). (a) Gombe, (b) Issa, (c) Mahale. (*) indicates a significant difference between proportions where P < .05. Plants of the genus *Grewia* were combined into a *Grewia* sp. taxon as it was not always possible to identify individual species.

general abundance within source species near mounds. Results showed that at Gombe, *M. poggei*, *Grewia* spp. and *U. angolensis* were preferentially used (Appendix, Table B.7; Figure 3.3), while at Issa and Mahale source species were equally selected (except for *A. garckeana* at Issa). Interestingly, *D. lucida* at Gombe and *A. garckeana* at Issa revealed a significant but inverse difference, with more individuals available than sourced, suggesting that these species, even if exploited for tool manufacture, were not preferred.

Re-use of source plants

The number of *scars* left as a result of chimpanzees removing tool material from an individual plant (Pascual-Garrido 2018) can function as a proxy for determining sourcing intensity (i.e., how often a plant is procured) (Figure 3.4). At all sites, chimpanzees exploited sources once and multiple times, however, the intensity of use differed between sites.

At Gombe, chimpanzees sourced individual plants once (56.4%) and multiple times (43.6%) in almost equal proportions (Chi-squared: X^2 = 2.3143, df = 1, P =0.128, n = 140). At Mahale, plants were mostly procured once (73.3%; X^2 = 9.8, df = 1, P <0.05, n = 45), while at Issa more than half (63.1%) of all recorded sources utilised multiple times (X^2 = 8.3934, df = 1, P <0.05, n = 122). Likewise, the average number of parts removed per plant differed significantly between sites (Kruskal-Wallis: X^2 = 25.328, df = 2, P <0.001). Post-hoc pairwise Wilcoxon rank sum test revealed that this difference was maintained between all sites (Table B.6). While Gombe chimpanzees removed, on average, 2.4 parts per individual plant (range = 1-22, sd = 2.85, n = 140), Mahale chimpanzees detached on average 1.3 parts (range = 1-3, sd = 0.55, n = 44), while at Issa, individual sources had the largest number of removals, with an average of 3.2 parts detached (range = 1-23, sd = 3.6, n = 122).

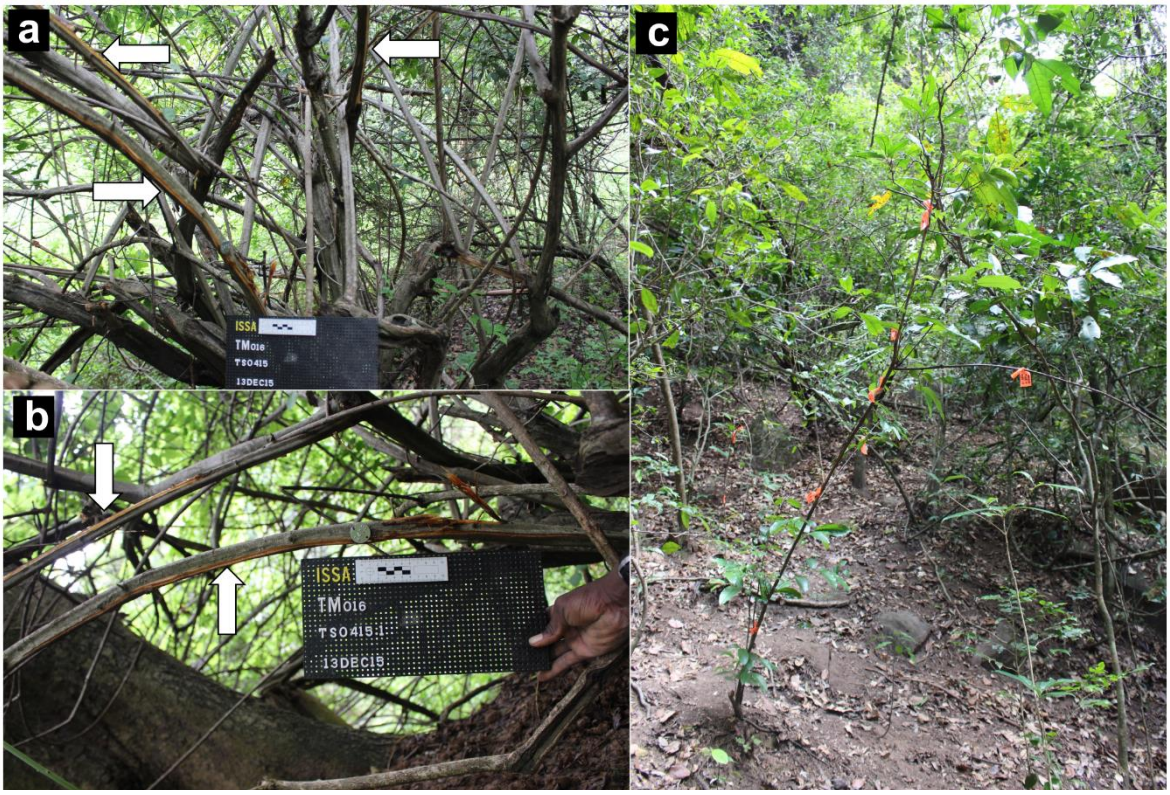


Figure 3.4. Examples of source plant locations at Issa from where chimpanzees removed tool material, indicated by white arrows (a, b) or orange tape (c). Photo credit: Katarina Almeida-Warren.

Use of source plants: effects of distance to mound and species abundance on number of removals

If the number of removals per individual plant decreases the further it is from the targeted mound, it seems likely that a transport-distance-cost-benefit effect is at play, whereby apes reduce the costs of transport by preferentially exploiting sources closer to the mound rather than turning to those located further away. Likewise, if the number of removals decreases the more abundant the plant species is, it is likely that chimpanzees are reusing more species more frequently.

Overall, distance to mound, species abundance and study site influenced number of removals (GLMM, full-null model comparison: $\chi 2 = 90.03$, df = 11, $P < 0.001$). In the full model, the three-way interaction between site, distance to mound and species abundance appeared non-significant ($P = 0.208$; Appendix B, Table B.1), as did the two-way interaction between distance to mound and species abundance ($P = 0.207$; Appendix C, Table B.2).

After removing the non-significant interactions, the resulting reduced model revealed that the influence of distance to mound and species abundance on number of removals differed significantly between the three study sites (Table 3.4; Figure 3.5). Distance to mound had a clear negative effect on the number of removals at Issa, while at Gombe and Mahale this effect was positive and neutral, respectively. Conversely, species abundance produced a negative effect on the number of removals at Gombe, while there was no evident correlation for Issa or Mahale.

Table 3.4. Results from the final reduced model (GLMM; lacking the non-significant three-way and two-way interactions) investigating potential predictors influencing number of removals.

term	estimate	SE	Lower CI	Upper CI	χ^2	*df*	P[c]
Intercept	0.258	0.244	-0.220	.736			NI[d]
SiteIssa[a]	0.417	0.288	-0.148	.982			NI[d]
SiteMahale[a]	-1.208	0.435	-2.060	-0.356			NI[d]
Distance[b]	0.121	0.287	-0.442	0.684			NI[d]
Abundance[b]	-0.523	0.106	-0.732	-0.315			NI[d]
SiteIssa*Distance	-0.740	0.295	-1.318	-0.162	7.747	2	0.021
SiteMahale*Distance	-0.081	0.517	-1.093	0.932			
SiteIssa*Abundance	0.565	0.129	0.313	0.817	2.538	2	<0.001
SiteMahale*Abundance	0.636	0.439	-0.223	1.496			

[a] Site was dummy coded with Gombe as the reference category.
[b] Variables were Z-transformed to a mean of 0 and SD of 1.
[c] Results from the likelihood ratio test using the 'drop1' function.
[d] Not indicated because it has a limited interpretation.

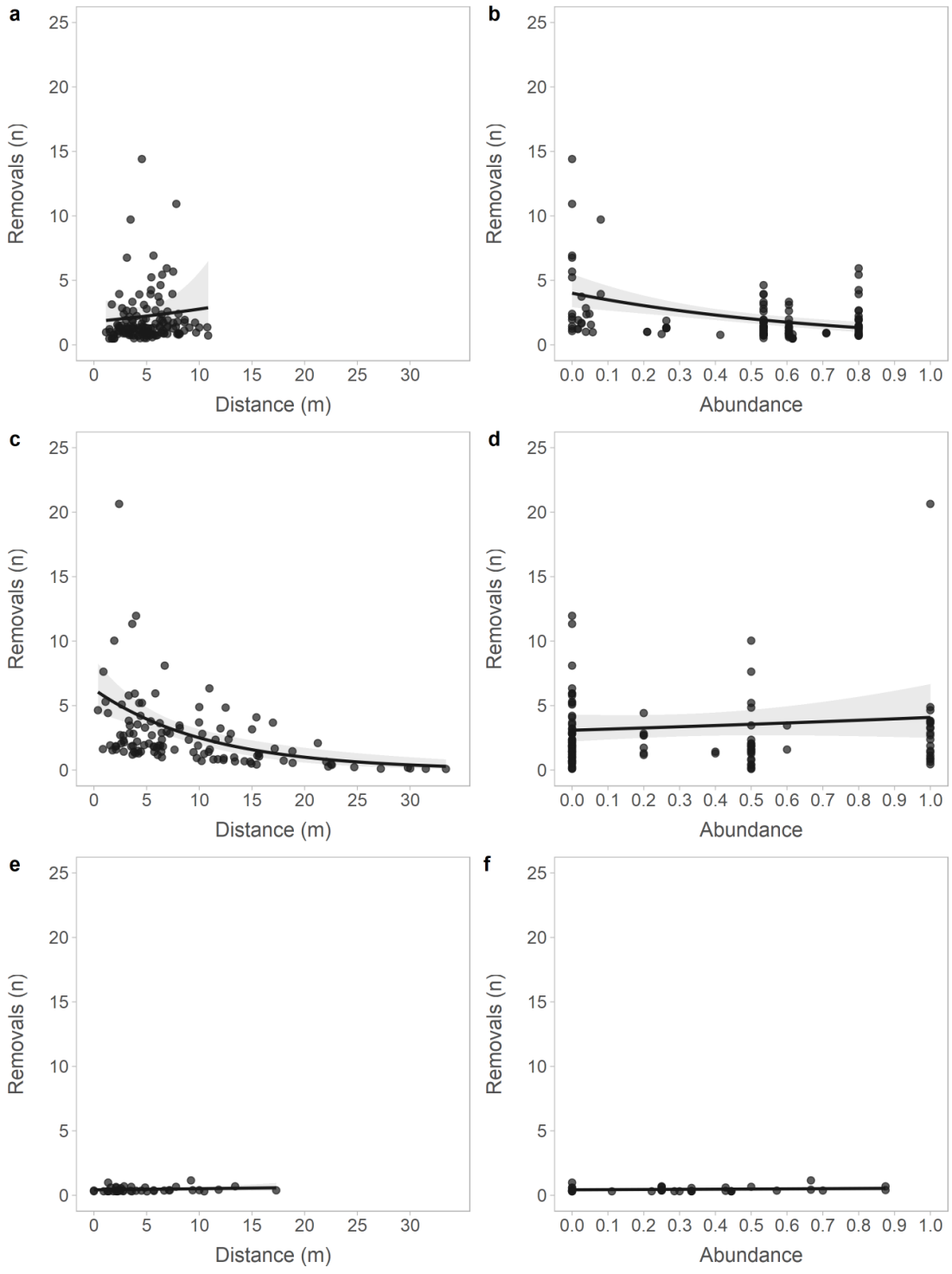


Figure 3.5. Comparison of number of removals per sourced plant by study site in response to distance to mound (a, c, e) and species abundance (b, d, f). At Gombe, (a, b); at Issa (c, d); at Mahale (e, f). Points represent individual sourced plants recorded at each study site (n: Gombe = 141; Issa = 113; Mahale = 44). The fitted GLMM model and confidence intervals are depicted by the line and grey area, respectively.

Discussion

The breadth and diversity of insectivory by modern non-industrialized human societies (Allsop & Miller, 1996; Raubenheimer et al., 2014) and wild ape populations (Bogart & Pruetz, 2011; Deblauwe, 2009; Hicks et al., 2019; Schöning et al., 2008), makes it likely that early humans were also exploiting this resource (Backwell & D'Errico, 2001; Lesnik, 2014; O'Malley & McGrew, 2014). Given the prevalence of perishable tools to harvest insects by chimpanzees (McGrew, 1992), it seems likely that early humans also used similar technologies (McGrew 2014).

Our previous studies indicate differences across study sites in material selection and transport for termite-fishing tools (Almeida-Warren et al. 2017; Pascual-Garrido 2018). In this study, we evaluate the extent to which raw material availability, and thus the local environment, dictates these differences. Our results show that chimpanzees living in a drier and more open habitat, with less raw material available nearby, exploited sources more intensively, with more parts detached per individual plant, and re-used them more frequently. Independent of habitat, Issa and Mahale chimpanzees preferred bark to fish termites, while Gombe chimpanzees used various materials. Unless other environmental differences, such as the efficiency of different raw material types influence this choice, this discrepancy may be socially driven. Our study shows that, as described for early humans (Braun et al. 2008, 2009; Goldman-Neuman and Hovers 2009, 2012; Harmand 2009) and chimpanzee stone technology (Carvalho et al. 2008; Luncz et al. 2016), raw material plays a major role in the variation of chimpanzee perishable technology. While part of this variation may be due to differences in the ecological context (in this case raw material abundance), other aspects, such as material selection, could not be attributed to the same ecologically

reasons, and thus, if socially learned and transmitted repeatedly across generations, as suggested by recent findings from Pascual-Garrido and Scheffrahn, 2020, may be termed as cultural (Koops et al., 2018; Lonsdorf, 2006; Musgrave et al., 2016, 2021; Van Schaik et al., 2003).

Raw material use and selection

We would expect that if chimpanzees show no selectivity of the raw materials they utilise to manufacture tools, the distribution of artefacts would reflect the distribution of available material types around the mounds. However, when we compared actual tool assemblage to an expected assemblage based on the percentage of raw material available around mounds, there are consistent differences. At all sites, twigs were the most abundant material, followed by bark, and, in much less proportion grass and vine (cf. Table 3.2). Despite this, only Gombe chimpanzees employed different materials for tools, while Issa and Mahale chimpanzees used only bark. If chimpanzee technology was positively correlated to the availability of materials, we would expect chimpanzees at Issa and Mahale to also incorporate other materials and, more importantly, for all three communities to favour twigs. This is clearly not the case.

Based on the recovery of chimpanzee assemblages, preference of materials has been described across sites (c.f. Stewart and Piel 2014). In some cases, their utilisation is linked to differences in tool functions (probe versus puncture; Sanz and Morgan 2007). However, this cannot be applied to our studied communities given the presence of termite-fishing probes alone. While the lack of use of grass and vines at Issa may correspond to a lower abundance or absence of these materials at mounds, the absence of twigs cannot be explained by the same ecological reasons. That *post-hoc* experiments with twigs showed that this material

was also suitable to termite fish (Almeida-Warren et al., 2017), further supports the lack of an environmental explanation for the absence of the use of twigs by the Issa community. Lack of knowledge or familiarity is also falsified as a possible explanation, given the use of twigs and other materials by the Issa apes to access underground tubers and fish for *Camponotus* ants (Hernandez-Aguilar et al., 2007; Wondra et al., 2016). Unless other environmental factors dictate the exclusive employment of bark by Issa chimpanzees (i.e., tool material efficiency, prey behaviour), social learning may be responsible for this 'speciality', particularly from mother (and older siblings) to offspring, which plays a fundamental role in the acquisition of termite-fishing skills, and is key for the development and maintenance of cultural behaviours and traditions (Koops, Schuppli, and van Schaik 2018; Lonsdorf 2005, 2006; Lonsdorf, Eberly, and Pusey 2004; Musgrave et al. 2016, 2020; Sanz and Morgan 2013; Sanz et al. 2014; Schuppli and van Schaik 2019).

At Mahale, while bark was also predominantly employed in the past, other types of materials were also utilised decades ago (McGrew and Collins 1985; Nishida and Uehara 1980; Uehara 1982). That only bark implements were recovered during this study (Pascual-Garrido, 2017) may correspond to the low sample size (n = 25) compared to the total number of tools collected by McGrew and Collins (1985) (n = 290) and Nishida and Uehara (1980) (n = 133). A larger sample size is necessary to assess if chimpanzees from Bilenge at Mahale have become exclusive bark users in recent decades. Historical data from Gombe (McGrew et al., 1979) also corroborates changes in the proportion of class of material employed. At that time, almost half (48%) of the artefacts were made from grass, while bark (21%), vine (17%) and twigs (10%), leaves of oil palms (4%) were less represented. This contrasts from the percentages reported in our study (bark 48.7%, twig 44.0%, vine 6.0% and grass 1.2 %). Changes in the raw material available might explain these differences. For example, at

Gombe, grass near mounds may have decreased during the past decades after the ending of annual burning, which allowed natural regeneration of vegetation (Collins and McGrew 1988; Collins, personal communication). Alternatively, previous studies might have focused on mounds residing in areas where grass was more abundant (McGrew et al., 1979). However, without a detailed description of the raw material available near mounds at that time, this is simply not possible to test. It could also be that changes in tool materials by Gombe chimpanzees occurred as a result of behavioural shifts towards greater material efficiency as recently documented for drinking sponges (leaf versus moss) manufactured by the Sonso community at the Budongo forest, Uganda (Hobaiter et al. 2014; Lamon et al. 2018). Future field experiments should aim to explore the potential role of efficiency in tool material selection for termite fishing by chimpanzees.

Source species

Plant species used for termite fishing have been recorded for various sites, including the current ones (Almeida-Warren et al. 2017; Pascual-Garrido 2018). Previous studies, indicate prevalence of plant species in tool assemblages (Bermejo & Illera, 1999; Fay & Carroll, 1994; McGrew et al., 2005; McGrew & Collins, 1985; Sanz & Morgan, 2007; Sugiyama, 1985; Suzuki et al., 1995). However, without a detailed record of the raw material available, these studies could not assess species selection empirically. McBeath and McGrew (1982) were the first to address the influence of plant variety on chimpanzee biodegradable technology. These authors found that chimpanzees at Mt. Assirik, Senegal, concentrated their termite fishing at mounds with abundant *Grewia lasciodiscus* nearby, the species most represented in tool assemblages. Likewise, botanical surveys conducted at Goulaougo, Republic of Congo (Sanz et al., 2004) and at the Issa valley (Almeida-Warren et al., 2017), indicate selection for plant

species to make termite-fishing implements. Our study provides further evidence supporting this, but also reveals differences across the study communities.

At Gombe, chimpanzees seem to be more 'generalist', exploiting almost 90% of all suitable species available in the vicinity of mounds — while at Issa and Mahale apes were more 'specialists', utilising only 12% of the total suitable species accessible (cf. Appendix B, Table B.4). These differences may likely correspond to the exclusive use of bark by Issa and Mahale chimpanzees, further evidenced by the differential sourcing of materials from the same plant species (i.e., *U. angolensis*, *Grewia* spp., and *Allophylus congolanus*) between the study communities (Table 3.3). Interestingly, *M. poggei*, *U. angolensis* and *G. forbessi*, three species preferentially utilised by Gombe chimpanzees, also provide termite-fishing material for apes living in West Africa (Mcbeath & McGrew, 1982; McGrew et al., 2005). Perhaps these taxa hold still unexplored mechanical and physical characteristics that make them ideal for termite fishing.

But what makes a 'good' material for termite-fishing tools remains largely unexplored and deserves further investigation. As McGrew, Tutin, and Baldwin (1979:205) pointed out decades ago: "The nature of the task defines the material to be used". At Goualougo, for example, puncturing sticks are manufactured mostly from branches of *Thomandersia hensii*, a rigid and straight tree, while *Sarcophrynium* spp., a species with sufficiently flexible twigs, is mostly sourced for fishing probes (Sanz & Morgan, 2007). The same holds true for chimpanzees at Bai Hokou and the Ndoki forest, Republic of Congo: tool types are manufactured from plant species which offer specific physical characteristics (Fay and Carroll 1994; Suzuki, Kuroda, and Nishihara 1995). Most of the source species at our studied sites belong to the Annonaceae and Tiliaceae families (Pascual-Garrido, 2018). These families may

embody physical and mechanical characteristics ideal for termite fishing, although we still do not know what characteristics are being selected by chimpanzees, nor if and how the selection criteria are passed on, for example via tool transfers or peering observation of users (Biro et al. 2003; Musgrave et al. 2016, 2020; Schuppli and van Schaik 2019; Whiten 2019).

Still, within the set of optimal species for tool manufacturing, why should chimpanzees at Gombe use bark and twigs, while those at Issa specialize on bark when twigs are predominant at this site? While still unexplored local ecological factors may shape preferences for tool material types (e.g. termite nest structure), we suspect that differences in tool materials used between our study sites are culturally influenced and thus reflect socially-learned variants (i.e., population-specific socially transmitted behaviours; Whiten et al. 1999; Koops, Schuppli, and van Schaik 2018; Lonsdorf 2006; Musgrave et al. 2020a, 2020b). Cultural differences as a driving factor in primate technology should not be overlooked (Boesch et al., 2020; Humle & Matsuzawa, 2002; Koops et al., 2015; Luncz et al., 2015; Möbius et al., 2008; Pascual-Garrido, 2019; Schöning et al., 2008; Whiten, 2019). In his pioneering studies at Gombe, Teleki (1974) concluded that selection proficiency for tool manufacture is a learned skill. This may be information acquired solely through repetitive individual trial and error, but may also be accompanied through social learning via stimulus enhancement, peering behaviour, and/or active facilitation, such as tool transfers (Hobaiter et al. 2014; Lonsdorf 2005; Lonsdorf et al. 2004; Musgrave et al. 2016, 2020; Sanz et al. 2014; Sanz and Morgan 2013; Schuppli and van Schaik 2019). Given that material selectivity often improves tool efficiency, it would be advantageous to retain this information (Sanz et al. 2014; Musgrave et al. 2016, 2020; Lamon et al. 2018).

Re-use of source plants: distance of transport and species abundance

Re-use of stone tools to crack nuts by chimpanzees reduces the energetic costs associated to the procurement and transport of new material (Boesch & Boesch, 1984b; Carvalho et al., 2008; Luncz et al., 2016). While the lifetime of perishable implements is comparably short, reutilisation of organic tools has been documented for types which require specific materials, not always readily available, and require several modifications. This is the case for puncturing sticks at the Goualougo Triangle, Republic of Congo, which are *cached* for later utilisation (Sanz and Morgan 2007). But perhaps because of their more delicate physical characteristics, and thus quicker deterioration, carrying and re-using fishing probes by chimpanzees is less frequent, and reduced to only a few hours or at most a day (Davidson and McGrew 2005; Sanz and Morgan 2007; Teleki 1974). Likewise, the repetitive use of individual sources might help reduce the time invested in searching for a new source, especially for species which may not be abundant nearby. Such is the case for *Thomandersia* trees which Goualougo chimpanzees repeatedly exploit for puncturing sticks. This genus of tree, though being one of the most common in the study area, is not always located close to the tool-use site (Sanz & Morgan, 2007). In this study, we provide new evidence that chimpanzees re-use sources of raw material for the manufacture of termite-fishing tools, with differences emerging between sites.

At Issa, chimpanzees not only extracted on average more parts per individual plant, but the distance of the source to the mound was negatively correlated with the number of parts removed, with fewer parts detached from sources found further away (cf. Table 3.4; Figure 3.5). This may reflect a strategy to minimize transport costs from source to tool-site (Blumenschine et al., 2008; R. Potts, 1994) in an environment where suitable sources are not

only less abundant (Appendix B, Table B.2), but also further away (Pascual-Garrido 2018). Such a strategy would enable Issa apes to maximise the procurement of tool material with the least investment of energy (Carvalho et al., 2008; Luncz et al., 2016). Abundance did not seem to affect the number of parts removed, perhaps due to the overall rarity of source species in the mound vicinity; Issa chimpanzees target all source species equally.

At Mahale, sources were exploited mostly once, and neither the distance of the source to the targeted mound nor the abundance of the source species seem to have an effect on the number of parts taken per source. With abundant bark sources available nearby, approximately 80% of plants around mounds providing suitable bark (cf. Appendix A, Table A2), Mahale apes have abundant sources from which to choose, which they do, given that only 12% of all available species are utilised (cf. Appendix A, Table A4). Similar findings have been described for chimpanzees at Mt. Assirik, Senegal, where 90% of all sources were located in close proximity to targeted mounds (McGrew et al., 1979).

At Gombe, where raw material was the most abundant of all study sites (cf. Table 3.1), a slightly different picture emerged: Even when apes obtained their material from a relative close distance, and at similar distances as chimpanzees at Mahale (Pascual-Garrido, 2018), species abundance showed a negative trend relative to the number of times it was sourced. Rare species were procured more often.

Use and re-use of tool materials provide valuable insights into hominoid technological patterns. Boesch and Boesch (1984) proposed that the transport of stone tools to *Panda* nut cracking sites by chimpanzees living in the Taï forest, Cotê d'Ivoire, follows a least-distance-strategy, with hammerstone weights decreasing with increasing distances to the nearest

location of tool material sources (Luncz et al. 2016). Optimal utilisation of resources with flexible, dynamic, opportunistic, and low-energy strategies to solve problems, which share affinities to the Oldowan, have also been described for nut-cracking chimpanzees in Bossou, Guinea (Carvalho et al. 2008). While perishable implements do not impose a similar weight constraint to that of stones ("A chimpanzee carrying a 3 kg stone walks on three limbs and carries the stone in one arm", Boesch and Boesch 1984:164) and so can be carried in the mouth, the distance travelled from a suitable source to the tool-site could still demand extra energetic costs, especially for sources that are rare and at a considerable distance (Sanz & Morgan, 2007). That chimpanzees at Gombe, Issa and Mahale selected and transported different materials for termite-fishing tools, and reutilised sources in ways that seemed to be influenced by the abundance of raw material available, suggests that, as described for lithic technology (Carvalho et al., 2008), different resource exploitation strategies might also be at play for organic technology. Further investigations including individual follows are necessary to corroborate this.

Conclusion

Besides the human lineage, selection and transport of materials for tool manufacture has been documented across many species. For example, New Caledonian crows (*Corvus moneduloides*) select and carry materials to fish *larvae* from tree holes (Bluff et al., 2010; Klump et al., 2019; Rutz et al., 2007); woodpecker finches (*Cactospiza pallida*) employ twigs, cactus spines, or leaf petioles to probe for insects inside tree holes, sometimes carrying the tool from branch to branch (Hundley, 1963); while orangutans (*Pongo abelii*) prefer certain lining materials to construct their nests which they may carry for as far as 50 m from the nest site (*leaf-carrying*) (Russon et al., 2007; Van Casteren et al., 2012). This suggests that selection

and transport of materials is a vital component of the tool use or manufacture. However, what probably sets apart chimpanzees from the rest of non-human tool manufacturers, including other apes, is their prolific and flexible use of materials for a diverse range of implements, more akin to humans than to any other living non-human species (McGrew, 1992; McGrew et al., 2019; Rolian & Carvalho, 2017).

Stone tool use by Plio-Pleistocene hominins involved selectivity and transport behaviours dependent on the raw material available, with patterns of variation reflecting their cultural diversity (Braun et al. 2008, 2009; Goldman-Neuman and Hovers 2009, 2012; Kimura 1999; Stout et al. 2005, 2010). In this study, we provide evidence that part of what archaeologists have reconstructed about the behaviours associated to the Oldowan can be accommodated within the perishable technology used by wild chimpanzees, and thus likely were present in the last human-chimpanzee common ancestor (McGrew, 2010b), before the advent of the Oldowan (Carvalho & Beardmore-Herd, 2019; Panger et al., 2002). These commonalities include: selection and transport behaviours for tool manufacture (Braun et al., 2009; Braun, Tactikos, et al., 2008; Goldman-Neuman & Hovers, 2009, 2012; Schick, 1987), tool-using strategies dependent on the raw material available (Kimura, 1999), and techno-cultural diversity (Stout et al., 2005, 2010). Our studies continue to support Wynn and McGrew (1989) and Wynn et al. (2011) assertions that everything archaeologists have reconstructed about the behaviour of the Oldowan can be accommodated within the 'ape adaptive grade' (more recently updated to the 'simian adaptive grade,' McGrew et al. 2019), except for two specific behavioural patterns which still remain unknown for modern apes, one of which is relevant here: Oldowan hominins carried raw material and implements farther than any living ape, sometimes for up to tens of kilometres, and that they competed with large carnivores for animal prey.

Given the predominance of biodegradable material in chimpanzee (McGrew, 1992) and hunter-gatherer's material culture (González-Ruibal et al., 2011; Hoffecker & Hoffecker, 2018), the prevalence of C_4 grassland since the late Miocene (Faith et al., 2019), and the possible exploitation of termite mounds early in our own lineage (Backwell & D'Errico, 2001), it is likely that early humans also made use of this resource with a much richer, diverse and varied tool kit (and associated technical behaviours) than is currently visible in the archaeological record (Backwell & D'Errico, 2001; Carvalho & Almeida-Warren, 2019; Domínguez-Rodrigo et al., 2001; Panger et al., 2002; Toth & Schick, 2009). It is largely thought by the palaeoanthropology community that the advent of flaked stone tool technology marked a qualitative leap in human evolution (Braun et al. 2019; Shea 2017). However, this and other studies call for the placement of our early ancestors in their appropriate evolutionary context, seeking to understand the Oldowan as being on a continuum of a way of life that might have been in place for millions of years (Carvalho & Beardmore-Herd, 2019; Panger et al., 2002; Wynn, 1981; Wynn et al., 2011).

Acknowledgments

We are grateful for: permission to conduct research in Gombe Stream National Park, Mahale Mountains National Park, and Issa valley by Tanzania National Parks (TANAPA), Tanzania Wildlife Research Institute (TAWIRI), and Tanzanian Commission for Science and Technology (COSTECH); field assistance at Issa from Shedrack Lucas, Patrick Hassan, Godfrey Stephano, Mashaka Kalutwa, Busoti Juma, Mlema Juma, Msigwa Rashid, Sebastian Ramirez-Amaya, and Eden Wondra, at Mahale by Shaka and Singa Kabugonga, and at Gombe by Matendo Msafiri Katoto and Nasibu Zuberi Madumbi; logistical support from Jane Goodall Institute, Greater Mahale Ecosystem Research and Conservation Project, and Mahale Mountains Chimpanzee

Research Project; plant identifications by Frank Mbago, Botany Department, University of Dar es Salaam. Special thanks go to Anne Pusey, Anthony Collins, Deus Mjungu, Michio Nakamura, and Alex Piel for aiding logistics in the field; Edward Kohi, Pius Kavana and Maria Mbogo for safekeeping APG's equipment in Kigoma town; and to Alex Mielke and Thomas Püschel for assistance with data analysis. We are very grateful to Luis da Silva for providing the illustration of chimpanzees sourcing raw material for termite-fishing tools. William C. McGrew, Volker Sommer, two anonymous reviewers, and the editorial team at *Current Anthropology* provided much constructive critique and greatly improved the article. This research greatly benefited from discussions with Susana Carvalho, Anthony Collins and William C. McGrew. APG was supported by a Leverhulme Trust Early Career Fellowship and received further funding for fieldwork from The Boise Trust Fund, University of Oxford. During writing APG was supported by The John Fell Fund, University of Oxford.

Chapter 4

Landscaping the behavioural ecology of ape stone tool use

The content of this section is currently under consideration by the *International Journal of Primatology*. It is also available as a pre-print at BioRxiv: https://www.biorxiv.org/content/10.1101/2021.08.24.457369v1

Abstract

The physical environment is fundamental to the development, transmission, and perpetuity of primate technology. Previous studies on tool site selection have addressed the relevance of targeted resources and raw materials for tools, but few have considered the broader foraging landscape. In this landscape-scale study of the ecological contexts of wild western chimpanzee (*Pan troglodytes verus*) tool-use, we investigate the conditions required for nut-cracking to occur and persist over time at discrete locations in Bossou, Guinea. We examine

this at three levels: selection, frequency of use, and inactivity. We find that, further to the presence of a nut tree and availability of raw materials, abundance of food-providing trees as well as proximity to nest sites were significant predictors of nut-cracking occurrence. This suggests that the spatial distribution of nut-cracking sites is mediated by the broader behavioural landscape and is influenced by non-extractive foraging of predictable resources, as well as non-foraging activities. Additionally, the number of functional tools was greater at sites with higher frequency of nut-cracking and was negatively correlated with site inactivity. Our findings indicate that the technological landscape of the Bossou chimpanzees shares affinities with the 'favoured places' model of hominin site formation and provides new insights for reconstructing ancient patterns of hominin landscape use.

Introduction

Ecology plays an important role in shaping non-human primate behaviour from foraging strategies, to ranging patterns, and sociality (Robbins & Hohmann, 2006; Strier, 2011). Tool-use, particularly for extractive foraging, is no exception. Recent studies have highlighted that ecology is key in determining whether tool-use emerges in a population, how it manifests itself, and how it is maintained once it is established (Carvalho et al., 2007, 2011; Grund et al., 2019; Koops et al., 2013, 2014).

Stone tool-use is often recurrent in spatially discrete locations, frequently involves the reuse of tools, and leaves a recognisable archaeological footprint that can be traced back thousands of years (Carvalho et al., 2009; Falótico et al., 2019; Mercader et al., 2007). However, little is known about the ecological factors influencing selection and repeated use

of specific locations for these activities and how they fit within the broader foraging landscape. Lithic-based foraging technology has been recorded in several wild, non-human primate species including chimpanzees (*Pan troglodytes verus* and *P. t. ellioti* formerly *P.t. vellerosus*; Whiten *et al.*, 1999; Abwe and Morgan, 2008), bearded capuchin monkeys (*Sapajus libidinosus;* Ottoni and Izar, 2008), Burmese long-tailed macaques (*Macaca fascicularis*; Gumert, Kluck and Malaivijitnond, 2009), and, most recently, in white-faced capuchins (*Cebus capuchinus*; Barrett *et al.*, 2018).

Chimpanzees are of particular interest because they are one of our closest living relatives(*P. paniscus*; (Langergraber et al., 2012), and they present one of the largest, most diverse and ecologically adaptable technological repertoire among non-human species, reflecting a level of cognitive flexibility akin to the earliest hominin toolmakers (Carvalho et al., 2013; Pascual-Garrido & Almeida-Warren, 2021; Rolian & Carvalho, 2017). Chimpanzee nut-cracking assemblages are very similar to the low-density assemblages characteristic of the early hominin record (Carvalho et al., 2008; Carvalho & McGrew, 2012). Thus, understanding how patterns of nut-cracking behaviour accumulate across the landscape can provide valuable insights into the formation and spatial distribution of early hominin assemblages and allow the modelling of ancient landscape use and resource exploitation.

Research on chimpanzee nut-cracking has established that the spatial availability of nut trees and raw materials for tools influences site location and reuse, as well as frequency and distance of tool transport (Boesch & Boesch, 1984a; Carvalho et al., 2007, 2011; Luncz et al., 2016). Nevertheless, nut-cracking assemblages are yet to be explored within the context of the broader ecological and foraging landscape. This requires the study of nut-cracking sites not only in relation to direct ecological correlates such as access to raw materials and nuts,

but also in relation to ecological requirements of other daily activities critical to survival such as food, water, and shelter.

Chimpanzees living in forested environments spend approximately 50% of their waking hours foraging and travelling between feeding locations (Pruetz & Bertolani, 2009). Studies have shown that chimpanzee ranging patterns are dynamic and are affected by the spatial distribution and seasonality of food (Trapanese et al., 2019; Wrangham, 1977), which may also influenced where non-foraging activities, such as nesting, take place (Basabose & Yamagiwa, 2002; Hernandez-Aguilar, 2009; Janmaat et al., 2014). Their diet mainly consists of fruit, followed by leaves and terrestrial herbs (Goodall, 1963; D. B. Morgan & Sanz, 2006), but high-energy foods such as insects, nuts and honey acquired through tool-assisted foraging are also important staples or nutritional supplements for many chimpanzee populations (Sanz & Morgan, 2013). Yet, little is known about how extractive foraging interacts with other feeding activities and the broader behavioural landscape.

Water is essential to life (Popkin et al., 2010). For non-human primate species living in extremely arid conditions, such as savannah-dwelling chimpanzees and baboons, water is a critical resource that constrains movement patterns and landscape use (Barton et al., 1992; Lindshield et al., 2021; Pruetz & Herzog, 2017; Wessling, Deschner, et al., 2018; Wessling, Kühl, et al., 2018). At face value, water provides hydration and a medium in which primates, and other living organisms, can stay cool. However, when examined in the broader foraging and behavioural context, other equally important qualities emerge. Most notably, water sustains plant species. These not only give shade but also provide a range of foods, some of which may not be encountered elsewhere. For some chimpanzee populations, water is also a source of aquatic resources such algae (Boesch et al., 2017; Humle & Matsuzawa, 2009)

and fresh-water crabs (Koops et al., 2019). Finally, free-flowing water can transport stone cobbles, and therefore serve as a source of raw materials for stone tools. This relationship has been proposed to explain the correlation between chimpanzee nut-cracking sites and hydrological features in Diécké, Guinea (Carvalho et al., 2007; Carvalho, 2011), although this remains to be empirically tested. Similarly, water has been spatially linked with early hominin stone tool sites (Rogers et al., 1994) and has also featured in many discussions surrounding early hominin evolution and behaviour (Joordens et al., 2019)..

Chimpanzees habitually make a sleeping nest at the end of every day, and sometimes make day nests for resting (Koops et al., 2012). They have been an important focus of research since Sept (1992) recognised that they form clusters of debris akin to early hominin assemblages, and saw their potential for understanding patterns of early hominin landscape use and the origins of human shelter (McGrew, 2021). Nesting locations have subsequently been linked with a range of ecological parameters such as tree species and tree architecture, as well as surrounding topography and vegetation types (Badji et al., 2018; Carvalho et al., 2015; Hernandez-Aguilar, 2009; Hernandez-Aguilar et al., 2013; Koops et al., 2012; Ndiaye et al., 2018; Stewart et al., 2011). Other studies have found additional links between nest sites and proximity to areas of high fruit availability (Basabose & Yamagiwa, 2002; Furuichi & Hashimoto, 2004; Goodall, 1962; Janmaat et al., 2014), and that these correlations are not universal (Koops et al., 2012). While the exact conditions determining nest site suitability appear to be population-specific, these findings demonstrate that nesting activities shape chimpanzee landscape use, and, in turn, are shaped by resource distribution and the local environment. Nevertheless, little is known about how nesting relates to other activities such as spatially discreet forms of tool use (e.g., nut-cracking and termite-fishing).

In this study, we explore the relationship between primate tool use and the broader behavioural and ecological landscapes by investigating the ecological drivers of chimpanzee nut-cracking. We examine, at a landscape-scale, the conditions required for nut-cracking to occur and persist over time in discrete locations at the long-term field site of Bossou (Guinea). This is divided into three points of enquiry: 1) tool site selection; 2) tool site use; 3) tool site inactivity.

Tool site selection explores the environmental conditions that determine where nut-cracking sites occur within the Bossou chimpanzee home-range. This is critical to understanding how technical activities occur within the broader behavioural landscape, and how these activities produce locally discrete assemblages that can remain archaeologically identifiable for thousands of years (e.g. Falótico et al., 2019; Mercader et al., 2007). There is a growing body of research on habitat selection for daily activities such as foraging, travelling, socializing and sleeping, particularly in relation to human-modified landscapes and implications for conservation (Bryson-Morrison et al., 2017; K. B. Potts et al., 2016). However, regarding technological activities, although we are beginning to learn more about raw material selection for tools (Carvalho et al., 2008; Pascual-Garrido & Almeida-Warren, 2021), the selection of locations for tool use remains unexplored.

Tool site use focuses on the ecological factors that influence the frequency with which established sites attract nut-cracking activity. How often a site is used can serve as a proxy for inferring preference in relation to other sites. From an archaeological perspective, generally the more a location is used for debris-generating activities, the larger and more conspicuous an archaeological signature becomes. This has important implications for understanding the spatial clustering of activities and material evidence over time and can

offer many insights into the formation and perpetuity of early hominin archaeological assemblages (Carvalho & Almeida-Warren, 2019; McGrew, 2010b). Ethoarchaeological studies of chimpanzee nests have found that sleeping sites are frequently revisited and the nests themselves may be reused (Hernandez-Aguilar, 2009; Sept, 1992; Stewart et al., 2011). However, comparable literature on the use of tool sites is scarce, except for the reuse of stone tools (Carvalho et al., 2009), and sources of perishable raw materials (Pascual-Garrido, 2018; Pascual-Garrido & Almeida-Warren, 2021).

Tool site inactivity investigates the ecological conditions that may cause the cessation of nut-cracking activity at an established tool site. Chimpanzees live in dynamic landscapes shaped by environmental change. Whether natural or anthropogenic, these shifts often result in changes in resource distributions that may in turn lead to the development of new behavioural adaptations and ranging patterns (e.g. Kalan et al., 2020). New opportunities may arise (e.g., foraging food from crops: Hockings et al., 2015, 2012; nesting in novel plant species: McCarthy et al., 2017), while formerly habitual activities may shift to new locations or become obsolete (Gruber et al., 2012; Kühl et al., 2019). Environmental changes have been identified as important drivers of our own evolutionary history (Bobe et al., 2002; Bobe & Carvalho, 2019; Joordens et al., 2019; R. Potts, 1998; R. Potts et al., 2020; Reed, 1997), but few studies have addressed empirically how these changes may have affected patterns of landscape use and the distribution of early hominin tool sites (e.g. Rogers et al., 1994). Thus, investigating the conditions that influence the cessation of activity at chimpanzee tool sites, can provide important clues as to the factors that lead to their temporary or long-term abandonment.

Throughout these steps we assess the effect of ecological parameters that have been found to correlate with nut-cracking activities (nut availability; abundance of raw materials; distance to water) as well as variables that encapsulate two key aspects of chimpanzee activity patterns: non-extractive foraging (abundance of food resources: wild food trees; wild fruit trees; THV - terrestrial herbaceous vegetation) and sleeping (distance to nesting site).

Methods

Study site and subjects

Bossou (7° 39′ N, 8° 30′ W) is located in the southeasternmost corner of the Republic of Guinea (West Africa), 6 km from the foothills of Mount Nimba Strict Nature Reserve (Figure 4.1) (Humle, 2011a; Yamakoshi & Sugiyama, 1995). The chimpanzee community has been studied continuously in both natural (since 1976) and experimental (outdoor laboratory since 1988) settings (Matsuzawa, 2011; Sugiyama & Koman, 1979). Between 1976 and 2003 the community was composed of 18 to 23 individuals (Sugiyama, 2004), but has since declined largely due to a catastrophic flu-like epidemic from which it never recovered (Humle, 2011b; Sugiyama & Fujita, 2011). At the time of this study, the population consisted of seven individuals. The Bossou chimpanzees habitually crack and consume oil-palm nuts (*Elaeis guineensis*) and are currently the only community known to use portable stones as both hammers and anvils (Carvalho, Matsuzawa and McGrew, 2013; but see Ohashi, 2015 for recent discoveries in liberia). Bossou has two seasons – a short dry season lasting from November to February, and a long rainy season extending from March to October (Humle, 2011a; Yamakoshi, 1998). Nut-cracking occurs year-round, but is most prevalent during peak

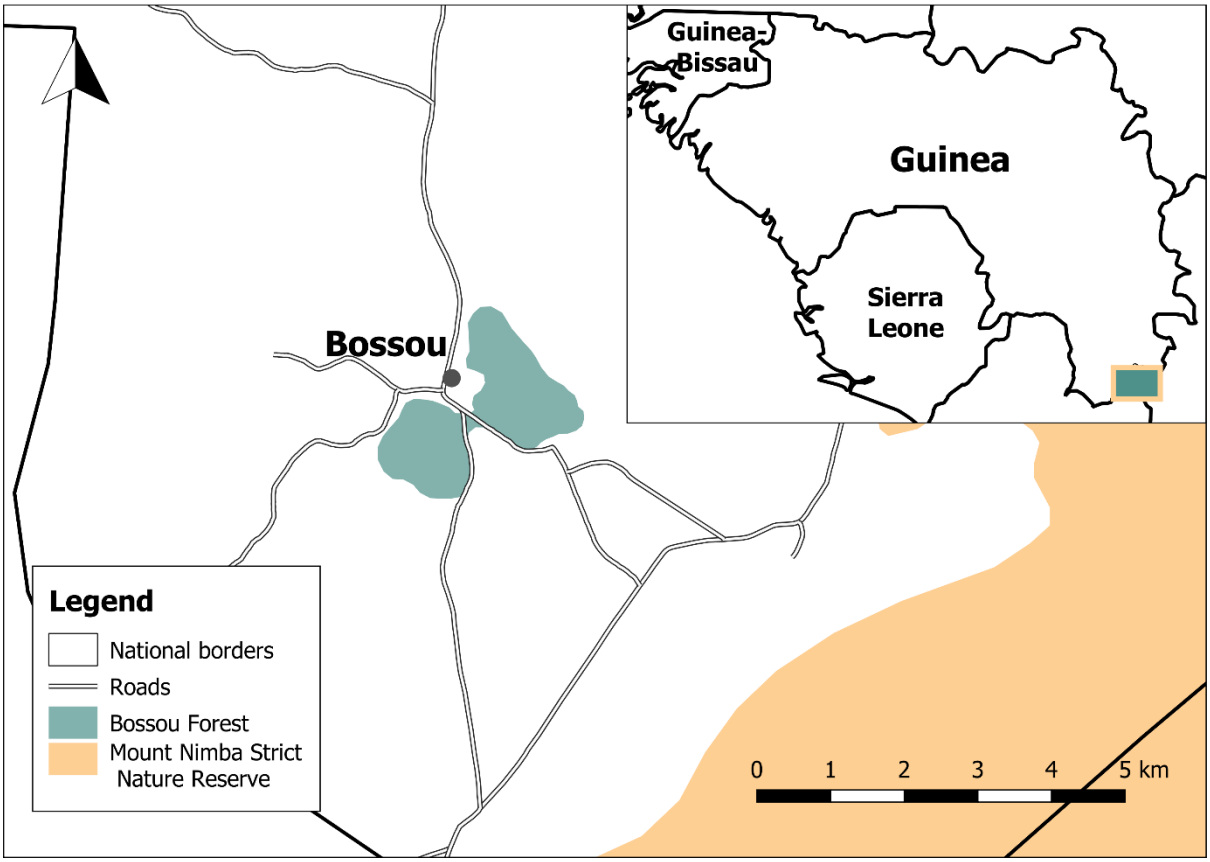


Figure 4.1. Map of the Bossou Forest and surrounding area. Mount Nimba Strict Nature Reserve shapefile adapted from the WDPA database (UNEP-WCMC and IUCN 2019).

wet season (June – August) and at the start of the dry season (November – December) when fruit is less abundant (Yamakoshi, 1998).

The Bossou forest has an estimated area of 16 km^2 and is intersected by roads (Figure 4.2; Hockings et al., 2006). Within this, the chimpanzees range in a core area of approximately 7 km^2 (Hockings et al., 2006). The habitat is comprised of a composite of primary, secondary and riverine forests, savanna and cultivated fields (Hockings et al., 2012). The northern slope of Mont Gban, in the Eastern part of the forest, is considered a sacred area – forêt sacrée –

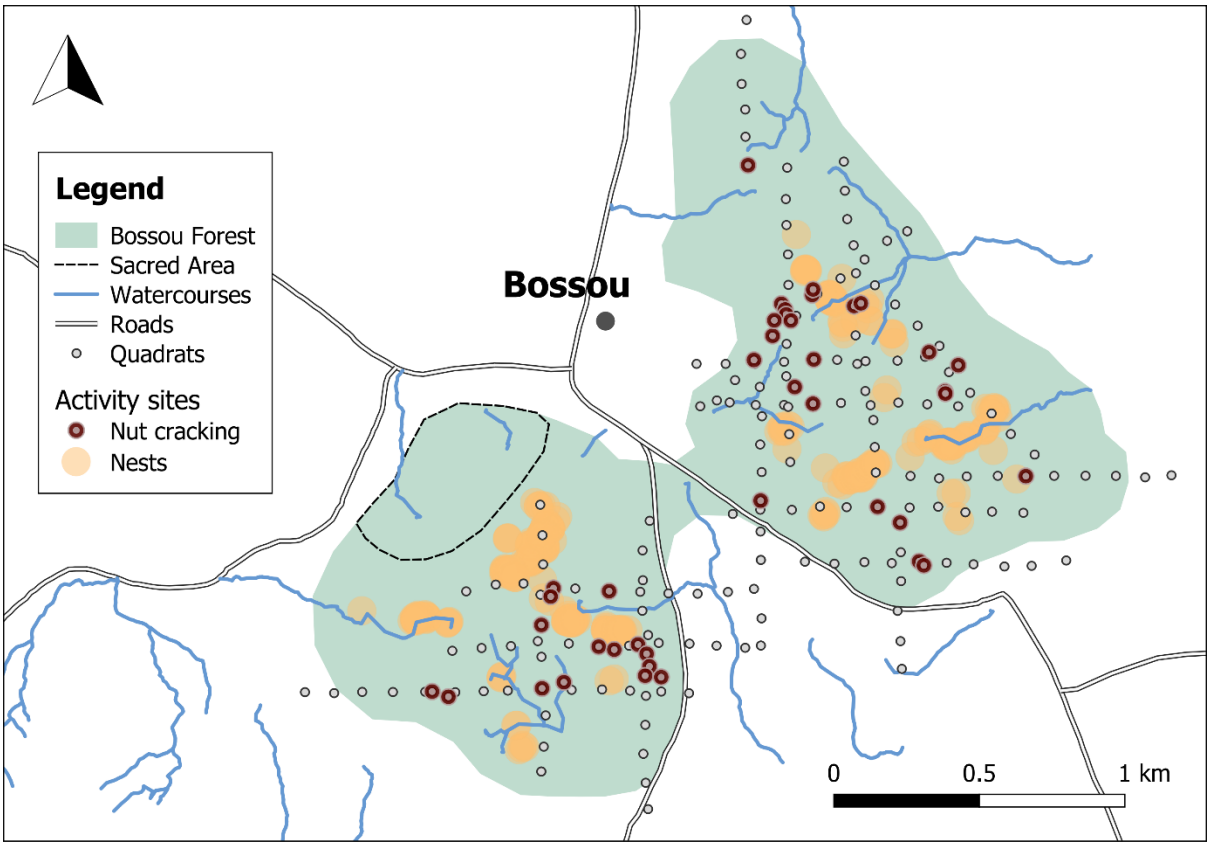


Figure 4.2. Map of the study area and surrounding area, highlighting the locations of recorded nut-cracking sites, quadrats, nests, and watercourses.

by the local *Manon* culture, and access is forbidden to outsiders. Out of respect to this tradition, we did not conduct any research in this area.

Data collection

Data were collected over two field trips: 14Dec2017 - 01May2018 and 28Oct2018 - 13Dec2018, encompassing 160 days of fieldwork. We employed a mixed-method approach that combined direct behavioural observation through group follows of the chimpanzee community, with archaeological documentation of nut-cracking sites (indirect behavioural observations as per Carvalho and Almeida-Warren, 2019), and ecological research using the

transect and quadrat method (Carvalho et al., 2011). Initially, we targeted nut-cracking sites that had previously been documented by SC in 2006 and 2008-09 and expanded this sample to include any new nut-cracking sites that were discovered during the ecological surveys and group follows. For each nut-cracking site we established 1-km transects intersecting the site datum at 500 m. Nut-cracking sites within 100 m of a pre-established transect were either assigned to that transect or became the mid-point of a new perpendicular transect in cases where those areas had not yet been recorded, to ensure even forest coverage. All transects (N = 18) were oriented N-S or E-W, except for two that were oriented NE-SW and NW-SE due to access difficulties (Figure 4.2). We established 5-metre radius survey quadrats (N = 195) at 100-m intervals along the transects starting from the midpoint where the nut-cracking site was located. At each quadrat nut-cracking specific and general ecological and vegetation data were collected (further details below).

We employed a fully digital method of data collection. Quadrat mid-points and all data entries (food-providing vegetation, tools, raw materials) were georeferenced using an Arrow Gold GNSS receiver (μ_{HRMS} = 2 m; Almeida-Warren et al., 2021; EOS Positioning Systems Inc., 2017). Coordinates were instantly downloaded via Bluetooth into the GeoGrafi-M application (Mobile GIS Services, 2019) on an android device where further data could be entered through custom made forms.

OIL PALMS

For each oil palm encountered during quadrat surveys we measured the diameter at breast height (DBH) with a diameter tape and counted the number of fruit bunches (total and ripe) visible from the ground with the naked eye. For the nut trees associated to nut-cracking sites we also collected weekly information on new traces of nut-cracking and the availability of

edible nuts on the ground. With aid from field assistants, we determined nut edibility by collecting a random sample of nuts within a 2-metre radius of the oil palm to estimate how many contained an edible kernel or were rotten (following Koops *et al.*, 2013). Nuts were not opened so as not to affect future availability, but the local people harvest palm fruits and nuts and are able to identify whether or not they are edible (Humle & Matsuzawa, 2004). As per Koops *et al.* (2013), we scored presence of edible nuts as: (0) nuts absent; (1) 1-50 nuts; (2) 51-100 nuts; (3) > 100 nuts.

We monitored the nut-cracking sites every week during the first field season (22JAN18-03MAY18) and once at the beginning and end of the second season (weeks of 29OCT18; 10DEC18) to record evidence of nut-cracking activity and availability of oil palm fruits and nuts. Additional monitoring data were collected by Henry Didier Camara during the weeks of 30SEP19, 27APR20, and 25MAY20. However, only the nut-cracking sites documented prior to the 22nd of January (N = 25) were checked for the full 15 weeks.

TOOLS AND RAW MATERIALS

We scored all lithic material according to size (the length of the longest axis), raw material type, and portability (whether loose or imbedded in the ground). Adapted from Koops *et al.* (2013), we scored size into six categories: (1) 1-2 cm; (2) 3-5 cm; (3) 6-10 cm; (4) 11-20 cm; (5) 21-30 cm; (6) >30 cm. Tools and by-products of nut-cracking were defined as stones that showed at least one of the following: a) traces of wear from nut-cracking; b) nutshell remains on or around them; c) could be refitted with another stone with evidence of a) or b). For this study, the variable *Tools* included all lithic materials used for nut-cracking except for fragments that could no longer be used for nut-cracking.

The collective tool assemblage was also scored for status of nut-cracking activity: (Active) New signs of nut-cracking activity were recorded during the fieldwork period. Shell fragments or nut powder or were visible on top of or around tools, and there was at least one hammer and anvil pair with impact points that lacked signs of chemical or organic weathering (i.e., rust, moss); (Inactive) There were no signs of recent nut-cracking activity during the entire fieldwork period. Cracked nut kernels were either absent or present but showed clear signs of decay. Iron oxide or moss had developed on tool impact points.

VEGETATION

We recorded all wild plant species known to be consumed by the chimpanzees of Bossou, that were encountered during quadrat surveys. We then cross-referenced the recorded species with the current list of chimpanzee food resources to identify those which were sources of fruit – the preferred food-type of chimpanzees. We considered trees with a DBH ≥ 5 cm (Hockings et al., 2009), lianas and shrubs with a DBH ≥ 2 cm (Gerwing et al., 2006), and THV of any dimensions. However, while THV is a frequently consumed food item by the chimpanzees of Bossou (Humle, 2011a), it differs from other wild plant foods in that they have a lower calorific value (Bryson-Morrison et al., 2020) and an individual plant often can only be sourced once, after which it is permanently depleted. To distinguish these types of food sources (perennial versus ephemeral), THV was documented as a separate variable. We also encountered a small number of domesticated or crop foods that are eaten by chimpanzees. This largely consisted of cassava tubers (*Manihot esculenta*) and banana plants (*Musa* sp.). While crops are frequently consumed by Bossou chimpanzees, especially during the wet season when wild fruit is scarce, use of these areas is conditioned by additional factors such as the high risk of antagonistic interactions with humans (Bryson-Morrison et al., 2017; Hockings et al., 2009). Such species would therefore warrant allocation to a third

vegetation category. However, due to the small sample size (N = 46), we did not include them in the present study.

NESTS

Because few nests were documented at the quadrat level or along transects (N = 4), additional forest-wide surveys were conducted, targeting areas that were known nesting locations. When a nest was encountered, elevation and direction of travel were maintained and all nests within 50 m of the nest and either side of the projected route were documented until no further nests were visible over a 50 m stretch in any direction (modified from Hernandez-Aguilar, 2009). We documented nests of all ages, excluding any recent nests that could have been built for daytime resting. Day nests are typically smaller and simpler in construction (Koops et al., 2012), but are more easily identifiably when most of the leaves are still green. We also only surveyed each area once to ensure nests were not recorded multiple times. For data analysis, nests were divided into spatial clusters. Chimpanzees in Bossou typically nest together within 30 m of each-other (Humle, 2003). To accommodate variation between multiple nights, a cluster was defined as a 100 m diameter area with a minimum of 21 documented nests, representing a minimum of three sleep-events for the collective chimpanzee population (N = 7) as a proxy for a habitual nesting location. This was achieved on QGIS (Version 2.18.4), by creating a 50 m buffer zone around each nest and using the 'count points in polygon' function to identify zones with a minimum of 21 nests. The *distance to nearest nest cluster* variable used in the following analyses was computed with the 'distance to nearest hub' function and was defined as the distance from a quadrat datum to the centre of the nearest nest cluster.

WATERCOURSES

Watercourse data were collected once in 2008/2009 by Henry Didier Camara. Streams, and rivers large enough for small amounts of water to be drawn year-round were traced on foot and recorded using the track feature on a hand-held GPS device (Garmin Oregon 700; accuracy = ± 3 m). The *distance to nearest river* variable used in the following analyses was computed in QGIS and was defined as the distance between a quadrat datum to the nearest point along the mapped watercourses.

Data analysis

TOOL SITE SELECTION

Initial inspection of the data revealed that no nut-cracking occurred in quadrats where nut trees were absent. This is consistent with previous literature describing that nut-cracking occurs in close proximity to a nut tree (Carvalho et al., 2008). We, therefore, restricted data analysis to quadrats where an oil palm was present, as the absence of an oil palm would mask the potential effect of the other variables of interest. Additionally, there was very little variation in the number of oil palms in each quadrat with only 15% of oil palm quadrats documented with more than one oil palm – only two of which were quadrats where nut-cracking was present. For this reason, we also did not include the number of oil palms as a predictor. The final dataset had a total of 82 quadrats, 40 of which had traces of nut-cracking activity. We used a binomial generalized linear model (GLM; Zuur *et al.*, 2009a) with a logit link function to investigate, using quadrat data, the effect of five main predictors: raw materials, wild food trees, wild food THV, distance to nearest nest cluster, distance to nearest river, on the presence (1) versus absence (0) of a tool site in a given quadrat. A full description of these variables is summarised in Appendix C1. We began through a process of model

selection where we analysed three additional sub-models to determine whether more restricted variables yielded a better model fit – see Appendix C2, Table C.2. The first sub-model replaced raw materials with a subset of raw materials of size class corresponding to the three most common tool size classes (95% of tools. Size class: 3, 4, 5; Appendix C2). The second sub-model replaced wild food-providing trees with a subset formed only of fruit-providing trees. The third sub-model included raw materials of size class 3-5 and fruit-providing trees. Akaike's Information Criterion for small sample sizes (AICc) was used to compare models (Burnham & Anderson, 2004), whereby the model with the lowest AICc was selected as the final model.

TOOL SITE USE

We investigated whether the hypothesized ecological variables (i.e., nut availability, raw materials, food trees, distance to nearest nest cluster, and distance to nearest river) influenced the frequency with which a nut-cracking site was used. From a total of 361 monitoring observations, only 35 cases of recent nut-cracking events were identified for 17 out of the 25 monitored nut-cracking sites, where nut-cracking occurred between 1 and 4 times. Because of single (N = 1) sample sizes for 2 and 4 events, frequency of activity was recoded as "Low" (≤ 2 events; N = 10) and "High" (> 2 events; N = 7). The small sample size (N = 17) was deemed too small to justify a GL(M)M, therefore we only discuss inferential statistics for this question using two-sample t-tests (or Mann-Whitney U tests when assumptions of normality were not met).

TOOL SITE INACTIVITY

We used a binomial GLM with 'logit' link to investigate the effect of mean nut availability, raw materials, and food trees, on tool-site inactivity. The response variable included nut-cracking sites that were classified as active (response = 0; N = 24) with those classified as inactive (response = 1; N = 16). The final dataset included 40 tool sites. Akin to the model for tool site selection, we also performed model selection by running four additional sub-models with raw materials of size class 3-5, tools, and fruit tree subsets (Appendix C4, Table C.6). The model with the lowest AICc was then chosen as the final model.

GENERAL CONSIDERATIONS

All analyses were processed in R Studio (version 1.1.383; R Studio Team, 2016), using R (version 4.1.0; R Core Team, 2021). Data exploration for each GLM, following the protocol described in Zuur, Ieno & Elphick (2010), did not raise any concerns. Collinearity among the explanatory variables was assessed by calculating the Variance inflation factors (VIF) using the function 'vif' of the car package (J. Fox & Weisberg, 2011). None of the models indicated any multicollinearity issues (Maximum VIF = 1.39, Quinn and Keough, 2002). To assess the significance of the full models and sub-models, we ran likelihood ratio tests (LRT) using the 'anova' function which compared each model to a corresponding null model from which all fixed effects were excluded (Dobson, 2002). The AICc for model selection was calculated using the 'MuMIn' package (Bartón, 2020). We tested the significance of main effects for each model by systematically dropping them one at a time and comparing the resulting model with the full model using the 'drop1' function (Dobson, 2002). P-values for the individual effects were based on the LRT results from the 'drop1' function. Model assumptions were verified by plotting residuals versus fitted values and versus each

covariate in the model (Zuur and Ieno, 2016). Influential observations were assessed by calculating and plotting the Cook's distance (Smith & Warren, 2019); all values were under the recommended threshold of 1, suggesting no evidence of influential points (J. Fox, 2002; Smith & Warren, 2019).

For tool site use, comparisons between low and high frequency of nut-cracking activity were computed for each of the variables of interest using unpaired two-sample t-tests or the non-parametric equivalent, Wilcoxon rank-sum test (i.e., Mann-Whitney U test). Normality assumptions were assessed using the Shapiro-Wilk test. Threshold for statistical significance was set to $p \leq 0.05$, but we also report trends up to $p \leq 0.07$.

Data availability

The datasets generated during and/or analysed during the current study will be available from the corresponding author on reasonable request. Source code will be made available at https://github.com/katarinawarren/bossou-chimps-analysis [to be replaced with DOI].

Ethical statement

All tool site and ecological data were collected when chimpanzees were absent from the survey locations. Efforts to ensure minimal disturbance of nut-cracking sites included: keeping all tools in their original locations; not removing or cracking nuts; collecting stone samples from existing tool fragments whenever possible. To ensure the safety and health of the chimpanzee community, all members of the research team wore surgical masks and maintained a distance of at least 10 m when observing them. Research was conducted in accordance with all the research requirements of Guinea, and the ethical protocols set out

by The University of Oxford, the Kyoto University Primate Research Institute (KUPRI), and the Institut de Recherche Environmentale de Bossou (IREB).

Results

Tool site selection

The sub-model in which raw materials were replaced by a subset of size class 3-5 was the best fitted model according to the AICc (Appendix C2, Table C.2) and had a clear effect on

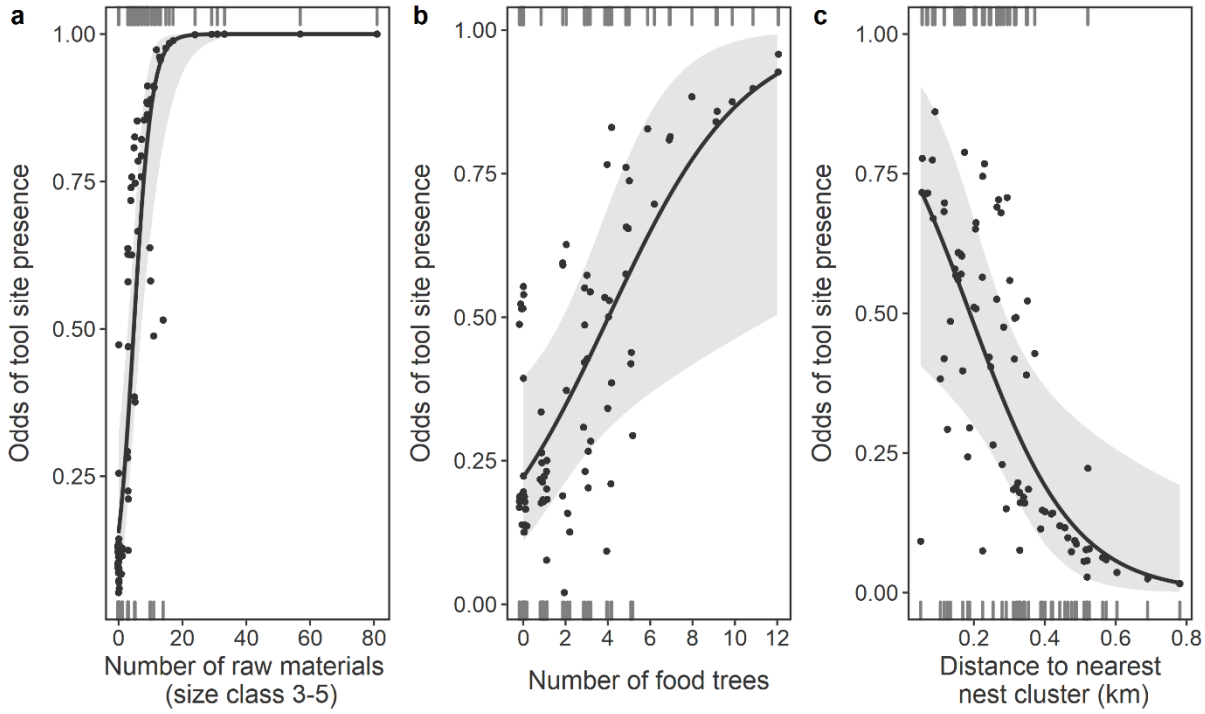


Figure 4.3. Probability of tool site presence in response to: a) Raw materials of size class 3 – 5; b) Trees that are sourced by chimpanzees for food; c) Distance to the nearest nest cluster. Points represent partial residuals (N = 82), and shaded areas indicate a 95% CI. Lower grey bars indicate the distribution of negative residuals, and upper grey bars indicate the distribution of positive residuals.

the probability of a nut-cracking site occurring in a location where at least one oil palm was present (full-null model comparison, LRT: *df* = 5, *deviance* = 56.52, $p < 0.001$). Raw materials had a significant positive effect on tool site prediction, as did food trees, while distance to nest cluster had a significant negative effect (Table 4.1; Figure 4.3). All other fixed effects were non-significant (Table 4.1). The sub-model replacing wild food trees with the fruit trees subset yielded the worst model fit in which fruit trees were not a significant predictor (Table C.4).

Table 4.1. Results of the final GLM investigating potential predictors influencing tool site selection.

Term	Estimate	SE	χ^2	p[a]
Intercept	-1.139	0.472		NI[b]
Raw materials (size class 3-5)	0.358	1.298	21.929	<0.001
Wild food trees	0.313	0.407	5.758	0.016
THV	-0.103	0.383	0.392	0.531
Distance to nearest nest cluster	-0.007	0.485	6.109	0.013
Distance to nearest river	0.005	0.411	1.397	0.237

[a] Results from the likelihood ratio test using the 'drop1' function.
[b] Not indicated because it has a limited interpretation.

Tool site use

Over 15 weeks, only 33 cases of nut-cracking were recorded for 17 out of 25 monitored tool sites. At 10 of the 17 sites we recorded one to two nut-cracking events (low frequency), with the remaining seven showing recent traces between three and four times during the monitoring period (high frequency). In general, the number of tools was significantly higher at nut-cracking sites that registered a higher frequency of nut-cracking activity compared to

low-frequency sites (T-test: p = 0.03; Figure 4.4; Appendix C, Table C.5). Furthermore, distance to nearest nest cluster revealed a negative trend, whereby high frequency sites tended to be nearer to nesting locations (Wilcoxon rank-sum test: p = 0.07). For all other variables of interest (raw materials, mean fruit bunches, wild food trees and distance to nearest river), there were no significant differences between the two categories (p > 0.15; Figure 4.4; Appendix C, Table C.5).

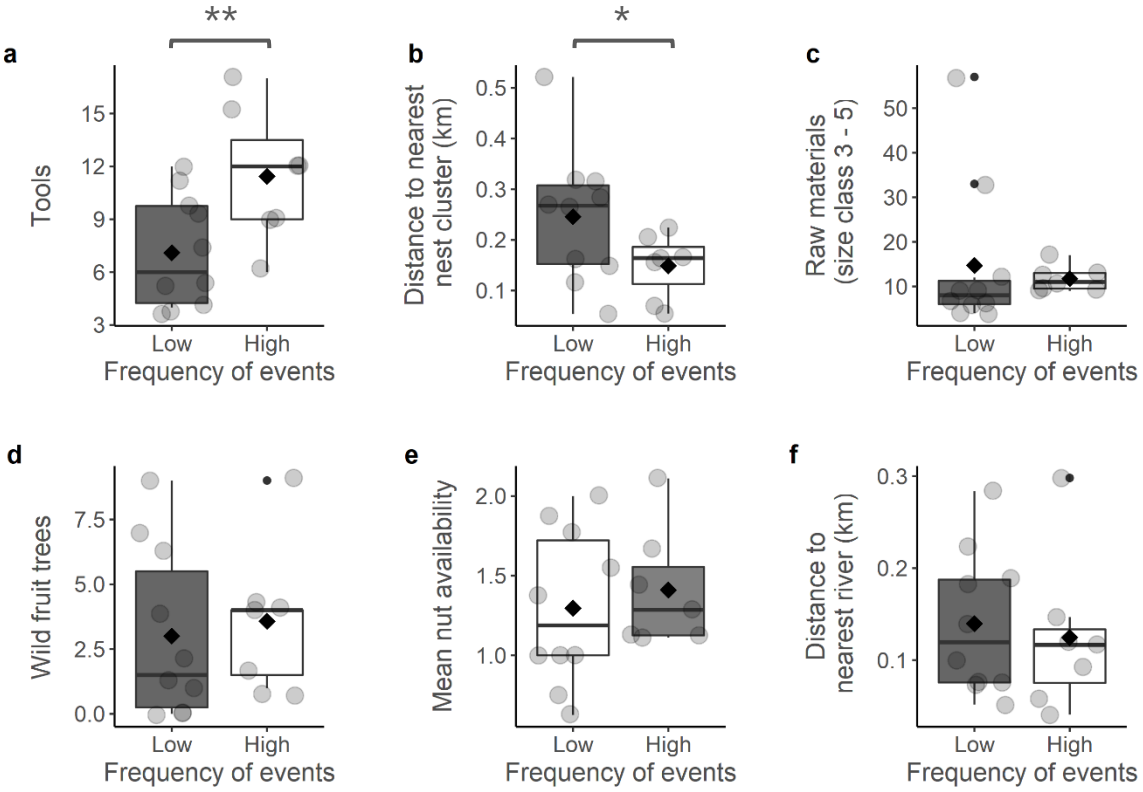


Figure 4.4. Frequency of tool site use relative to: a) Raw materials that have been used as tools; b) Distance to nearest nest cluster (km); c) Raw materials of size class 3 to 5; d) Wild trees that are sourced by chimpanzees for fruit; e) Mean availability of oil palm nuts; f) Distance to nearest river (km). Boxes illustrate the second and third quartiles, with whiskers indicating the first and fourth quartiles. Solid lines represent median values, and points indicate outliers. Grey circles specify individual points, and means are represented by diamonds. ** p < 0.05; * p < 0.07.

Tool site inactivity

Out of the sub-models, the tool subset model yielded the best fit, although the AICc for the tool and fruit trees model was only marginally higher and produced comparable results (Table B.7; Table B.8). Comparison of the tool subset model with the null model was significant (LRT: *df* = 3, *deviance* = 13.20, $p < 0.01$). Overall, we found that lower values of mean nut availability and a lower number of tools were both significant predictors of tool site inactivity, while wild food trees had no effect (Figure 4.5; Table 4.2). However, the data distributions suggest that the model is not very robust (Figure 4.5).

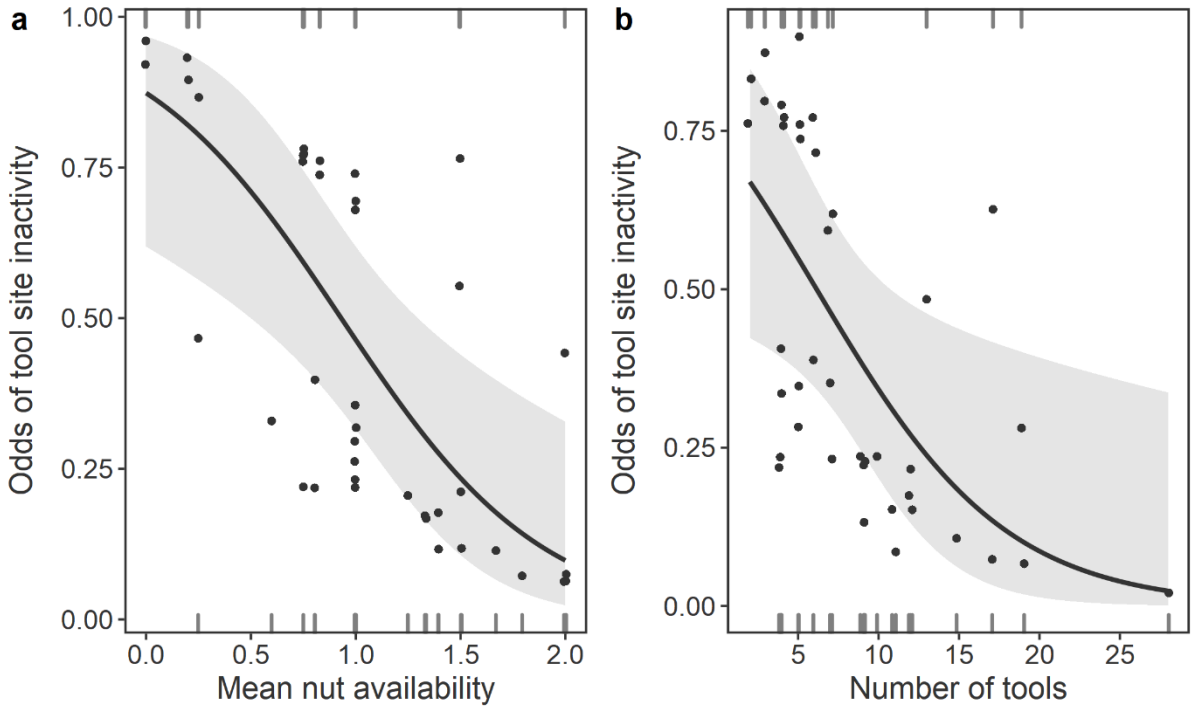


Figure 4.5. Probability of tool site inactivity in response to: a) Mean nut availability; b) Raw materials that have been used as tools. Points represent partial residuals for individual quadrats (N = 24) and shaded areas indicate a 95% CI. Lower grey bars indicate the distribution of negative residuals, and upper grey bars indicate the distribution of positive residuals.

Table 4.2. Results of the final GLM model investigating potential predictors influencing tool site abandonment.

Term	Estimate	SE	χ^2	p[a]
Intercept	2.957	1.263		NI[b]
Mean. nut availability	-2.186	0.851	8.947	0.003
Tools	-0.186	0.093	5.183	0.023
Wild food trees	0.093	0.109	0.752	0.386

[a] Results from the likelihood ratio test using the 'drop1' function.
[b] Not indicated because it has a limited interpretation.

Discussion

Tool site selection

From the initial inspection of the data, it is evident that at least one oil palm, specifically an oil palm in close proximity (within 10 m), is required for nut-cracking to occur in a given location. Our results further show that the abundance of raw materials and food trees as well as proximity to the nearest nest cluster are also important predictors for whether a tool site is established at an oil palm location. This suggests that, in addition to the *ecological pre-requisites* of nut-cracking, i.e., a producing oil palm and raw materials for tools, other perennial resources that form part of the chimpanzee diet (wild food-providing trees), as well as non-food related activities (sleep sites), are influential in the spatial distribution of nut-cracking locations. In contrast, THV had a non-significant effect on whether tool-sites occurred. Food trees are replenishable, often seasonally, and constitute reliable and perennial resources that can be returned to on a seasonal basis. The fact that THV does not bear a clear effect on tool site occurrence suggests that ephemeral food sources are not ecological drivers of tool site selection.

Many primate species have goal-orientated foraging trajectories towards spatially permanent resources and that they likely use mental maps to guide their resource exploitation strategies (Trapanese et al., 2019). Our results provide tentative evidence that the chimpanzees of Bossou may behave in a similar way, whereby nut-cracking activities take place within a foraging strategy that primarily targets perennial food sources (trees), while low-energy foods like THV act as part of an opportunistic strategy during forage-on-the-go.

Distance to nearest nest cluster was a significant predictor in all models, whereby the likelihood of a tool site occurring increased with proximity to nest locations. Research at other field sites has found that nests sites occur in areas of high food availability (Basabose & Yamagiwa, 2002; Carvalho et al., 2015; Furuichi & Hashimoto, 2004; Goodall, 1962; Janmaat et al., 2014). Given that nut-cracking sites are also located in areas with a greater number of food providing trees, and bearing in mind that the Bossou chimpanzees source oil palms for a range of other resources (e.g. fruit, pith, palm heart) and also nest in their crowns (Humle & Matsuzawa, 2001, 2004; Yamakoshi & Sugiyama, 1995), it is possible that the relationship between nut-cracking sites, proximity to nest sites, and food availability, is indicative that these areas are activity hotspots, rich in resources and with habitat characteristics that are suitable for a range of core chimpanzee activities.

Distance to the nearest river was not a significant predictor in any of the models. This contradicts previous research in the nearby forest of Diécké, that identified that nut-cracking locations occurred near waterlines (Carvalho et al., 2007). Equally, it would seem, at least in the case of Bossou, that water is neither the sole or primary provisioner of stones of tools. Given the proximity of the Bossou and Diécké field sites (approx. 50 km) and their similar

climates it is unlikely that this is due to differences in aridity or water availability. However, the chimpanzees of Diécké crack different nut species, *Panda oleosa* and *Coula edulis*, which are absent in Bossou and are likely more water dependent than the oil palm on account of being exclusively rainforest dwelling species (Burkill, 1985; Moupela et al., 2014). Thus, this discrepancy may be connected to the different plant species exploited and their respective ecology and distribution.

Emerging research on the role and importance of water in shaping primate behaviour, adaptations, and landscape use, is providing increasing evidence that there are differences in water-dependence between populations. Rainforest-dwelling apes can usually obtain their daily hydration requirements from the food they consume, and can go several days without drinking (Pontzer et al., 2021). However, for primates that live in predominantly arid habitats water is a critical resource that shapes movement patterns and landscape use (Barton et al., 1992; Lindshield et al., 2021; Pruetz & Herzog, 2017). Fongoli chimpanzees in Senegal usually drink water at least once a day and often spend time near water sources during dry months to stay cool (Lindshield et al., 2021; Pruetz & Bertolani, 2009). Conversely, the Bossou forest is much more humid, with a long-wet season. Its many streams, and small forest area provide a hydrological landscape in which chimpanzees are rarely more than 300 m away from water. Furthermore, during a total of ~500 hours of focal follows, the Bossou chimpanzees were only seen to drink water on eight occasions, suggesting that they can get most of their fluids from the foods they consume, in line with the general trend for non-human apes (Pontzer et al., 2021).

While water was not a significant factor for Bossou, we hypothesize that it could be a major ecological driver regarding the spatial distribution and reuse of tool sites by savannah-living

chimpanzees. The Fongoli chimpanzees do not crack nuts, but they engage in termite-fishing, which is also a spatially discrete technological activity tethered to the location of termite mounds (Bogart & Pruetz, 2008, 2011), much like nut-cracking.

Tool site use

Number of tools was the only variable of interest that differed significantly between sites with low or high frequency of nut-cracking events. This could indicate that the visible traces of nut-cracking found on tools act as visual cues for stimulating further nut-cracking behaviour, and potentially also lead to the transport of further raw materials for tools to these locations. The repeated use of discrete locations through stigmergy – the principle that behavioural traces left in the environment can stimulate the occurrence of further activity – has been suggested to have led to the emergence of persistent places during the Middle Pleistocene (Pope et al., 2006; Pope, 2017; Shaw et al., 2016). Similar hypotheses featuring local and stimulus enhancement in chimpanzees have also been discussed as processes of social learning (e.g. in the development of technical skills; Musgrave et al., 2020; Tennie et al., 2020; Whiten, 2021) as well why some plants are sourced more intensively than others for the manufacture of termite fishing tools (Almeida-Warren et al., 2017). Conversely, it could indicate that chimpanzees prefer sites with material that they are already familiar with. Previous, experimentally-induced research in Bossou has demonstrated that chimpanzees reuse hammer-anvil pairs (tool-sets) more often than others, that there is both group- and individual-level preference for certain tool-sets (Carvalho et al., 2009), and that chimpanzees are selective of the types of materials they use for nut-cracking (Carvalho et al. 2008). Analogous studies on chimpanzee plant technologies, suggests similar patterns in the selection of materials for termite-fishing, ant-dipping, honey gathering and water

extraction (Pascual-Garrido *et al.*, 2012a; Koops *et al.*, 2015b; Almeida-Warren *et al.*, 2017; Lamon *et al.*, 2018; Pascual-Garrido and Almeida-Warren, 2021; See also Chapter 3).

Distance to nearest nest cluster showed a weak yet noteworthy difference, whereby the frequency of nut-cracking events was marginally greater at tool sites that were closer to nest locations. These results mirror those found for tool-site selection and offer further tentative support that active tool sites and their frequency of use is influenced by their distribution relative to current activity hotspots.

The number of wild food and fruit trees was largely the same for all active nut-cracking sites. This suggest that, while food providing trees are good indicators of tool-site selection, they may not be good predictors of site use because the data collected did not capture temporal changes in food availability or frequency of foraging activity. On the other hand, nests are temporary features that, on average, rarely preserve for longer than six months in non-savannah environments (Ihobe, 2005; Kamgang et al., 2020; Zamma & Makelele, 2012). Therefore, they are a better spatial proxy for recent ranging patterns and possibly explains why differences were found for nests, but not for vegetation.

Some consideration needs to be given as to the low number of weekly traces of nut-cracking events recorded per tool site during the 15 weeks of monitoring. This is partially due to the fact that not all active tool sites were monitored, with a further seven traces found through indirect observations at non-monitored sites. Another contributing factor could be that monitoring largely took place during the dry season when primary foods such as wild fruits are in abundance. Our data indicates that a minimum of 40 nut-cracking events took place at natural nut-cracking sites during the 15-week monitoring period, averaging

approximately three events per week, which may be sufficient for the existing chimpanzee population.

Furthermore, out of the nine nut-cracking events witnessed during group follows, six took place at the outdoor laboratory, where nuts and stones were being artificially provisioned for another project. The outdoor laboratory is located very close to an active natural nut-cracking site (~ 80 m) and is at the intersection of several routes which the chimpanzees frequently travel through to access different parts of the forest. As a location that has always experienced a high degree of natural thoroughfare (Matsuzawa, 2011), it likely represents a pre-existing activity hotspot that has been enhanced by the guaranteed encounter of tools and edible nuts. This could explain why a comparatively higher number of nut-cracking events were observed there, similar to patterns recorded by Hockings et al. (2009).

Due to small sample sizes and the limitations of the statistics employed, more data are needed to explore these hypotheses further, including spatial information of food availability across both dry and wet seasons. For future research, it would be important to investigate over a longer timescale whether and how often chimpanzees visited the part of the forest where the tool site is located. This could make use of complementary data from camera traps placed in strategic locations, as full-day focal follows are not permitted in Bossou.

Tool site inactivity

Understanding the contexts of tool site inactivity is an important step in investigating the conditions required for nut-cracking to occur and persist over time in a particular location, and the factors that might lead to their abandonment. Our data suggest that mean nut

availability, used as a proxy for tree productivity, and a high abundance of tools are important in maintaining the active status of a nut-cracking site. However, there are clear exceptions that appear to not fit the model (Figure 4.5), suggesting that other factors that were not considered in the analysis may also be at play.

The Bossou forest suffers from a great deal of human activity, particularly slash-and-burn agriculture, which leads to frequent and rapid changes in the spatial distribution of resources and localized vegetation composition (Hockings, 2011). While oil palms are not cut down during this process and are highly resistant to fire (Yamakoshi, 2011), the changes in the surrounding landscape and the increase in human presence may deter chimpanzees from visiting those areas, especially if they are near the forest boundary. Conversely, cultivated land that contains desirable food items (e.g. banana, mango, papaya) can often attract chimpanzees (Hockings, 2011), and perhaps, under these conditions, the chimpanzees prioritize the prized fruit over nuts that can be found almost anywhere. Site inactivity could also be an artefact of population decline, whereby fewer resources are sufficient to sustain the entire population. Previous literature has suggested that the Bossou forest has a carrying capacity for around 20 chimpanzees (Sugiyama & Fujita, 2011), so it is possible that the current population may no longer need to depend as highly on nuts to supplement their diets. A future longitudinal comparison drawing from historical and contemporary data will help investigate and test this further.

Conclusions

Our results indicate that proximity to a nut tree, an abundance of raw materials and perennial resources, as well as proximity to a nesting site are important ecological parameters for the

establishment of a nut-cracking site in a given location. Distance to nearest nest cluster was also correlated with frequency of nut-cracking, which could potentially indicate that nesting sites are important anchors for ranging and activity patterns. Similarly, tool availability was significantly correlated with tool site use, as well as tool site inactivity, suggesting that familiarity of materials used for tools or the visual cues of tool use could be important in the persistence of nut-cracking activities once a site has been established. While there was no significant difference in nut availability among oil palms at active sites, the odds of tool site inactivity were greater when mean nut availability was low, potentially indicating that a decline in oil palm productivity at nut-cracking sites is driver of site disuse. Together, these results postulate that nut-cracking in Bossou is not only tethered to locations that provide the necessary resources for this activity but is also intimately connected to a broader foraging and behavioural landscape that is mediated by the spatio-temporal availability of primary target resources, such as food-providing trees, as well as the distribution of frequently used nesting locations.

Preliminary comparisons with other sites regarding the importance of ecological features such as the effect of water on tool use and ranging patterns, suggests that the ecology of chimpanzee technology is context-specific and should be examined with this in mind. Further studies investigating the technological landscapes of other chimpanzee populations, as well as the integration of long-term data, will help better understand the effect of different environmental and demographic contexts on the factors driving the spatial distribution and reuse of tool sites, adding further detail to this picture.

While current evidence suggests that early hominin and chimpanzee lithic technologies differ in form and function (Arroyo & de la Torre, 2016; Toth et al., 2006), it is likely they had

similar plant-dominated diets supported by invertebrates and sporadic meat consumption (Panger et al., 2002). Thus, it is plausible that, like chimpanzees, early hominin tool-use operated within behavioural landscapes influenced by localized environmental parameters, where foraging strategies were shaped by the distribution and availability of predictable food sources, the dietary dependence on extractive foraging and the availability of the necessary raw materials, as well as the location of places for sleeping. With the aid of primate archaeological inference, visualizing the spatial distribution of hominin lithic assemblages within this framework will be instrumental in providing crucial insights for reconstructing the patterns of landscape use and resource exploitation.

The present study suggests that the technological landscape of the chimpanzees of Bossou shares affinities with the 'favoured places' model (Schick, 1987; Schick & Toth, 1993), which proposed that hominin tool sites formed at the centre of foraging areas where hominins would process and consume food, rest and socialize, with sites being used more intensively in areas with higher resource abundance. Such 'activity hotspots' would have acted as ecological tethers, shaping early hominin movement and foraging patterns, which, in turn, would have led to the formation and repeated use of tool sites over time. As the most conspicuous evidence of these locations, stone tool assemblages may hold important clues for uncovering behaviours beyond those associated to lithic technology and serve as starting points to search for traces of other activities, such as sleeping, foraging, and insectivory, that are currently extremely rare in the archaeological record. This research draws upon the work of Glynn Isaac (Isaac, 1981b; Isaac et al., 1981; Isaac & Harris, 1980) who pioneered the application of landscape-scale approaches to the study of hominin assemblages, from which the first concrete models of hominin site formation were developed. Further studies will help guide future human origins research and provide an empirical framework for modelling and

testing hypotheses of early hominin behaviour associated to the archaeological record of our earliest ancestors.

Acknowledgements

We are grateful to Vincent Mamy, Lawe Goigbe, Boniface Zogbila, Gouanou Zogbila, Jules Doré, Henry Didider Camara, and Pascal Goumi for support in the field; Dr. Jesse van der Grient and Dr. Alexander Mielke for statistical advice; Dr. Dora Biro and Dr. Bronwyn Tarr for helpful comments and feedback on the original manuscript. We also thank the Direction Nationale de la Recherche Scientifique, the Institut de Recherche Environmentale de Bossou (Guinea), and the Kyoto University Primate Research Institute, for research permissions and logistical support. KAW was funded by the Fundação pela Ciência e Tecnologia (grant number: SFRH/BD/115085/2016), supported by the Programa Operacional Capital Humano (POCH) and the European Union; the Boise Trust Fund (University of Oxford); and the National Geographic Society (grant number: EC-399R-18); TM thanks the Japan Society for the Promotion of Science (JSPS) Leading Graduate Program (U04-PWS), JSPS core-to-core CCSN, and the Ministry of Education, Culture, Sports, Science and Technology of Japan (MEXT)/JSPS-KAKENHI (grant numbers: #07102010, #12002009, #16002001, #20002001, #24000001, #16H06283); SC thanks the Leverhulme Trust (grant number: PLP 2016-114) which supported part of the field equipment and logistics.

Chapter 5

Simulating the formation of chimpanzee technological landscapes

Perspectives from agent-based modelling

Abstract

Archaeological assemblages are the product of a dynamic relationship between humans and their natural environment. As such, understanding how the archaeological record forms can provide important insights into the lifeways of past populations, including how the environment shaped patterns of landscape use and resource exploitation. In human origins research, this is being explored through the observation of living primates and computer simulation. Nevertheless, while our knowledge of the role of stone tool resources (e.g., raw materials) has greatly expanded, comparatively little has been achieved regarding the

broader behavioural and environmental contexts. Here, we use agent-based modelling (ABM) to explore how different ecological scenarios may influence the landscape-scale patterns of stone tool use, with a focus on three key resources: food, water, and shelter. Using chimpanzees as our study species, and nut-cracking as our focal behaviour, we developed an empirically derived, spatially-explicit, ABM that aggregates site-specific ecological data from Bossou (Guinea), species-wide biological and behavioural data, and artificially generated landscapes. We found that the spatial patterning of nut-cracking did not change with variations in the spatial distribution of resources. However, our results also show that variations in wild food distribution and water availability had significant effects on other measures such as daily caloric intake, distance travelled per day, and rates of fission-fusion. This suggests that the dynamic relationship between the environment, behaviour and the formation of technological landscapes may be even more complex than originally thought.

Introduction

One of the biggest challenges faced by archaeologists is deciphering the dynamic relationships between humans and their natural environment from the material record they leave behind. This is particularly evident when dealing with early records from the Plio-Pleistocene, where much of the material evidence is limited to palimpsests of stone tools and incomplete skeletal remains (Reeves, Proffitt, et al., 2021). Indeed, since the discovery of the first Oldowan tools in the 1930's (M. D. Leakey, 1971), archaeologists have developed a multitude of different interpretive models of early hominin site formation and the patterns of behaviour they infer (Isaac, 1989; Plummer, 2004; Schick & Toth, 1993). Yet, while new

archaeological approaches to the study of assemblage composition are providing new, empirically-driven, insights into site formation in the context of raw material selection, sourcing and transport (Braun, Rogers, et al., 2008; Braun, Tactikos, et al., 2008; Douglass et al., 2018; Reeves, Braun, et al., 2021), comparatively little has been achieved regarding the relationships with broader behavioural and ecological contexts that are not directly related to stone tool use, but nonetheless critical to hominin survival (e.g., food, water, and shelter).

In attempts to disentangle this archaeological conundrum, some archaeologists have sought living modern analogues in present-day hunter-gatherers and, more recently, non-human primates for exploring ancient hominin behaviours and patters of landscape use (see Chapter 1 for overview; Carvalho and Beardmore-Herd, 2019; Holdaway and Davies, 2020). The burgeoning field of Primate Archaeology has further paved the way forward regarding the integration of archaeological practices into a non-human primate context, enhancing our understanding of tool manufacture and use, as well as raw material acquisition and transport (Almeida-Warren et al., 2017; Carvalho & Almeida-Warren, 2019; Haslam et al., 2009, 2017; Luncz et al., 2016; Pascual-Garrido & Almeida-Warren, 2021; Proffitt et al., 2016; Also Chapter 3 of this thesis). For instance, studies on the spatial distribution of chimpanzee nesting sites have provided the first glimpse of how such debris-generating activities can produce spatially discrete archaeological assemblages without a 'home-base' or 'central-place' foraging system comprised of an activity-hub in the heart of the home-range (Hernandez-Aguilar, 2009; Sept, 1992). More recently, landscape archaeology approaches to the study of chimpanzee stone tool use are providing insights into the broader behavioural contexts of site formation, revealing that the distribution and use of nut-cracking sites across the chimpanzee home-range is influenced both by the local abundance of food-providing trees as well as the proximity to sleep sites (Chapter 4).

Nevertheless, the study of modern analogues has its own limitations when attempting to reconstruct the formation of archaeological landscapes and the environmental and behavioural processes that shaped them in deep time. The first is that 'living archaeology' occurs in real-time, and therefore it would take several human generations to witness the formation of time-averaged assemblages comparable to the Plio-Pleistocene record (Cegielski & Rogers, 2016). The second is that there is no single primate-habitat system, human or non-human, that can accurately replicate every aspect of a hominin species' paleo-biology as well as its paleo-environment.

Computer simulations, such as agent-based models (ABMs), can serve as artificial laboratories where real-world populations and environments can be recreated, modified, and explored under controlled *in silico* experiments. In essence, ABMs are generative models that facilitate the study of emergent phenomena generated by dynamic systems that operate over spatio-temporal scales and levels of complexity that cannot be captured purely from observations of the natural world (Cegielski & Rogers, 2016; Holdaway & Davies, 2020; Lake, 2015; Lucas, 1979). They can be used for proof-of-concept exercises, theoretical testing, hypothesis formulation and methodological experimentation to guide future data collection (Gilbert, 2019; Romanowska et al., 2019). In archaeology, ABMs have been employed to explore a broad range of topics including social complexity (Alden & Choi, 2007), cultural transmission (Premo, 2015), dispersal patterns (Romanowska, 2015), trade networks (Crabtree et al., 2016), adaptations to environmental change (Wren et al., 2020), and, most pertinently, the formation of archaeological assemblages (Brantingham, 2003; Reeves, Proffitt, et al., 2021).

One of the earliest simulations of hominin site formation was developed by Potts (1984) to examine the energetic efficiency of using multiple sites as raw material repositories for tool manufacture (described by the 'stone cache model'), as compared to using a single location as the main hub of technological activity (proposed by the 'home base model'; Isaac, 1976). More recent agent-based models have explored this topic by testing whether observed archaeological patterns could be generated simply through random patterns of raw material acquisition and discard (Brantingham, 2003; Oestmo et al., 2020). These so-called 'neutral models' do not make any assumptions about behaviours or biological and physiological properties of individuals (e.g., daily energetic requirements; costs of travel) and, therefore, can serve as null hypotheses, but also be used as heuristic benchmarks from which to develop and test more complex behavioural models. However, by their very nature, such models have typically only examined the relationship between a limited number of entities, such as individuals, raw materials, and sources of raw materials.

The potential role of other ecological variables, such as the distribution of resources that are the object of stone too; use, has only recently been explored in a model inspired by chimpanzee nut-cracking in the Taï forest, Côte d'Ivoire (Reeves, Proffitt, et al., 2021). Here, landscape-scale patterns of archaeological site formation are examined in the context of raw-material (stone) and nut tree (*Panda oleosa*) densities where pounding stones for nut-cracking can be acquired through short-distance transport (<200 m), as observed at Taï (Boesch & Boesch, 1984a; Luncz et al., 2016). The model factors in the empirical longevity of pounding tools and *Panda* trees, as well as the fragility of different types of stones, to determine the re-usability of tools and nut-cracking sites over time, with end of life of these resources serving as a driver for sourcing new raw materials or transporting tools to new nut-cracking locations. This model has provided a proof-of-concept that under certain

ecological conditions, long-distance transport is not necessary to generate landscape-scale archaeological patterns akin to early hominin assemblages, and could have resulted from short-distance redistribution of tool material over hundreds to thousands of years (e.g., Wynn & McGrew, 1989). Nevertheless, as with the neutral models, biological considerations are limited, and potential relationships with behaviours outside the technological realm were not explored.

A different approach to studying early hominin landscape-use through ABMs uses foraging decisions as the primary focus of model design (e.g. Griffith et al., 2010; Van Leeuwen, 2019). In these models, the movement of individuals is guided by their energetic (and thermoregulatory) needs as well as the characteristics of the surrounding environment, such as the distribution and availability of food. Crucially, these models harness a wide range of empirical data, from the foraging potential of different real-world micro-habitats and food types to population size and the daily calories needed to survive.

This approach has been used to explore early hominin dietary adaptations, such as meat-eating and the use of digging tools to access tubers, and their impact on nesting patterns as a proxy for the formation of the archaeological record (Griffith et al., 2010). The model landscapes and vegetation were built from paleo-environmental reconstructions and hominins were given some capacity to interact with each-other when encountering a carcass or deciding where to sleep. The study found that in the absence of tubers, hominin activity patterns tended to occur exclusively around channel and flooded zones. Conversely, the introduction of tubers to the hominin diet produced patchier and more dispersed ranging patterns, with both nesting and feeding activities becoming more concentrated in areas of tuber abundance (Griffith et al., 2010).

In a similar vein, van Leeuwen (2019) uses empirical data from modern chimpanzee landscapes to model and explore hominin climatic adaptations and how living in arid landscapes may have affected homeostasis, daily activity patterns and the types of habitats targeted for these activities. In addition to foraging, this model also integrates drinking and resting, bringing together all three physiological requirements for an individual's survival. The model results found that chimpanzee behaviour and habitat use changed when environments shifted from dense forests through forest mosaics to savannah. In general, chimpanzees were able to adapt their activities by increasing their travel, drinking, and feeding, reducing sleeping and resting, and shifting vegetation type usage, such as relying more on forest vegetation types in forest mosaic environments. It was also found that behavioural adaptations to maintain homeostasis were considerably harder to achieve in Savannah landscapes. Nevertheless, this study focuses exclusively on the habitat types that are preferentially used and did not examine the spatial patterning of activities across the landscape.

Here, we combine elements of both approaches to examine landscape-scale patterns of stone tool use within the broader behavioural and ecological contexts and address: How do variations in the spatial distribution of food, water, and shelter affect the formation of lithic assemblages? Using chimpanzees as our study species, and stone tool use for nut-cracking as our focal behaviour, we developed an empirically-derived, spatially-explicit ABM that aggregates site-specific ecological data from Bossou (Guinea; See also Chapter 4 in this thesis) with species-wide biological and behavioural data. We then created an experiment where ecological variables were artificially modified to examine their combinatorial effect on the spatial patterning of chimpanzee nut-cracking activities. In doing so, this model builds upon previous ABMs and provides a complementary approach to archaeological and

actualistic studies, enhancing existing data to enable the controlled exploration of hypothetical scenarios that would otherwise not be possible through traditional approaches.

The model has been designed using the principles of extensibility such that it can be used as a developmental environment for researchers to explore other real-world landscapes, such as hominin paleoenvironments, and introduce other variables and behaviours for consideration. Accessibility was also a central design criterion to enable its employment as an educational tool.

Methods

Overview

The purpose of the model is to explore how ecological and foraging landscapes affect the distribution of tool-using activities by primates within their home range. The environment and behaviour relate to the use of stone tools by wild chimpanzees for nut-cracking, with a focus on the influence of the distribution of food, water and shelter.

The model was developed and implemented in NetLogo 6.2.1 (Wilensky, 1999), with use of the *gis*, *nw*, *rnd*, *dc*, *profiler* and *csv* extensions. The landscape used for empirical validation of the model was based on the Bossou forest, where the chimpanzee home range spans approximately 3.11 km. The resulting model landscape consists of a 26 x 28 grid of one-hectare cells, with 311 cells representing the home range in which entities are active (Figure 5.1). There are five types of entities in the model: habitat patches, and three types of agents

(chimpanzees, groups, and nests). Here, a group refers to an aggregate of chimpanzee-agents that move together as one unit.

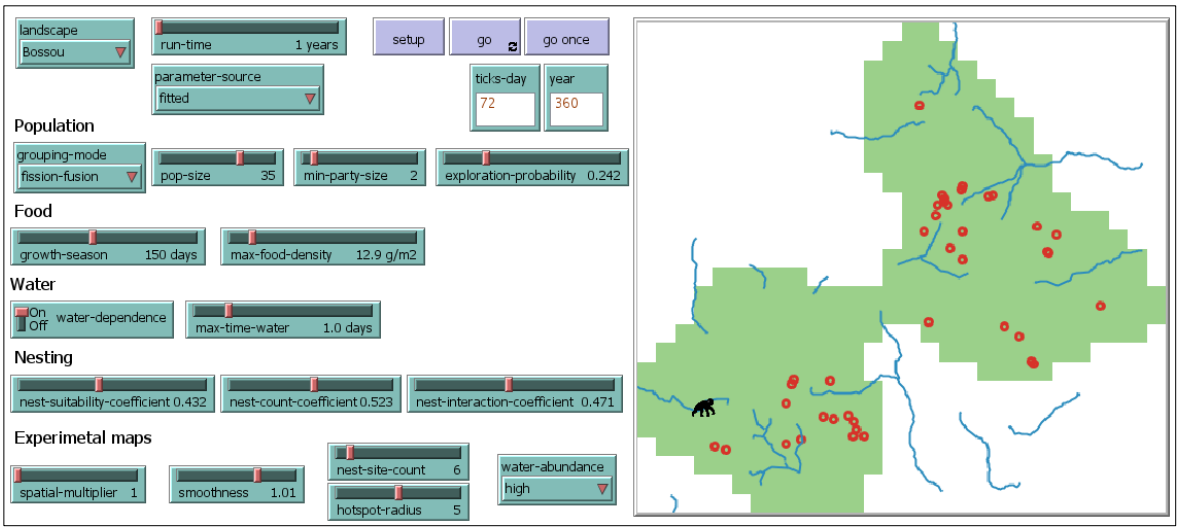


Figure 5.1. NetLogo interface of the empirical model based on the Bossou landscape. Parameter options are displayed on the left. The panel on the right shows the chimpanzee home-range (green), water courses (blue lines), and known nut-cracking sites (red circles).

Each habitat patch corresponds to a cell in the landscape grid and contains information relating to availability of raw materials for tools, nuts, wild food, nests and water. Availability of wild foods follows a seasonal cycle (see **Wild food availability and seasonality.**). Chimpanzee-agents represent individual primates, who log their daily caloric intake from foraging, the daily distance they have travelled, the number of nuts cracked over time, and the frequency permanent water sources (i.e., year-round watercourses) are encountered. Chimpanzees move in groups, as defined by group-agents, and the activity of chimpanzee-agents is determined at the group level. The activity options include travelling, foraging (including seeking, obtaining, processing and ingesting food), cracking nuts, snacking (defined as a short 10-minute bout of foraging), drinking, and making a nest. Group sizes

and member composition can vary over time (See Grouping.), however, the total chimpanzee population remains constant throughout the simulation. Nest-agents represent individual nests that are constructed by each chimpanzee-agent at the end of each day. This type of agent is stationary and impermanent, whereby its chance of durability in the landscape decreases with time since construction (see Nesting. and Nests)

The model has two cycles – a day-cycle that delineates chimpanzee daytime activities between waking and sleeping; and a year-cycle that is used to define the seasonality of wild food availability. A one day-cycle consists of 72 10-minute blocks (time-steps), representing 12-hour day. For simplicity, a year was set to 360 days (12 30-day months), which corresponded to 25920 time-steps. Throughout the day, chimpanzees move in groups between patches to forage and crack nuts in order to acquire their daily caloric targets.

Goals and assumptions

The primary goal of this model is to investigate how chimpanzees forage, use stone tools for extractive foraging, sleep, and travel across the landscape within an optimal foraging framework and how different ecological habitats may influence the spatial distribution of nut-cracking activities (studied here, as a proxy for extractive stone tool use). This version of the model is intended to represent generic wild chimpanzee physiology and behaviour, with the integration of details that are specific to the Bossou fieldsite and/or artificially generated data. The objective of the chimpanzee-agents is to maintain their energy (and hydration) levels throughout the day by foraging for wild foods, cracking and eating nuts, snacking on wild foods, and drinking (Figure 5.2).

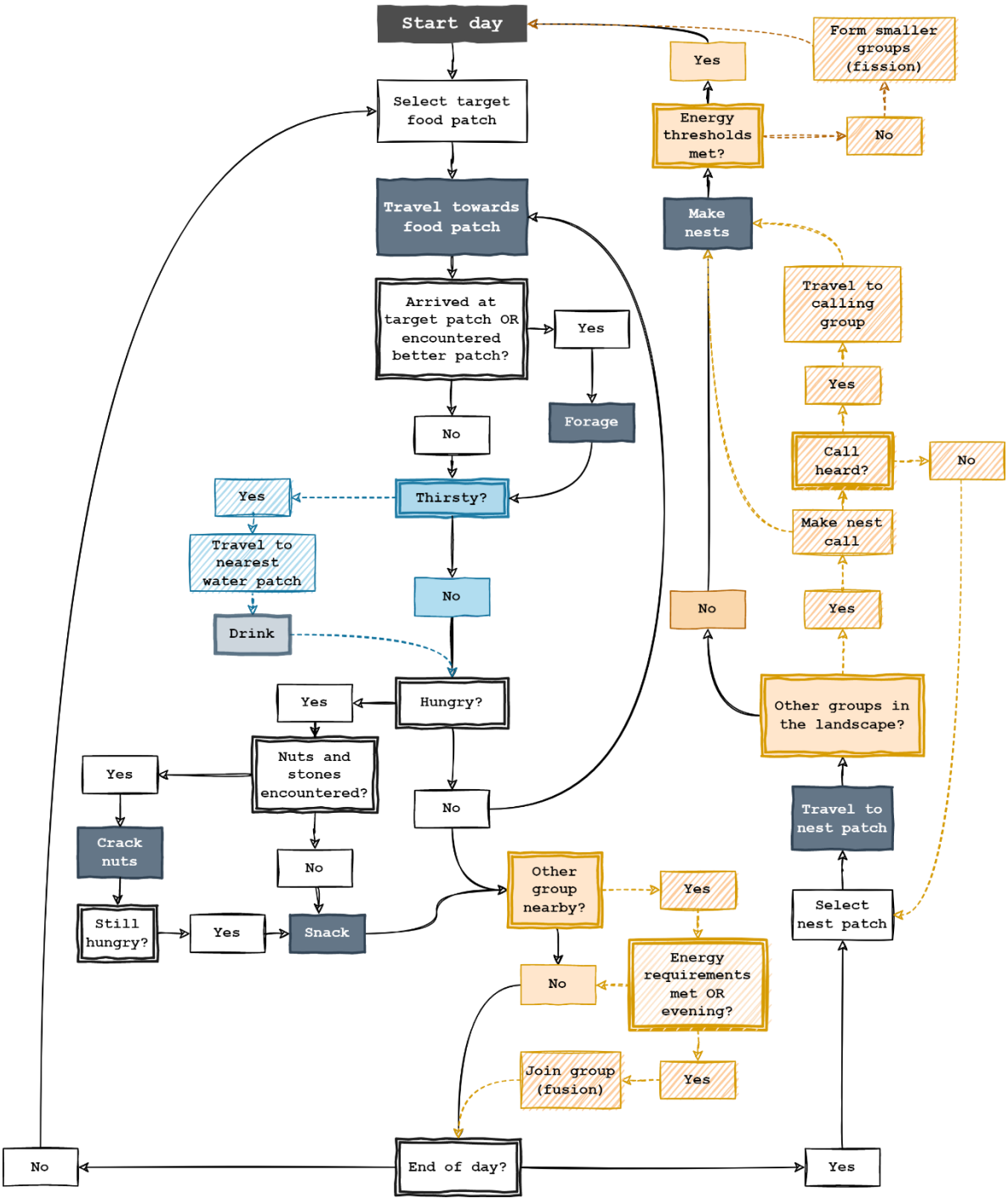


Figure 5.2. Overview of chimpanzee-agent procedures. Dashed arrows and hashed boxes indicate steps that are only available under certain conditions. Light blue procedures are only available only when water-dependence is activated. Yellow procedures are active only when grouping-mode is set to "fission-fusion".

All chimpanzee and group foraging decisions are guided by an optimal foraging strategy with the additional ability of storing knowledge about the food availability and updating it over time. While current field research is demonstrating that chimpanzee foraging decisions and planning are likely more complex (Green, Boruff, & Grueter, 2020; Green, Boruff, Bonnell, et al., 2020; Janmaat et al., 2021; Trapanese et al., 2019), our understanding is still emerging. This model reproduces an intermediate scenario whereby agents can make foraging decisions relative to a pre-defined level of knowledge accuracy. This enables the attribution of some degree of ecological knowledge without making explicit cognitive assumptions about the agents.

In general, the chimpanzee diet is mainly composed of fruit, leaves, and other wild foods that do not require the use of tools (Goodall, 1963; Hockings et al., 2009; Humle, Maisels, et al., 2016; Uwimbabazi et al., 2019). In this model it is assumed that agents will always prefer to consume wild foods before targeting nuts that need to be cracked with tools. Following an optimal foraging strategy, agents will seek to crack nuts when availability of wild foods does not meet their energetic requirements. To integrate elements of on-the-go foraging (Furuichi, 2009; Jang et al., 2019), chimpanzee agents may also snack for a 10-minute period (one time-step) during travel between target food patches, if they are hungry and neither nuts or the materials for cracking them are encountered.

As per wild chimpanzee populations, the default form of social organization is fission-fusion (Goodall, 1986; Humle, Maisels, et al., 2016), whereby a community will split up into smaller parties (fission) and join into larger groups (fusion) throughout the day. There are potentially a wide range of underlying factors driving fission-fusion dynamics (see Lehmann et al., 2007). However, because we are mainly interested in energy regulating activities (i.e., eating,

drinking, sleeping), in this version of the model fission-fusion is solely dictated by the energetic returns of individuals in the group under the assumption that when individuals are unable to meet their energetic requirements (i.e., food availability is low), it is more optimal for individuals to forage in smaller parties (Anderson et al., 2002; Furuichi, 2009; Itani & Suzuki, 1967; Wrangham, 1977). Nevertheless, the model also provides the option to explore alternative grouping patterns by switching to solitary or single-group organisation. When solitary, chimpanzees move entirely independent from each other across the landscape. Under single-group organisation, the entire population remains together throughout the simulation.

There is now a significant body of evidence that supports the idea that chimpanzees select nesting locations based on specific properties pertaining to the environment, topography and tree canopy and that they frequently nest the same locations and even re-use pre-existing nests (e.g., Stewart et al., 2011; Hernandez-Aguilar and Reitan, 2020). Therefore, chimpanzee agents choose a nesting patch based on a nest suitability parameter and the number of nests present in the patch under the assumption that the presence and number of visible nests can act as visual cues to agents about the suitability of a patch for nesting (see Nesting.). Integrating the specific underlying factors of nesting suitability was beyond the scope of this model and research question, but it is something that could be explored in a future version of the model. The nests themselves decay over time, with an increased probability of disappearing as they approach their maximum lifespan. Studies indicate that among some chimpanzee populations parties may come together to feed and nest in the evening, potentially to reduce the predation risk from large nocturnal carnivores such as lions and leopards (Ogawa et al., 2007). This is also considered in the model by inducing

fusion in evening group encounters and allowing nesting parties to make nest vocalizations to other groups present in the landscape.

Wild food availability follows an annual cycle with two distinctive seasons – growth and decay. The start and duration of the seasons is modelled after the empirical data from Bossou (see Parameters and empirical data). No distinction between wild food types is made in this version of the model, and it is assumed that all patches follow a similar seasonal pattern of food availability overall. To accommodate some variation, patches are programmed to reach their maximum and minimum values following a normal distribution based on the empirical data. In addition to these cycles, food consumed by chimpanzees is subtracted from patches in real time.

Oil palms (*Elaeis guineensis*) are productive year-round (Woittiez et al., 2017; Zeven, 1967) and, therefore, nut availability of nuts for nut-cracking is not modelled following seasonal patterns, but rather the empirical probability of a productive oil palm being encountered and the variation in the number of nuts available per productive palm in any given time (see Parameters and empirical data). The availability of raw materials does not change over time, and their probability of encounter in a patch is calculated relative to the highest value or raw materials available in the landscape.

Most chimpanzee populations, especially those living in tropical forests, can achieve their hydration requirements simply through the water contained in the food they consume (Pontzer et al., 2021). This also seems to be the case for Bossou (See Chapter 4). However, in some habitats where the climate is predominantly hot and arid, permanent water sources become a critical resource for chimpanzees to stay cool and hydrated (Lindshield et al.,

2021). Because empirical validation of the model was based on the Bossou landscape, the default setting is for chimpanzee-agents to simply log the number of times they encounter water and the time spent away from water, without adapting their behaviour to satisfy potential hydration needs. However, the role of permanent water sources in chimpanzee landscape use can be explored in alternative landscapes by activating the water-dependence feature which allows users to restrict the amount of time that agents can spend away from water. When this feature is activated, the model assumes that chimpanzees have precise knowledge of the location of permanent free-flowing water sources in their home range as these remain unchangeable throughout the model.

All these concepts and the empirical basis for these assumptions are explained further in the following sections, and a full model description using the standardized Overview, Design concepts, & Details (ODD) protocol as per Grimm et al. (2010) can be found in the Appendix D). The full model code will be made available online at comses.net and github.

Parameters and empirical data

Ecological parameters used to build the model landscape were obtained from ecological surveys conducted at the long-term chimpanzee field site of Bossou (Guinea) by KAW during 2018. Spatial information on the distribution and abundance of wild food trees, oil palms, and raw materials was collected using a transect and quadrat method where 5-m radius quadrats (N = 195) were sampled at 100-m intervals along 1-km transects (~ 18 km total). Here, food trees are defined as trees with a diameter at breast height (DBH) above 10 cm, that provide at least one type of resource that Bossou chimpanzees are known to eat. Data on nest frequency and distribution were collected using forest-wide surveys which targeted

areas that were known nesting locations. When a nest was encountered, all nests within a 50-m radius of the nest were recorded until no more nests were encountered over a 50-m stretch. We also mapped the location of all nut-cracking sites (N = 40) encountered during fieldwork and used GPS-tracks recorded during focal follows of chimpanzees to estimate the home range perimeter. Water availability data were drawn from hydrological data of free-flowing watercourses collected in 2008/2009. Further details on the data collection methods are provided in Chapter 4.

Table 5.1 - Summary of food seasonality and energetic parameter values used in the model.

Parameters	Value	Reference
Peak availability of wild foods	~ 90 day of the year	(Bryson-Morrison et al., 2016; Hockings et al., 2009)
Wild food growth period	~ 150 days	(Bryson-Morrison et al., 2016; Hockings et al., 2009)
Calorific intake per gram of wild food consumed	3 ± 0.6 kcal/g	(Bryson-Morrison et al. 2020)
Probability of nuts at an oil palm	0.7 (range 0 – 1)	This study; (Humle & Matsuzawa, 2004)
Nut availability	~ 75 ± 35 nuts/palm	This study; (Humle & Matsuzawa, 2004)
Nut kernel weight	3.0 g	(R. M. Davies, 2012)
Energetic value of nuts	18.45 kcal/kernel	(Bryson-Morrison et al., 2020)
Nut intake rate	2.02 ± 0.53 nuts/min	(Humle, 2003)

Data for food trees, oil palms, raw materials, nests and home range area were converted into gridded continuous landscapes with a 100 x 100 m resolution using spatial interpolation and rasterization tools in QGIS 3.10.9 (See Appendix D2 for a full description). Hydrology and nut-cracking sites were mapped as line and point data. The resulting rasters and shapefiles

were integrated into NetLogo using the *gis* extension and served as the base-maps for populating the patch variables of the model.

Seasonality and energetic parameters of wild foods and nuts were drawn from published academic literature as well as field data collected in 2018 (Table 5.1). All data derived from Bossou, except for dry kernel weight which was measured using palm kernels sourced from Nigeria (R. M. Davies, 2012).

Table 5.2. Summary of physiological and biological parameter values of ape-agents used in the model.

Parameter	Description	Value	Reference
min-kcal	Minimum calorific intake required per day	1200 kcal*	(Conklin-Brittain et al., 2006; Uwimbabazi et al., 2019)
target-kcal	Target calorific intake per day	2500 kcal*	(Conklin-Brittain et al., 2006; Uwimbabazi et al., 2019)
speed-travel	Speed of terrestrial travel	0.83 m/s	(Hunt 1989, as cited in Pontzer and Wrangham 2004)
travel-kcal	Energetic cost of terrestrial travel	0.085 kcal/m	(Pontzer & Wrangham, 2004)
climb-kcal	Energetic cost of climbing	0.195 kcal/m	(Pontzer & Wrangham, 2004)
food intake rate	Amount of wild food (in dry grams) consumed per minute of feeding	2.58 g/min	(Uwimbabazi et al., 2019)
nut intake rate	Amont of nut kernels consumed per minute of cracking	2.02 ± 0.53 nuts/min	(Humle, 2003)
water intake rate	Number of times water is drunk per day	0.2-1 drink/day	(Almeida-Warren, Matsuzawa, et al., 2021; Lindshield et al., 2021; Wrangham, 1977)
Hearing-range	Average hearing-range of pant-hoots and other long-range acoustic signals	~ 1 km	(Kalan et al., 2016; Piel, 2014)

Physiological and biological parameters of ape-agents including travel speed (m/s), energetic costs of travel (kcal/m), minimum daily energetic requirements (kcal/day), food intake rates (g/min), water intake rates (drink/day), and hearing range (km) of chimpanzees were sourced from published academic literature (Table 5.2). Only data on water intake rates and nut intake rates were available for Bossou.

Nest taphonomy, or the length of time a nest remains detectable, was sourced from data published for other field sites as data for Bossou was unavailable. Nest decay rates are highly site-specific and conditioned by climate, habitat type and plant species used for nesting (Ihobe, 2005; Kamgang et al., 2020; Kouakou et al., 2009; Zamma & Makelele, 2012). For this reason, we only collated values reported for field sites comparable to the Bossou habitat (i.e., forested, non-savannah habitats; Appendix D1, Table D.7). We used the mean (~ 130 days) as the value for nest longevity used to model nest decay.

Procedures and equations

PATCHES

Wild food availability and seasonality. At initialization, imported values of food trees are converted to food availability (g) to enable estimation of calorific returns and a more intuitive interpretation of the data. Because the exact conversion rates between tree abundance and food availability are unknown, this calculation is based on an adjustable upper limit of food density (g/m^2) for the environment. This becomes the value for the patch with the highest number of wild food trees, with the remaining patches scaled accordingly. This is then converted to total food available at patch, in grams, by multiplying by 10,000 m^2 (the total area of a patch).

Food availability and, by consequence, food density at both patch and global levels change over time in response to seasonal plant cycles, as well as food consumed by chimpanzee-agents during the simulation (see Foraging.).

The plant cycles in this model are broadly defined by a growth-period of five months (~150 days; Nov-Mar), and a decay-period of seven months (April-Oct). These, respectively, correspond to dry and wet seasons of Bossou (Bryson-Morrison et al., 2016; Hockings et al., 2009). As per Griffith et al. (2010), we calculate plant growth ($\boldsymbol{P_g}$) for each patch following a logistic function as defined by a modified Verhulst equation (Kingsland, 1985):

$$\boldsymbol{P(t) = \frac{K P_0 e^{rt}}{K + P_0 (e^{rt} - 1)}}$$

, where:

$\boldsymbol{P(t)}$ = proportion of plant food available on day t of the growth cycle

$\boldsymbol{K}$ = theoretical maximum proportion of plant food available

$\boldsymbol{P_0}$ = proportion of plant food available on the first day of the growth season

$\boldsymbol{r}$ = growth-rate

To allow food availability to reach its empirical maximum during the simulation ($\boldsymbol{P}$ = 1), we set $\boldsymbol{K}$ = 1.1. We set $\boldsymbol{P_0}$ = 0.25, according to published data on monthly food availability for Bossou which shows that minimum food availability is approximately 25% of food at peak availability (Bryson-Morrison et al., 2016). The resulting equation is therefore:

$$\boldsymbol{P_g(t) = \frac{1.1}{1 + 3.4\, e^{-rt}}}$$

The growth-rate is computed by solving the above equation for r:

$$\boldsymbol{r = \frac{\ln\left(3.4\,P(t)/(1.1 - P(t))\right)}{t}}$$

Plant decay ($\boldsymbol{P_d}$) is calculated in a similar manner, but with $\boldsymbol{t}$ replaced by -$\boldsymbol{t}$, such that:

$$\boldsymbol{P_d(t) = \frac{1.1}{1 + 0.1\,e^{rt}}}$$

, and decay-rate:

$$\boldsymbol{r = \frac{\ln\left((1.1 - P(t))/(0.1\,P(t))\right)}{t}}$$

Daily growth and decay are calculated as the change relative to the previous day and converted to grams by multiplying by the empirical maximum of wild food at that patch ($\boldsymbol{F_{max}}$):

$$\Delta = \big(\boldsymbol{P(t) - P(t-1)}\big) \times \boldsymbol{F_{max}}$$

Given that the model is set to initialize at the start of the year (January) we calculate initial food values using the plant growth equation ($\boldsymbol{P_g}$), with t computed relative growth season duration (150 days) and time to peak food availability (~ 90 days), which is determined for each patch using a normal distribution:

$$\boldsymbol{t = 150 - (90 + X)}$$

, where $X \sim N[0, 9]$. In Bossou food availability peaks at the end of March (Bryson-Morrison et al., 2016; Hockings et al., 2009).

Water availability. Water availability of patches is determined relative to the distance ($\boldsymbol{d_{min}}$) to the nearest patch that intersects a permanent water source. Patches that intersect a water line are attributed a water availability of 1. Water availability for the remaining patches ($\boldsymbol{W_a}$) is calculated using the following equation:

$$\boldsymbol{W_a = \frac{1}{d_{min} + 0.25}}$$

Unlike food availability, water availability at patches remains fixed throughout the simulation.

CHIMPANZEES

Travel and foraging decisions. At the start of the simulation chimpanzee-agents independently assume that every patch in their home-range has the same amount of wild food available. This is set to the mean value of wild food present in the home range. During the simulation, each chimpanzee-agent registers the current food availability values of the patches it travels across and updates its knowledge of the mean food availability of those patches. When a group initiates a travel-to-food activity, each member individually inspects the mean values they have stored of all the patches in their home-range and suggests a foraging patch using an epsilon-greedy algorithm (Sutton & Barto, 2018). This algorithm is typically employed to set the probability with which an agent explores unknown parameters (exploration) versus the probability of exploiting acquired knowledge (exploitation). In this case, we employ this algorithm to determine how well the chimpanzee-agents know their

environment, whereby the inaccuracy of their choice (i.e., that they will choose a random patch) is determined by an *exploration-probability* between 0-1.

The group then selects one of the suggested patches using a weighted factor ($\boldsymbol{w}$) conditioned by the distance ($\boldsymbol{d}$) to the suggested patch:

$$\boldsymbol{w} = \frac{\mathbf{1}}{\mathbf{1} + \boldsymbol{d}}$$

A weighted decision ensures that chimpanzees have a higher probability of selecting the patches that are closest to them, while allowing some selection of more distant patches to account for uncertainty and unknown parameters. For example, chimpanzees may not always choose the patch with the highest overall food, potentially because: a) they cannot always accurately predict which patches have the most food; and b) they prefer certain food types and/or species that occur in relatively lower value patches, but for which we do not have precise data.

Once a chimpanzee has identified its target patch, it calculates the most direct linear route and moves along the route, one patch at a time. At each intersected patch, chimpanzees may crack nuts (see Nut-cracking.), and snack if they are hungry (see foraging section). When they arrive at the target patch, they forage (see Foraging.).

Additional checks are made by the chimpanzees at each *en route* patch to evaluate whether they have encountered a better foraging patch. If the food available at the current patch is greater than the perceived food available at the target patch, then groups will reset their target foraging location to their current patch.

If the *water-dependence* function is activated, chimpanzees evaluate their hydration levels at the start of each step (see Hydration.). If they are dehydrated, their target patch is set the nearest patch where a permanent water source is located and move directly to that location, forgoing hunger checks and opportunities for nut cracking or snacking. Only after restoring their hydration levels, can they resume foraging activities.

Foraging. To calculate the amount of food consumed by each chimpanzee-agent at a patch, we used a modified type II functional response equation (Spalinger & Thompson Hobbs, 1992). This asymptotic equation produces values that are influenced by the local availability/density of food, while also considering two key conditions: a) there is maximum amount of food that can be consumed once an upper threshold of food density is reached; b) when food density is low, the food consumed is lower in response to the lower encounter-rates and the greater time spent searching for food. Using published estimates for chimpanzee travel rates and food intake rates (see Parameters and empirical data), the grams of food consumed per tick ($\boldsymbol{F_t}$) is calculated as:

$$\boldsymbol{F_t}\,(\boldsymbol{g}) = \frac{\mathbf{500} * \boldsymbol{D_p}}{\mathbf{50} + \mathbf{19.5} * \boldsymbol{D_p}}$$

, where $\boldsymbol{D_p}$ is the food density (g/m^2) in the chimpanzee's current patch. The food consumed is subtracted from the patch and is acquired by the chimpanzees as energy (kcal) using the following formula:

$$\boldsymbol{E_f}\,(\boldsymbol{kcal}) = \boldsymbol{F} \times (\mathbf{3} + \boldsymbol{X})$$

, where $X \sim N[0, 0.6]$. Values are based on the energetic return (kcal/100g) estimated for wild foods consumed by chimpanzees in Bossou (Table 5. 2). The normal distribution ($3 + X$) is employed to mimic the variation in the energetic yield of different food types and species.

Chimpanzees can forage at the same patch over several ticks while it remains more optimal than moving to another patch (i.e., food availability is greater than neighbouring patches; or forest mean). If chimpanzees get hungry while travelling between patches they may *crack-nuts* and/or *snack*, before moving to the next patch towards the destination.

Nut-cracking. If chimpanzees are hungry in between foraging bouts (as defined by the 'foraging' activity), they can obtain additional energy from cracking nuts if nuts and stones are detected. This procedure is designed to reproduce a nut-cracking strategy that is based on both foraging needs (necessity hypothesis; Grund *et al.*, 2019), and the encounter-rate of required resources within an opportunity hypothesis framework (Koops et al., 2013).

Using a three-step probability draw, the chimpanzees pick a random number between zero and one for oil palms, presence of edible kernels, and raw materials. If the value drawn is lower than the respective probability reported for the current patch in all three counts, the chimpanzees initiate nut-cracking activity.

The number of edible nuts available is calculated using the following equation:

$$\boldsymbol{N_{nuts} = 50 \times 1.5 + X},$$

where $X \sim N[0, 0.7]$. Values are estimated from nut availability recorded for oil palms in Bossou (Table 5.2).

Hungry chimpanzees will crack nuts until they are no longer hungry, or nuts are depleted. The resulting calories obtained from nut kernel consumption are added separately to the daily energetic intake record:

$$\boldsymbol{E_{nc}\ (kcal) = N_k \times 18.45},$$

Where N_k is the number of kernels consumed, and 18.45 is the kcal return of an average kernel weighing 3g (Table 5.2).

Snacking. If chimpanzees are hungry in between foraging bouts, but are unable to locate nuts and raw materials, or they are still hungry after nuts have been depleted, they are able to snack. This procedure is identical to *foraging*, except for a time restriction of 10 minutes (1 time-step).

Hydration. Throughout the simulation, chimpanzees check every patch visited for the presence of a permanent water source. If a permanent water source is encountered, *time-from-water* is set to zero; while if water has not been encountered within that time-step *time-from-water* increases by one unit.

If the *water-dependence* option is activated and *time-from-water* for a member of the group reaches the maximum threshold set by the corresponding initializing parameter (max-time-water; Table 5.1), then the entire group travels to the nearest water source to restore their hydration levels (as described in **Travel and foraging decisions.**).

Grouping. *Fission-fusion* is the default setting of the model and is conditioned by the number of chimpanzees in a nesting group that are satiated (i.e., reached the minimum

calorific threshold) at the end of the day (see Goals and assumptions section). If more than half the chimpanzees did not reach the targets, then the group will fission into smaller groups with a maximum party size set at the number of satiated chimpanzees, or the parameter value for min-party-size, whichever is largest.

Throughout the day, if groups are in the same neighbourhood (within two patches of each-other), they will fusion if one of the following conditions is met: 1) less than 50% of chimpanzees in those groups are hungry; 2) there are under 2 hours (12 time-steps) left until the end of the day. The second condition enables groups to get together into a larger party in anticipation of their nesting time.

Although not explored in the present study, we also provide two additional grouping options – *solitary* and *one-group*. When *solitary*, chimpanzees move entirely independent from each other across the landscape. When *one-group* chimpanzees move as a single unit and travel decisions are made collectively according to the status of the entire population.

Nesting. At the end of every day-cycle (71 time-steps), the chimpanzee-groups select the best nesting patch within the distance that can be covered during one time-step (*travel-per-tick*) to construct their sleep nest. This selection is based on a nest score ($\boldsymbol{\chi_n}$) calculated from the suitability of the patch for nesting ($\boldsymbol{S_n}$), the number of nests present in the patch ($\boldsymbol{N_n}$), and the relative importance ($\boldsymbol{C}$) given to each of the values and their interaction:

$$\boldsymbol{\chi_n} = (\boldsymbol{C_s} \times \boldsymbol{S_n}) + (\boldsymbol{C_N} \times \boldsymbol{N_n}) + (\boldsymbol{C_i} \times \boldsymbol{S_n} \times \boldsymbol{N_n})$$

, where:

$\boldsymbol{C_s}$= nest-suitability-coefficient

$\boldsymbol{C_n}$= nest-count-coefficient

$\boldsymbol{C_i}$= nest-interaction-coefficient

After the first group has nested, it makes a nesting call to remaining groups in the environment. Each of these groups will check if they hear the call according to a probability draw based on their distance to the nesting group ($\boldsymbol{D_{n \cdot g}}$) and a maximum hearing range of 10 patches (≈ 1 km; Table 5.2):

$$\boldsymbol{r < 1 - \left(\frac{D_{n \cdot g}}{10}\right)}$$

, where $\boldsymbol{r \in [0, 1]}$. If the condition is met, the group will move to the nesting group's location and form a nesting party with that group. Each group that did not hear the call will initiate a nesting procedure and make a nesting call to remaining un-nested groups until all groups have nested.

NESTS

Nest-decay. To reproduce effects of nest decay, we employ a condition where the probability of nest disappearance increases as nest age ($\boldsymbol{A_n}$) approaches 130 days (the average nest longevity; see Table D.7):

$$\boldsymbol{r < \frac{A_n + 1}{130}}$$

, where $\boldsymbol{r \in [0, 1]}$ and is randomly drawn. If the condition is met, then the nest is removed from the environment.

Analyses

MODEL CHECKS

The model was built incrementally by KAW, with frequent checks of the code following new additions or updates to pre-existing syntax. A thorough code-review was performed by NP at several key stages of the model building process to check for syntax errors, logic errors, and to improve running speed whenever applicable.

EMPIRICAL VALIDATION

While the model was built on current empirical and theoretical knowledge about the chimpanzees of Bossou as well as chimpanzees more broadly, some variables – such as the density of wild-foods per m^2 (*max-food-density*) or the accuracy chimpanzee ecological knowledge (*exploration-probability*) – could not be determined due to the lack of scientific knowledge on those subjects. Empirical validation enables the fine-tuning of these unknown parameters as well as the assessment of the accuracy of our model relative to the real-world Bossou environment that we are attempting to reproduce.

This process involves testing the model outputs against the empirical data (Cegielski & Rogers, 2016), and involves three steps: parameter estimation, sensitivity analysis, and model verification (J.-S. Lee et al., 2015; ten Broeke et al., 2016; Thiele et al., 2014). The purpose of parameter estimation is to find the parameter settings that produce model outputs that most closely match the empirical observations (Thiele et al., 2014). The goal of sensitivity analysis is to identify which variables and interactions have the greatest influence on the model and quantify how robust the model outputs are over multiple simulations (ten Broeke et al., 2016). Finally, following any necessary revisions and updates, we proceed to model

verification which involves running the model a final time to confirm that it produces the expected outputs.

All simulations performed during empirical validation were run in NetLogo using the BehaviourSpace tool. Data outputs were processed and analysed in R 4.1.2 using several specialized code packages. All model code and R-script necessary for replication of the present study are accessible at: https://github.com/katarinawarren/Bossou-ABM. Threshold for statistical significance was set at $p \leq 0.05$.

Parameter calibration. There were six unknown parameters in the model that required calibration: minimum party size; maximum food density; exploration probability; and the coefficients for nest suitability, nest count and nest interaction. The remaining parameters (i.e., population size, grouping mode, and growth season) were set to the known values for Bossou (Table 5.3).

Table 5.3. Fixed parameters used for empirical validation.

Parameter	Description	Value
Landscape	Chooser to set which model version to run	Bossou
Pop-size	The size of the population	7
Grouping-mode	Chooser to set population-level movement	Fission-fusion
Growth-season	The duration of the wild food growth season	150 days
Water-dependence	Switch to determine if movement is conditioned by water availability and distribution	Off

Parameter calibration was performed using a reference table approach (Carrella, 2021). This involved running 1500 iterations of the model where a value for each unknown parameter

was randomly sampled every time (see Table 5.4). Each iteration was run for a simulation period of 10 years (259200 time-steps), during which the information on daily caloric intake, daily travel distance, caloric efficiency (calculated as caloric intake / caloric expenditure), daily rates of fission-fusion, monthly food availability, location and frequency of nut-cracking activities, and location and frequency of nests was recorded.

Table 5.4. Unknown parameters and ranges used for parameter calibration.

Parameter	Description	Value range for random selection
Min-party-size	The minimum size of a party (group)	1-3 individuals
Exploration-probability	The probability of a chimpanzee-agent selecting a random foraging patch	0.000-1.000
Max-food-density	Sets the upper limit of food density for the environment	1-25 g/m2
Nest-suitability-coefficient	Relative importance given to the nest-suitability when choosing a nest patch	0.000-1.000
Nest-count-coefficient	Relative importance given to the number of visible nests when choosing a nest patch	0.000-1.000
Nest-interaction-coefficient	Relative importance given to the interaction between nest-suitability and the number of visible when choosing a nest patch	0.000-1.000

The outputs for each run were compared to the respective empirical data using Kolmogorov–Smirnov (KS) tests for discrete data (e.g., daily energetic intake, daily travel distances), Fréchet distance and dynamic time warping (dtw) for patterns of monthly food availability, and Pearson product-moment correlation for assessing spatial correlation

between simulated and empirical nut-cracking activity. To facilitate comparison of monthly food availability between datasets, values were z-transformed to a mean of 0 and standard deviation of 1 prior to analysis. The empirical and simulated rasters were generated by creating gaussian smoothed heatmaps of the corresponding nut-cracking event spatial data.

The results from all runs were then collated into a single meta-model which was analysed using a broad spectrum of statistical methods, including approximate Bayesian computation (ABC), linear models, generalized additive models (GAM), and random forests. We used the R package 'freelunch' to implement these analyses and evaluate their performance through cross-validation (Carrella, 2021). This is a necessary step as there is no single method that can provide the best estimates across models or even across parameters within the same model (Carrella, 2021). The method that most closely predicted the real-world observations for each input parameter was then selected to estimate the parameter value that would be used in the final model.

Sensitivity analysis. To investigate the effects of unknown parameters on the overall model outputs, we also performed a global sensitivity analysis where parameter values were varied simultaneously over their entire range (Thiele et al., 2014). The model settings and simulation followed a similar procedure to parameter calibration, with the parameter values being randomly varied and scrutinized. Parameter effects were evaluated using a regression-based method (ten Broeke et al., 2016; Thiele et al., 2014). In this study, we ran a multiple linear regression with 2-way interactions for each of the model outputs: daily caloric intake, daily travel distance, caloric efficiency, daily rates of fission-fusion.

Model verification. In the final step of empirical validation, the model was run again using the combined parameter values that best fit the empirical observations together with the default settings (Table 5.3) to verify the accuracy and consistency of the model outputs. This model was run repeatedly with the same fixed parameter values over 100 iterations with a duration of 10 years (259200 time-steps). Aggregated simulation outputs were assessed according to empirical observations as follows: Kolmogorov–Smirnov (KS) tests and t-tests to compare distributions and means of daily energetic intake, daily travel distances, and energetic efficiency; and Pearson's product-moment correlation coefficients for determining the model's accuracy at reproducing similar patterns of monthly food availability as well as spatial distribution of nut-cracking activities (Boero et al., 2010; J.-S. Lee et al., 2015). As with parameter estimation, this was achieved by comparing raster renderings of the spatial data, and z-transformed values of food availability.

EXPERIMENTAL DESIGN

To investigate how changes in water, food, and shelter availability may affect chimpanzee nut-cracking behaviour, we setup a new experiment where these variables could be modified and tested, while maintaining the original values for abundance of *raw materials* and *oil palms* that were sourced from the empirical Bossou data. To enable a more general view of chimpanzee populations as a whole, we increased the population size to 35 individuals, and increased the world dimensions to a 78 x 84 1-ha grid to approximate the average community (~ 35 members; Humle et al., 2016) and home-range size (~ 30 km^2; Humle et al., 2016; Lindshield et al., 2021) recorded for wild chimpanzees. Using these new dimensions, we generated artificial landscapes for permanent water sources, wild food trees, and nest suitability with parameters set to reflect low, medium, and high conditions.

Landscape algorithms. Artificial landscapes for food trees were generated using a diamond-square algorithm (a type of stochastic fractal algorithm). This algorithm produces realistic looking continuous resource landscapes with different levels of spatial heterogeneity (i.e., the degree at which low and high values are spatially segregated). In this model, this is determined by the *smoothness* parameter, where higher values correspond to greater environmental heterogeneity (see Appendix D, Figure D3). In effect this emulates landscapes with different degrees of resource patchiness that reflect the ecological diversity of chimpanzee habitats (Meijaard, 2016). To ensure the total number of wild food trees (and therefore food availability) in the home-range remained constant throughout all experiment runs, values were rescaled relative to the total of 5,184 – the amount that would be expected for a Bossou-like forest of these dimensions.

Wild chimpanzees often make nests in the same locations, resulting in the formation of nest clusters and the emergence of spatial hotspots. To reflect this pattern, nest-suitability was modelled using a hotspot-diffusion method whereby nest hotspots were allocated randomly across the landscape and the value for each patch in the home-range was calculated as a function of distance to the nearest hotspot. The number of hotspots is set by the *nest-site-count* parameter.

Maps of permanent water courses were created in QGIS using real-world digital elevation models (DEM) of the Bossou region. This data was sourced from the freely available Advanced Spaceborne Thermal Emission and Reflection Radiometer (ASTER) Global DEM (GDEM) 30-metre resolution dataset (NASA/METI/AIST/Japan Spacesystems and U.S./Japan ASTER Science Team, 2019). We used the adjustable variable for minimum flow accumulation (FA) – the minimum downslope surface area needed to produce a free-flowing body of water

– to generate maps with low (FA = 1000), medium (FA = 250), and high (FA = 50) water availability (See Appendix D2.2. for details). A full description of the procedures and algorithms is presented in the ODD (Appendix D1), and examples of the experimental landscapes can be found in Appendix D3.

Parameter settings. For each of the artificial landscapes we selected three values to represent low, medium, and high conditions. This would enable a broad sense of behavioural variation over large scales of ecological variation, without being too computationally intensive. The remaining parameters were fixed. These were set to the values used in the validated empirical model, except for population size which was increased to 35 (see above). All settings are listed in Table 5.5.

Table 5.5. Parameter settings used in the experimental setup.

Parameter	Value(s)
Landscape	Experimental
Pop-size	35
Min-party-size	2
Grouping-mode	Fission-fusion
Exploration probability	0.242
Growth-season	150 days
Max-food-density	12.9
Max-time-water	1 day
Water-dependence	On
Nest-suitability-coefficient	0.432
Nest-count-coefficient	0.523
Nest-interaction-coefficient	0.471
Spatial-multiplier	3
Smoothness	0.01 (low); 0.5 (medium); 1.01 (high)
Nest-site-count	6 (low); 18 (medium); 30 (high)
Hotspot-radius	9 patches
Water-abundance	Low; Medium; High

Simulation details and statistics. The experiment was run 100 times for each combination of low-medium-high inputs (i.e., clustering of wild food availability; water

availability; number nest sites). Each iteration ran for a duration of 10 years. To minimize the effects of spatial relationships emerging by chance, new landscapes for food-trees and nest-suitability were generated at the start of every run. The main output of interest was the spatial patterning and frequency of nut-cracking activity. To measure the spatial autocorrelation of nut-cracking events we use the global Moran's I index, which takes into consideration both the location and frequency of activity (Goodchild, 1986). Analyses were also conducted for: daily caloric intake, daily travel distance, and daily rates of fission-fusion, to check potential changes in overall patterns of behaviour. Each of these outputs were analysed using a linear regression with food distribution (*smoothness*), level of water availability, number of nest sites, and the 2-way interactions between them as explanatory variables.

Results

Parameter calibration

The performance of the eight methods used for parameter calibration was generally high, ranging 0.867-1.000. However, the random forest algorithms consistently ranked the best overall, with performance values > 0.950 for all parameters (Appendix D4.1). For minimum party size, two other methods performed equally well, also yielding the same estimated value (Appendix D4.1). The values predicted by the selected models were used to set the parameter values that would be used for model validation (Table 5.6).

Table 5.6. Parameter calibration results, including mean parameter values, estimation method used, and performance outputs.

Parameter	Mean	Method	Performance
Min-party-size	2	Quantile random forest	1
Exploration probability	0.242	Quantile random forest	0.960
Max-food-density	12.9	Quantile random forest	0.986
Nest-suitability-coefficient	0.432	Random forest	0.965
Nest-count-coefficient	0.523	Random forest	0.972
Nest-interaction-coefficient	0.471	Random forest	0.960

Sensitivity analysis

Global sensitivity analysis showed that the randomized parameters had different effects on the model outputs (Figures 5.3 – 5.5). All regressions produced good fits overall (Table 5.7), with variations in *max-food-density* and *exploration-probability* predicting the greatest changes in foraging- and travel-related measures. Daily caloric intake was greater when *max-food-density* ($ß$ = 741, p < 0.001) and, to a lesser extent, *exploration-probability* ($ß$ = 73, p < 0.001; Table D.17) were higher (Figure 5.3). *Max-food-density* maintained a positive effect on caloric efficiency ($ß$ = 8.0, p < 0.001), while *exploration-probability* yielded a negative effect ($ß$ = -1.1, p < 0.001; Table D.18). These patterns were inverted for distance travelled per day (*max-food-density*: $ß$ = -0.1, p < 0.001; *exploration probability*: $ß$ = 0.08, p < 0.002; Figure 5.4; Table D.19).

Table 5.7. Summary of overall multiple regression results assessing the sensitivity of model outputs to parameter variations.

Measure	R^2	AIC	Residual SE[a]
Kcal/day	0.922	20,432	218
Kcal-efficiency	0.891	7,413	2.84
Km/day	0.661	-2,789	0.095
Prop-fusion	0.865	2,936	0.090

[a] SE = standard error

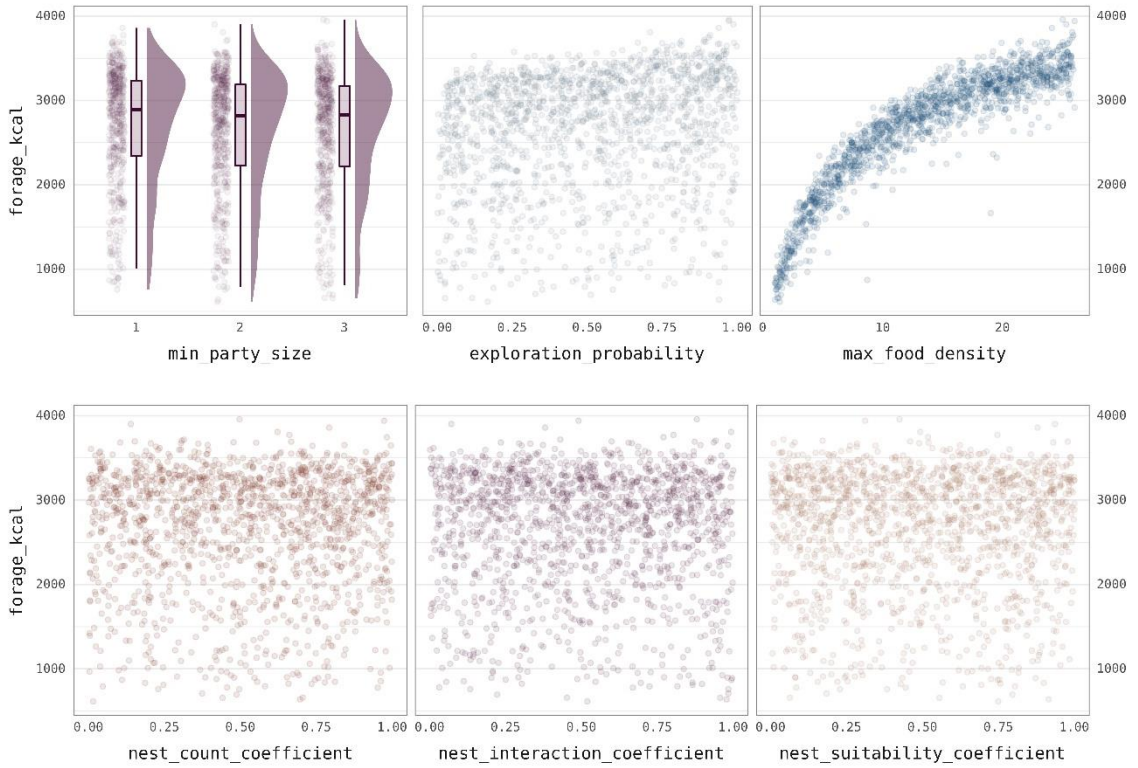


Figure 5.3. Results of the sensitivity analysis for daily caloric intake (kcal).

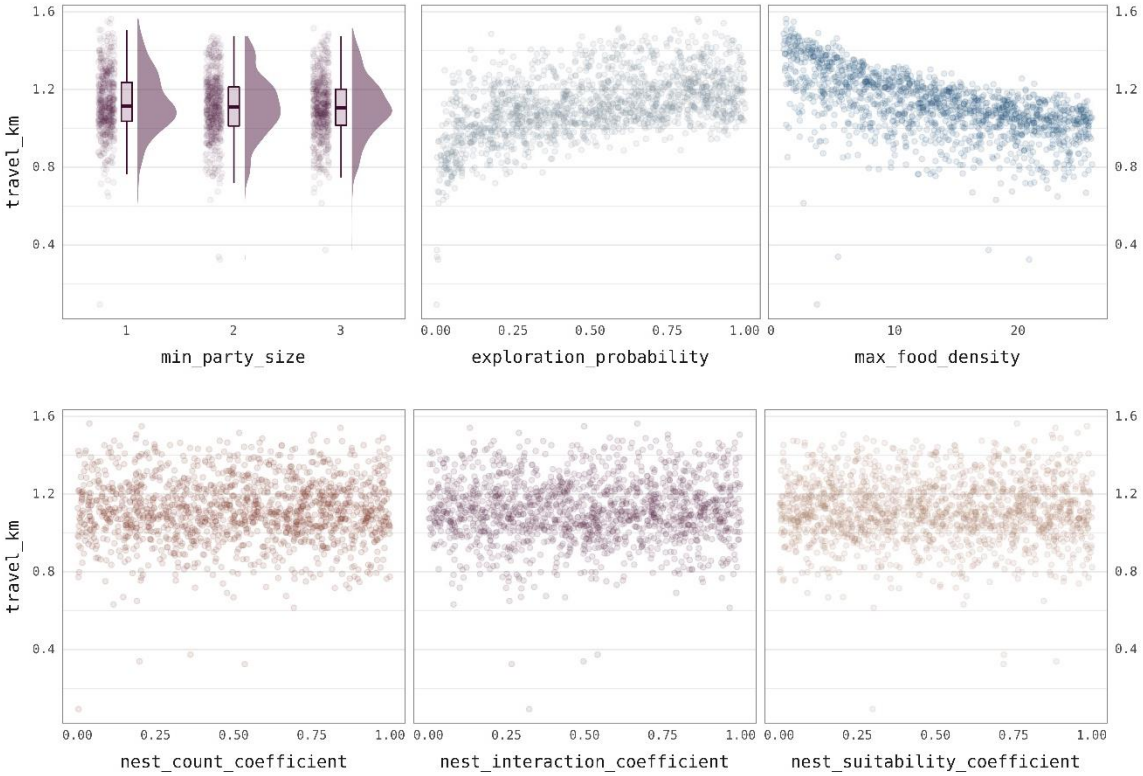


Figure 5.4. Results of the sensitivity analysis for daily distance travelled (km).

Max-food-density had a significant positive effect on the proportion of time the chimpanzee population stayed together in a single unit (β = 0.21, p < 0.001), with *min-party-size* also showing a significant, yet weaker positive effect (β = 0.06, p < 0.001; Figure 5.5). This was also the case for *exploration-probability* (β = -0.04, p < 0.001) and the interaction between *min_party_size* and *max_food_density* (β = -0.05, p < 0.001), which showed a small but significant negative effect. Significant interactions were detected in all models, but their effects were relatively small and therefore will not be discussed further (Appendix D4.2). No significant effects were reported for the nest-related variables by any of the models (Appendix D4.2). < 0.002; Figure 5.4; Table D.19).

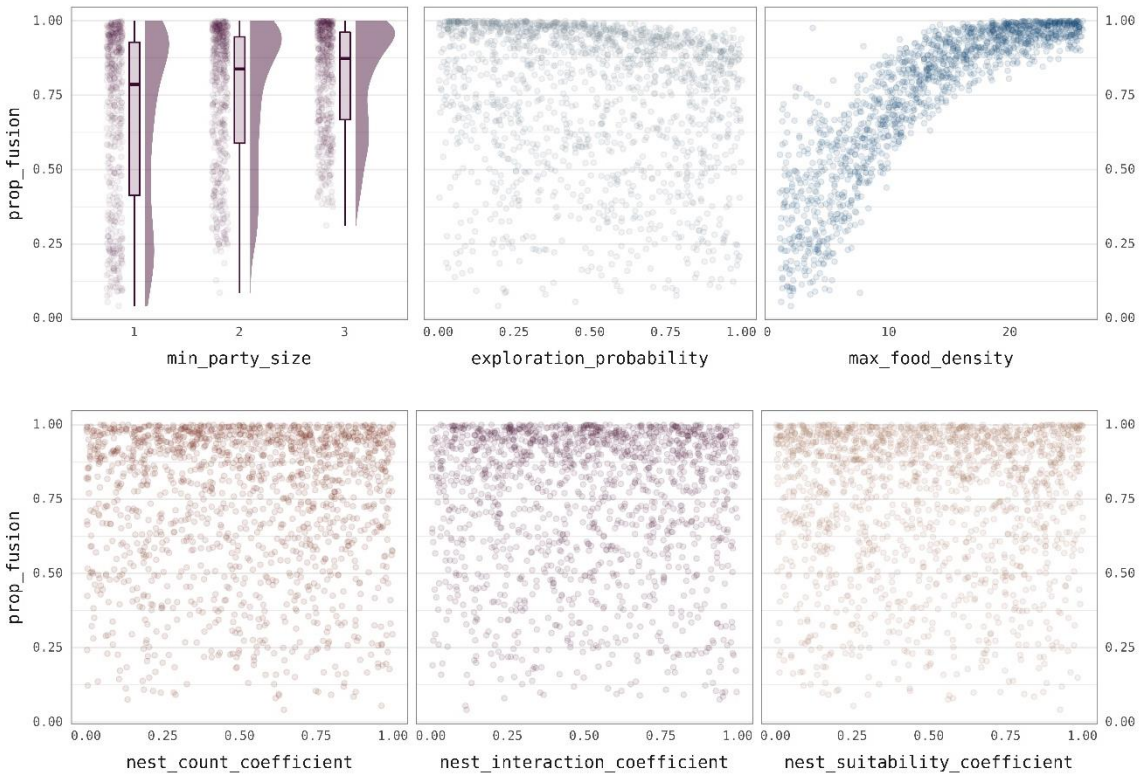


Figure 5.5. Results of the sensitivity analysis for the proportion of time the group remained as one single unit.

Model Verification

The final model, using the calibrated parameters, produced daily caloric intake values that did not differ significantly from the empirical mean or data distribution, although the simulated output had a wider range (Figure 5.6a; Table 5.8). Conversely, the average distance travelled per day was significantly lower than the real-world observations, with the respective distributions also differing significantly (Figure 5.6b; Table 5.8).

Table 5.8. Statistical results of the comparisons between empirical data and simulation outputs. Statistic + sd and p-value + sd, indicate the mean and standard deviation of the test statistic and p-value, respectively.

Measure	Method[a]	Statistic ± sd	p-value ± sd
kcal/day	KS test	0.228 ± 0.081	0.629 ± 0.338
	WT	-0.068 ± 0.291	0.796 ± 0.096
km/day	KS test	0.781 ± 0.054	<0.001
	WT	-11.851 + 0.458	<0.001
Spatial distribution of nut-cracking activities	PC	0.321 ± 0.222	0.004 ± 0.009
Monthly food availability	PC	0.727 ± 0.006	0.007 ± 0.001

[a] KS = Komilgorov-Smirnov; WT = Welch's two-sample t-test; PC = Pearson product-moment correlation

The spatial distribution of simulated nut-cracking events showed a significant moderate correlation with its empirical counterpart (Figure 5.7; Table 5.8), generally producing patterns that were larger and less dispersed than the observations recorded for Bossou. Regarding patterns of monthly food availability, there was a high correlation between simulated and empirical values, with only four months deviating by more than 0.5 units (Figure 5.8; Table 5.8). With the exception of nut-cracking, standard deviations for all

statistical outputs were low. This demonstrates that there was minimal variation between the 100 model runs, indicating a good level of model robusticity.

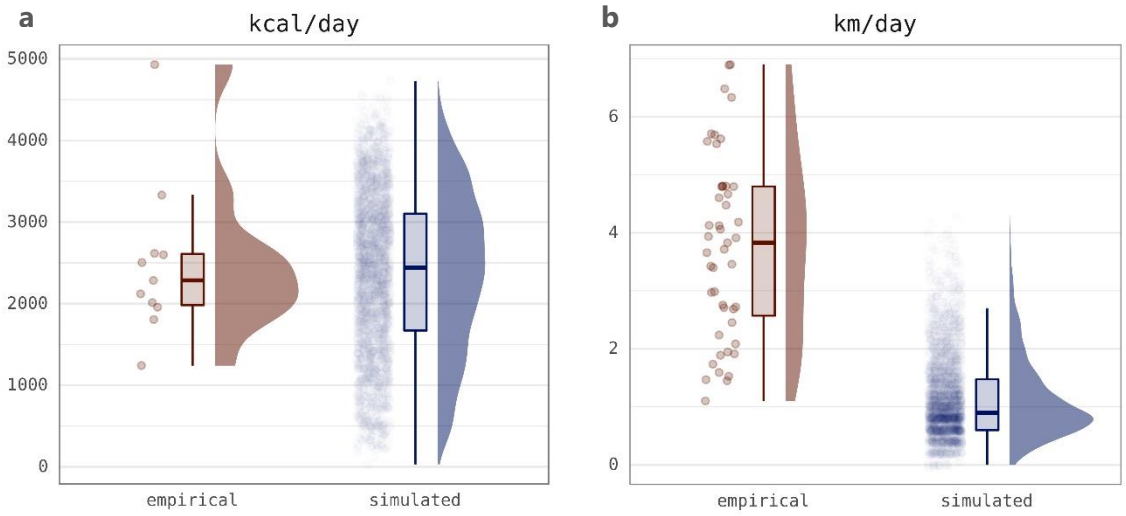


Figure 5.6. Empirical data distributions compared to the corresponding simulated outputs: a) caloric intake per day (kcal); b) distance travelled per day (km).

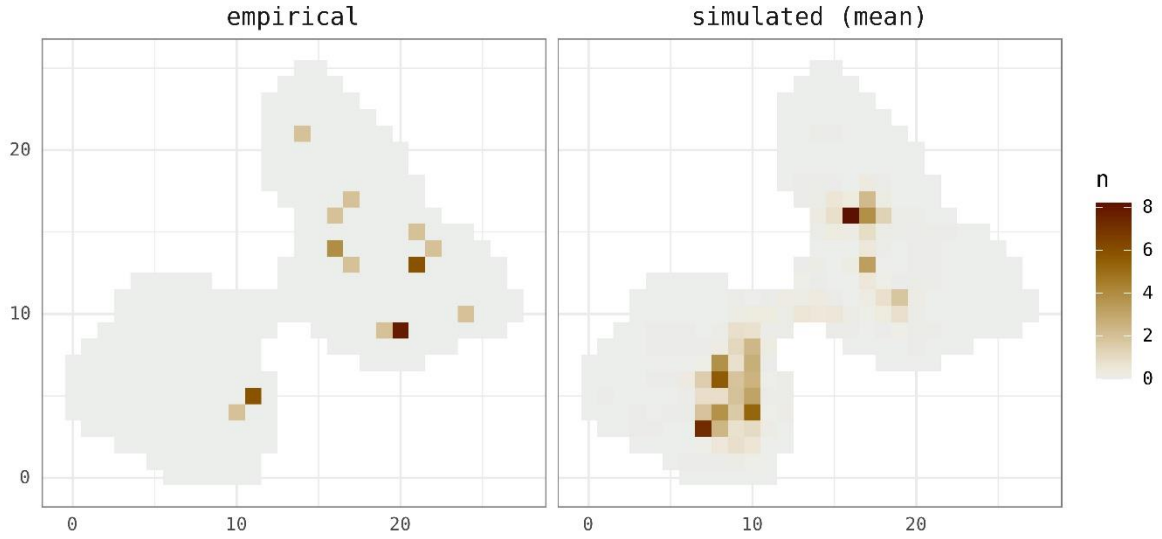


Figure 5.7. Spatial distribution of nut-cracking activities. Left: empirical data; Right: simulated data.

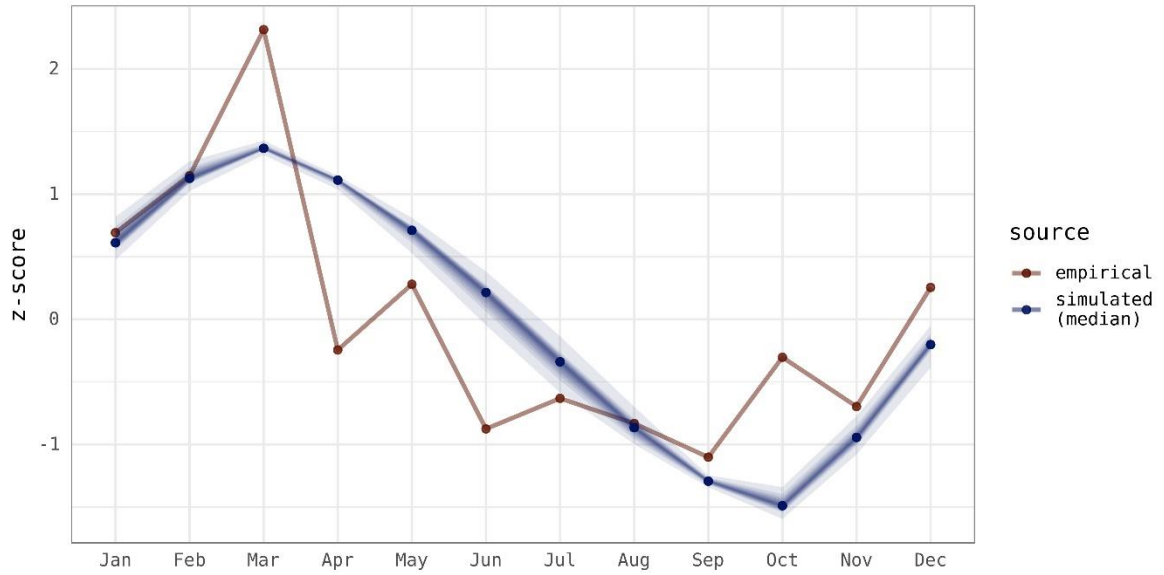


Figure 5.8. Empirical and simulated patterns of monthly food availability. Values have been z-transformed to a mean of 0 and standard deviation of 1 to enable comparison between the datasets. Simulated datapoints are the median values from each of the model runs.

Experimental outputs

In the experimental version of the model, which included artificially generated maps for water, food and nests distributions, variations in *water-abundance* and *smoothness* (of food distribution) had the largest predictive effect on the model outputs (Figures 5.9 – 5.14). On average, calorific intake increased with higher water abundance (medium: $\beta = 26$, $p = 0.013$; high: $\beta = 23$, $p = 0.029$), as well as higher spatial clustering of food ($\beta = 26$, $p = 0.018$; Figure 5.9; Table D.21). Conversely, higher water abundance significantly correlated with lower daily travel distances (medium: $\beta = -0.29$, $p < 0.001$; high: $\beta = -0.43$, $p < 0.001$), while the degree of spatial clustering had a positive, yet comparably smaller effect ($\beta = 0.05$, $p = 0.007$; Figure 5.10; Table D.22). The significant interaction between *water-abundance* and *smoothness* also indicates that the estimated travel distance was lowest when water abundance was high and

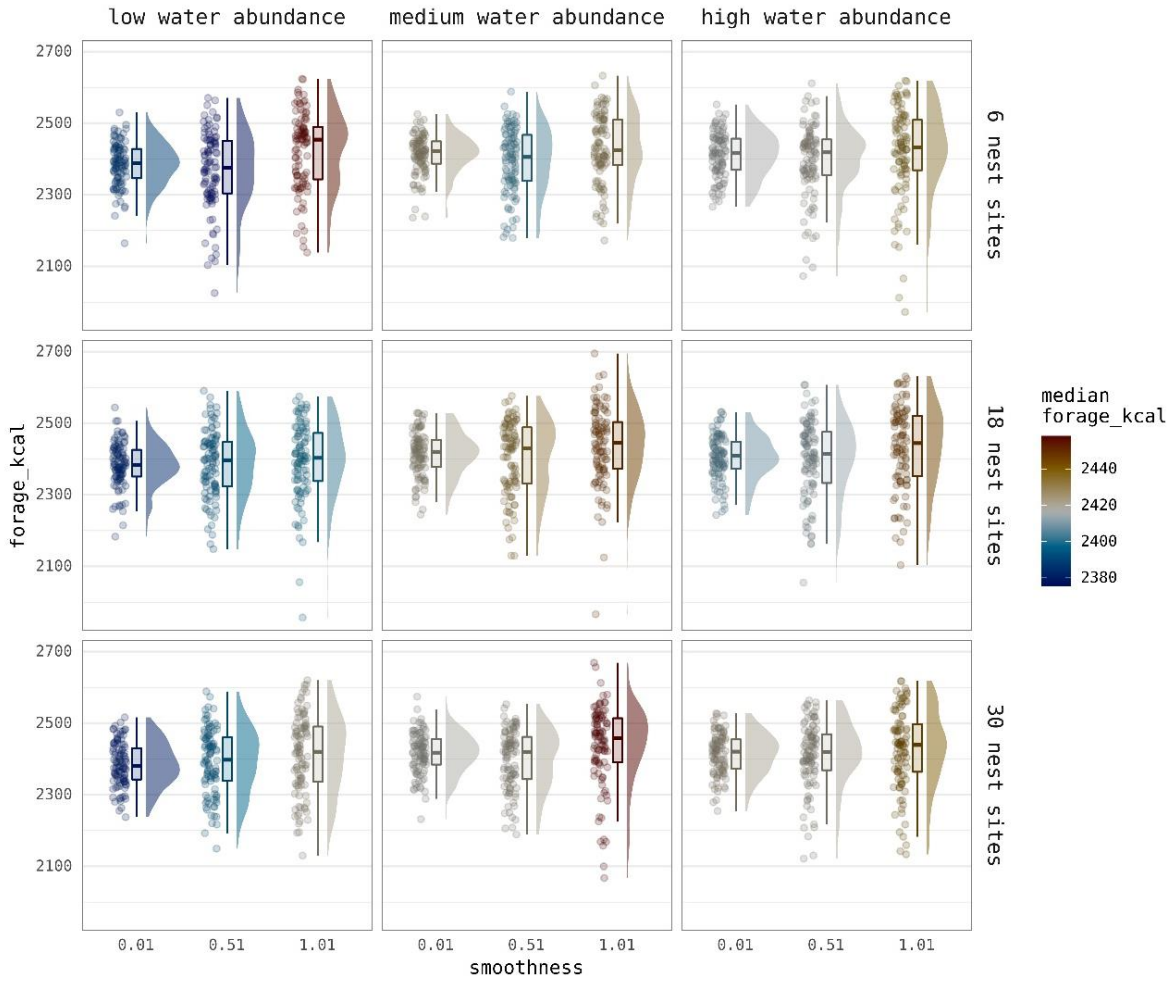


Figure 5.9. Daily caloric intake (forage_kcal) relative to the spatial clustering of food (smoothness), number of nest sites (rows), and water abundance (columns).

spatial clustering of food was low (medium * smoothness: β = 0.006, p = 0.001; high * smoothness: β = 0.04, p = 0.013).

Smoothness was the only variable that had a significant effect on the proportion of time the chimpanzee population travelled as one unit (Table D.23), revealing a small positive influence (β = 0.06, p = 0.001; Figure 5.11). For all parameter combinations, the spatial distribution of nut-cracking events (determined by the Moran's I) revealed a moderate

degree of spatial clustering which in all cases differed significantly from what would be expected from a random distribution (range: 0.428-0.469; $p < 0.001$). However, the spatial clustering of nut-cracking activities and the total number of nut-cracking events, did not vary significantly between the different conditions and parameter combinations (Table D.24; Table D.25). Equally, the number of nesting sites did not appear to have an influence on any of the model outcomes (Appendix D4.3; Figures 5.9 - 5.11).

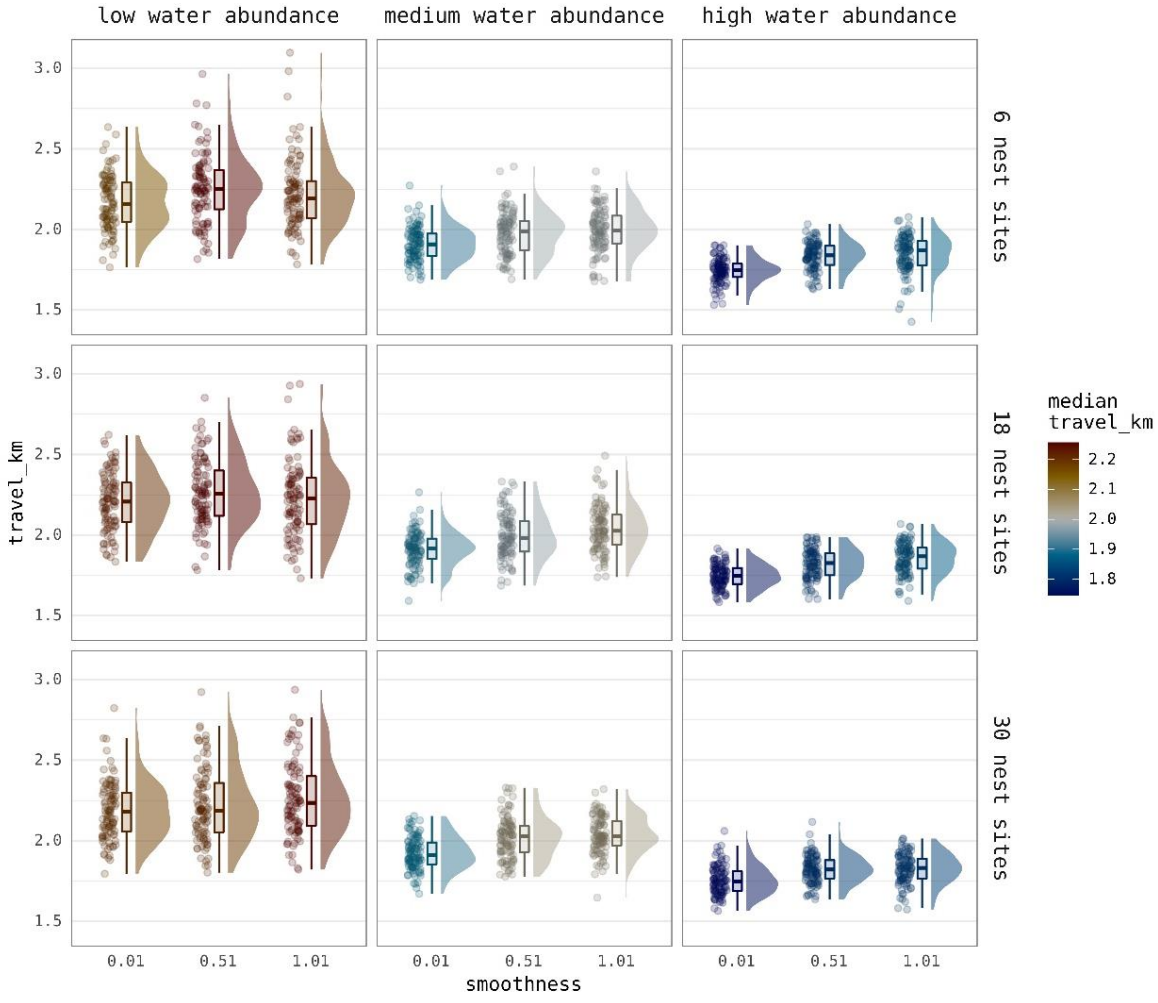


Figure 5.10. Distance travelled per day (km) relative to the spatial clustering of food (smoothness), number of nest sites (rows), and water abundance (columns).

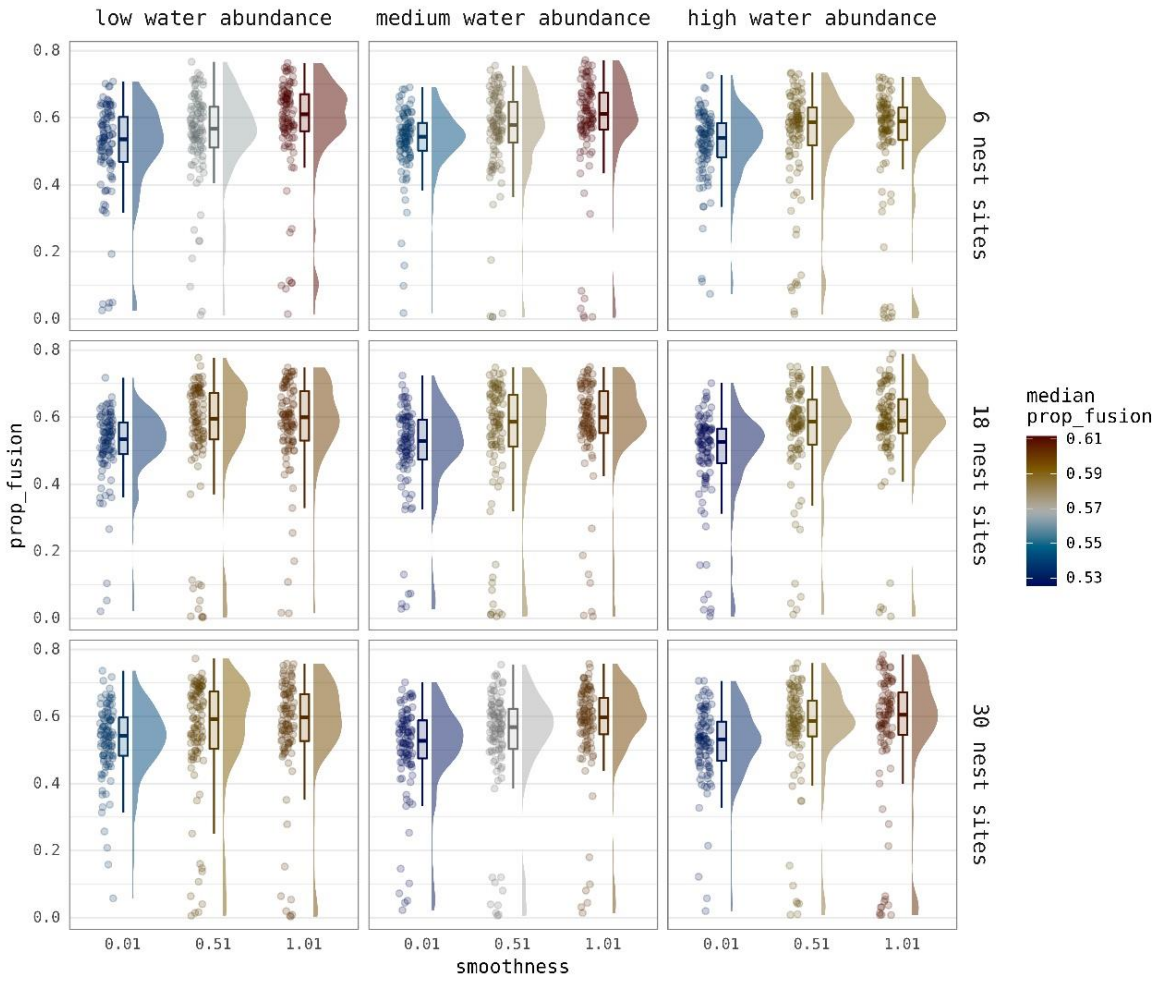


Figure 5.11. Proportion of fusion relative to the spatial clustering of food (smoothness), number of nest sites (rows), and water abundance (columns).

Discussion

Empirical validation

Parameter estimation and sensitivity analysis revealed that the model outputs were sensitive to all parameters except for the nest-related variables. This suggests that in the current version of the model, the process of nest site selection operates independently from other

activities and does not appear to affect any measures of energetic intake, travel, fission-fusion, or the spatial distribution of nut-cracking events. This appears to contradict the initial results presented in Chapter 4 which showed a relationship between nut-cracking sites and proximity to nesting locations, as well as other research that has linked the choice of nesting sites with proximity to morning foraging spots (Janmaat et al., 2014).

Exploration-probability is the parameter that determines how well a chimpanzee knows about the distribution of wild food in their environment and their ability to choose the best foraging patch (i.e., the patch with the most food). Low values indicate a high degree of knowledge exploitation, while high values reflect a greater degree of randomness when selecting a foraging destination. The estimated value was relatively low (0.242), indicating that having largely but not entirely precise knowledge of the forest produced the best model fit. This provides further support to the hypothesis that chimpanzees have intimate ecological knowledge of their home range, consistent with the latest findings concerning chimpanzee ranging patterns and foraging decisions (Ban et al., 2014; Green, Boruff, Bonnell, et al., 2020; Janmaat et al., 2016). .

The final Bossou model performed well regarding the estimates for monthly food availability and daily energetic intake, demonstrating a high level of fidelity with real-world observations. The small deviations from the empirical data are likely due to the small sample sizes of the real data. Monthly food availability was sampled over the course of one year and the addition of further data, once collected, will likely generate a smoother curve akin to the simulated output. In the case of the energetic intake, the sample while small, was also collected at a different field site, and therefore can only be considered an approximate rather than exact representation of Bossou.

Spatial patterns of nut-cracking activity only moderately correlated with the empirical patterns. Visual inspection of the raster data (Figure 5.8) shows there is good degree of overlap with some of the active nut-cracking sites, but the patterns are generally more clustered and spread over a wider area. Inactive sites (i.e., locations that did not show sights of nut-cracking activity during the fieldwork period) were not considered in this analysis to avoid potential discrepancies between ecological variables and tool site use. However, subsequent visual inspection of the data alongside the distribution of all 40 nut-cracking sites recorded at Bossou (Figure 5.12), reveals additional similarities. If true, this would be consistent with previous findings (Chapter 4) that site inactivity is not linked to any of the ecological variables considered in this study. The lack of a strong correlation suggests there are additional processes driving the spatial patterning of nut-cracking activity that have not been explored or implemented in the current model. For example, it is possible that pre-existing evidence of nut-cracking activity may stimulate the occurrence of further nut-cracking in that location (See Chapter 4). Also not considered, is the possibility that chimpanzees might prefer to revisit established nut-cracking sites, if reasonably nearby,

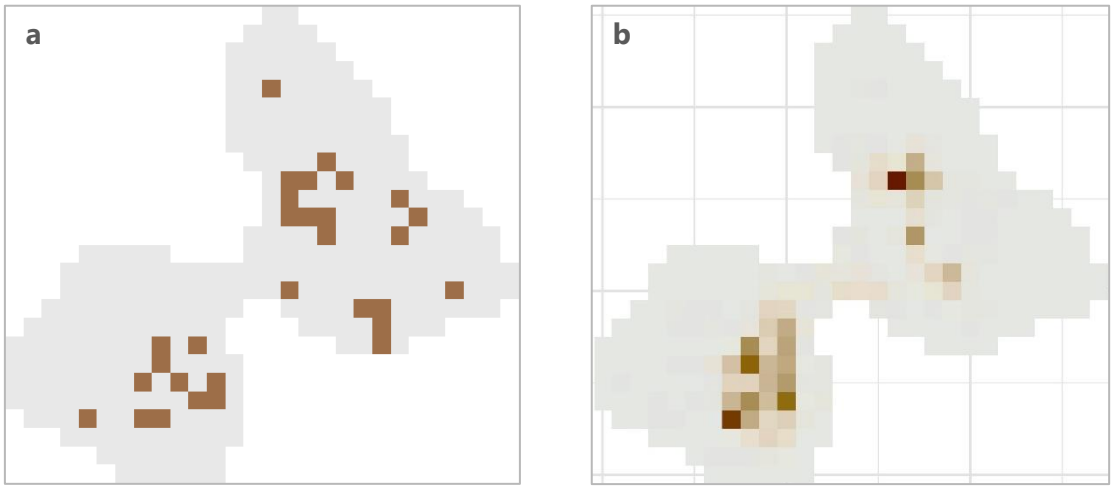


Figure 5.12. Rasterized distribution of all Bossou nut-cracking sites (a); Rasterized simulation output of the distribution of nut-cracking activity (b).

rather than rely on the probability of encountering the right resources at their present location.

The average distance travelled per day was the variable that diverged the most from the empirical values, with simulated travel paths appearing nearly 75% shorter than observed values. This discrepancy could be due to several reasons. In line with an optimal foraging approach, the group algorithm for selecting the next foraging patch, always chooses the nearest of the "best patches" suggested by the group members. . Additionally, chimpanzee-agents travel in straight lines between their current patch and the patch they have chosen to travel to. The model assumes the landscape is topographically flat, and that there are no obstacles or barriers to movement except for the home range boundaries. In reality, chimpanzee habitats occur in landscapes of varying topographical complexity, with steep mountains and cliffs at the upper extreme (Green, Boruff, & Grueter, 2020). There may also be other obstacles, such as rivers that may be too wide to cross, or areas of high risk due to human or predator presence. Therefore, the fastest and most direct travel routes may not be the shortest trajectories. In the case of Bossou, the chimpanzee home-range spans two large hills that are separated by a main road and parts of their habitat are intersected by cultivation fields (Humle, 2011a). While the Bossou chimpanzees have no natural predators, crossing anthropogenic areas and human encounters do pose some degree of threat, so such areas are often avoided unless they are crop raiding (Bryson-Morrison et al., 2017; Hockings, 2011). Often chimpanzees may also reuse pre-existing trails, establishing "forest highways" that link different parts of the forest, instead of creating a new route every time (personal observations; Bertolani, 2013; Green, Boruff, & Grueter, 2020).

Some of the divergence may also be attributed to the accuracy of the empirical data. Due to the field policies in place, chimpanzees could only be followed up to a maximum of 6 hours in any given day. The logged GPS travel distances were converted to an hourly rate and then to a 12-hour day. Although GPS tracks were cleaned prior to conversion, the resulting travel distances are likely to be over-estimates.

Taking all validation outputs into account, the model performed within acceptable margins of error relative to the behaviour of the Bossou chimpanzees. Therefore, it can confidently be used to explore how different ecological conditions affect landscape-scale patterns of nut-cracking activity of the simulated chimpanzee population under constant behavioural rules.

Experimental Results

None of the parameter variations or combinations appeared to influence the landscape-scale patterns of nut-cracking activity. This could indicate that the underlying patterns of oil palm and raw material distributions, which did not change between model runs, exert a comparably stronger effect on where nut-cracking takes place. This is consistent with empirical findings presented in Chapter 4 which show that nut-cracking cannot occur without the presence of an oil palm or a minimum number of stones. Further investigation under a controlled agent-based modelling environment, has revealed that variations in density and durability of resources can generate different landscape-scale patterns of stone tool use (Reeves, Proffitt, et al., 2021). The influence of these resources could be tested further by running a neutral model as a null hypothesis, where the distribution of these two resources is constant throughout the environment (i.e., the chance of encounter is the same

for all patches within the home-rage). Nut-cracking frequency did not vary between conditions. This is likely because total food availability was kept constant for all model runs, and therefore the need to acquire additional calories through nut-cracking is expected to have remained largely unchanged.

However, the lack of variation in spatial patterning presents some interesting questions and avenues for further research. Firstly, might the introduction of raw material transport change nut-cracking patterns? The transport of raw materials and tools over large distances is considered a hallmark of early hominin lithic technology (Braun, Plummer, et al., 2008; Braun, 2012). The chimpanzees of Bossou transport materials over very short distances, but research from the nearby site of Tai has suggested that raw materials and tools may become substantially spatially displaced through a series of short transport events (Luncz et al., 2016; Reeves, Braun, et al., 2021). The present model assumes that nut-cracking can only occur when tools and nuts converge in the same place. Integrating transport capabilities would help explore further the role of raw material procurement behaviours within the broader environmental and behavioural context.

Secondly, does the similar clustering of nut-cracking activities indicate equally uniform patterns of landscape use across different ecological conditions? It has long been assumed that the different distributions of archaeological sites reflect differences in overall patterns in landscape-scale behaviour (Plummer, 2004). Therefore, under this premise, we would expect landscape use to show very little variation. However, the examination of other model outputs suggests that this may not be the case. For example, lower water availability correlated with greater daily travel distances – a pattern that has been associated with chimpanzees living in drier and hotter savannah landscapes (Lindshield et al., 2021). Travel

distances are even greater when this is combined with higher spatial clustering of food, likely because areas of high food availability may not always overlap with watercourses, thereby leading to more frequent long-distance travel. Lastly, greater dispersion of food leads to an increase in the proportion of time the chimpanzee population remains in smaller parties, which is likely to also impact overall patterns of landscape use. It is possible that the material traces of tool use may only be able to reveal one part of the behavioural multiplex of chimpanzee landscape use. While empirical evidence points to clear spatial relationships between ecological variables and where nut-cracking sites occur (Chapter 4), further investigations through agent-based modelling in this study suggest the dynamic relationship between the environment, behaviour and the spatial patterning of stone tool use may be even more complex than originally thought.

Conclusion

Understanding how hominin lithic assemblages formed and what they represent in terms of landscape-scale patterns of early hominin behaviour has been one of the biggest challenges of archaeological inference. In this study, we attempt to shed light on this question by combining primate archaeology approaches with agent-based modelling to investigate how key resources, such as food, water, and shelter, may have shaped spatial patterns of stone tool use. Our experimental results revealed that under the same behavioural conditions, variations in the environmental parameters did not produce different landscape-scale patterns of stone tool use. On the other hand, environmental parameters, such as water availability and the spatial distribution of food, had an effect on travel and group fission-fusion, likely resulting in different spatial patterns of overall behaviour. This suggests that

changes in landscape use do not necessarily correspond directly to changes in spatial patterns of tool use. This could have important implications as to how archaeologists perceive the relationship between early hominin lithic assemblages and overall patterns of landscape use.

Acknowledgments

This work was funded by the Fundação para a Ciência e Tecnologia (FCT) [grant number: SFRH/BD/115085/2016], with support from the Programa Operacional Capital Humano (POCH) and the European Union; the National Geographic Society [grant number: EC-399R-18]; and the Boise Trust Fund (University of Oxford).

Chapter 6

Revisiting the second largest forest of Guinea a decade later

Chimpanzee presence, conservation status and threats in Diécké, Korohouan area

Abstract

The Diécké Forest is the second largest forest in Guinea and home to a population of nut-cracking chimpanzees (*Pan troglodytes verus*). It has attracted several research expeditions focusing on chimpanzee presence and tool use since 1993, until the Ebola outbreak of 2013. We visited Diécké in November 2018 on a reconnaissance expedition to check the current chimpanzee presence and nut-cracking activity. We report our findings along with an up-to-date overview of the historical, socio-political, environmental, and scientific

developments around the Diécké Forest. Our survey took place in the Korohouan area where research on chimpanzee nut-cracking had previously been conducted. We found that the chimpanzee presence in the area continues to decline with no recent evidence of nutcracking or other activities. We also found that hunting was one of the major threats to wildlife, but small-scale agriculture, as well as commercial activities in the region, are also having an impact on forest fragments outside the protected area. Our study highlights the need for concerted conservation action and provides an important case study on the disappearing cultural heritage of a chimpanzee population in decline.

Introduction

The Diécké Forest in Guinea was first recognized as an important area for studies of chimpanzee culture following a nationwide chimpanzee and large mammal census in the late 1990's, which found evidence of chimpanzee nut-cracking activities alongside other indirect traces of chimpanzee presence (Ham, 1998). Subsequent surveys focusing on chimpanzee tool use identified a number of nut-cracking sites where chimpanzees were using stone and wooden pounding tools, including outcropping stones and embedded tree roots, to extract *Panda oleosa* and *Coula edulis* kernels (Carvalho et al., 2007; Carvalho, 2011; Humle & Matsuzawa, 2001; Matsuzawa et al., 1999). The techno-cultural contrast with the nearby long term field-site of Bossou, located approximately 50 km East, where chimpanzees exclusively crack oil palm (*Elaeis guineensis*) nuts and only use movable stone tools, established Diécké as a locality of interest for comparative research on chimpanzee technology and culture (Carvalho et al., 2007, 2008; Carvalho, 2011; Humle & Matsuzawa, 2001). The primate archaeology 2006-2009 expeditions (see Carvalho et al., 2007) in the vicinity of the Nonah and Korohouan villages offered the first insights into Diécké's research

potential for investigating technological diversity at a regional scale, and announced plans to establish a longer term research presence in the area (Carvalho, 2011).

Despite these promising beginnings, partly due to a period of political instability and the 2013 Ebola outbreak, research on the chimpanzees of Diécké, their technology and culture remained stagnant between 2009 and 2018, except for a short visit by field assistants in 2012. We returned to Diécké in November 2018 on a reconnaissance expedition to check the current status of chimpanzee presence and nut-cracking activity in the forest nearby the Korohouan locality. In the present study, we provide the first up-to-date review of the historical, socio-political, environmental, and scientific developments around the Diécké Forest, and examine our findings within this context. We assess the potential for resuming research and discuss implications for conservation.

Diécké Forest

The Diécké Forest is located in the Yomou prefecture of the Guinée Forestiére region (Figure 6.1; Ham, 1998). It extends over 700 km^2, spanning approximately 35 km across North-South and East-West (Humle & Matsuzawa, 2001; Kormos et al., 2003), and borders Liberia to the south-east. The landscape is characterized by a large collection of small hills with elevation ranging 50-800 metres above sea level (Carvalho et al., 2007; Carvalho, 2011). It is part of the Western Guinean lowland forests ecoregion and is composed predominantly of a moist evergreen forest, where trees of large girth timber species form a dense canopy, interspersed by areas of riparian forest and swamp-forests dominated by *Raphia* palms (Brugière & Kormos, 2008; Carvalho, 2011; Haba & Couch, 2018; Robertson, 2001). It has a high diversity of plant species which includes *Parkia bicolor* and *Piptadeniastrum africanum* and some

threatened species such as *Allophylus samouritourei* (Haba & Couch, 2018; Robertson, 2001). This region has an annual rainfall of 1,900-2,000 mm (Robertson, 2001), and experiences a very short dry season between December and March (Carvalho et al., 2007). It has two main rivers running South-West (See figure 3), but there are also many smaller streams that flood creating swamps which restrict access to some parts of the forest (Carvalho et al., 2007; Robertson, 2001).

Conservation status and initiatives

There are currently 162 classified forests ("forêts classées") in Guinea and Diécké is one of the 40 in Guinée Forestiére (Ministère de l'Environnement, 2019b). It was made a natural reserve by the French colonial administration in 1932 and was given classified status in 1945 (Akobi & Poissonnier, 2021), which includes a hunting ban within its boundaries (Brugière & Kormos, 2008). It is the second largest lowland evergreen forest in the region, and one of the few remaining near-pristine forest mosaics of the Upper Guinean Forest ecosystem

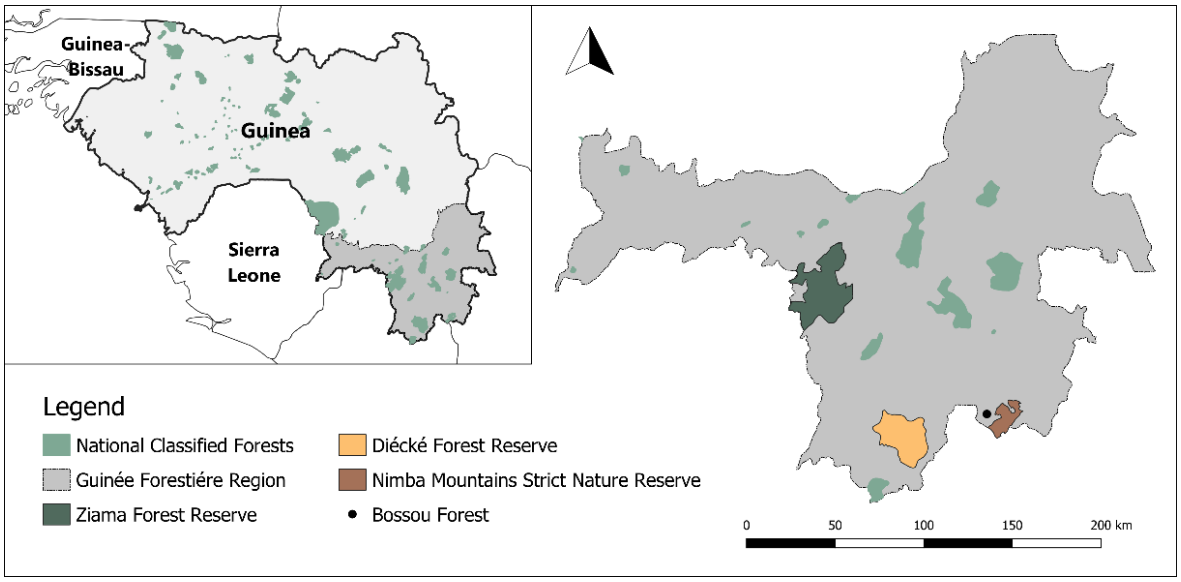


Figure 6.1. Map of the national classified forests of Guinea and the locations of the Ziama, Diécké, Nimba, and Bossou forests.

(Akobi & Poissonnier, 2021; Couch & Haba, 2018; Fauna & Flora International, 2021), a part of the lowland forests of western Africa that survived the glaciation cycles and global cooling of the Pleistocene (Carvalho et al., 2008; Kalan et al., 2020). As such, Diécké represents a relic of an important forest refuge that would have provided a stable tropical climate and habitat to a range of taxa, including chimpanzees, throughout the environmental fluctuations of the Pleistocene (Barratt et al., 2021; Kalan et al., 2020).

Along with the Ziama Forest, the forest of Diécké is of high conservation significance and a Key Biodiversity Area for West Africa, serving as an important refuge for a number of endemic species (Carvalho, 2011; Fauna & Flora International, 2021). Additionally, Diécké has been identified as part of one of four transboundary areas of importance for the conservation of the critically endangered western chimpanzee, *Pan troglodytes verus* (Heinicke, Mundry, Boesch, Hockings, et al., 2019; Humle, Boesch, et al., 2016).

In addition to chimpanzees, the forest is home to 61 species of conservation importance, including the dwarf crocodile (*Osteolaemus tetraspis*), the Tokba river frog (*Phrynobatrachus tokba*), and the tenth largest population of pygmy hippopotamus (*Hexaprotodon liberiensis*) (Akobi & Poissonnier, 2021; Kormos et al., 2003; Robertson, 2001). It is also an Important Bird and Biodiversity Area (IBA), with 141 avian species (Akobi & Poissonnier, 2021), such as the threatened Yellow-casqued hornbill (*Ceratogymna elata*), Yellow-bearded greenbul (*Criniger olivaceus*), Green-tailed bristlebill (*Bleda eximia*), and White-necked rockfowl (*Picathartes gymnocephalus*) (Robertson, 2001). The first comprehensive faunal surveys conducted as part of the DARWIN initiative (Haba et al., 2018), have also documented that the Diécké forest is one of the top 5 sites at a national level where a number of endangered or vulnerable plant species can be found (Haba & Couch, 2018).

Conservation efforts in the Diécké region have been supported by a series of fixed-term projects managed by the Centre Forestiére de N'Zérékoré (CFZ), aided by funds from the Guinean Government and financial institutions such as The World Bank, Kreditanstalt für Wiederaufbau (KfW; Germany), and the Canadian International Development Agency (Ministère de l'Environnement, 2019a; The World Bank, 1997). From 1990 to 2010, the Projet de Gestion des Ressources Forestières (PROGEFOR; 1991-1994), the Projet de gestion des Ressources Rurales (PGRR; 1996-2003), and the Projet de Gestion des Ressources Forestières (PGRF; 2004-2009), collectively sought to promote and facilitate sustainable rural development, reforestation and the monitoring of hunting activities (Diallo, 1996; Mano River Union, 2018; Ministère de l'Environnement, 2019a; The World Bank, 1997). However, the success of some of these initiatives has been put into question because of negative public perception with complaints by residents of enforced political agendas and the lack of consideration for local communities (Leach, 2008).

More recently, Diécké was part of a multinational conservation project of the Mano River Union (MRU), which includes Guinea and the neighbouring countries of Côte d'Ivoire, Liberia, and Sierra Leone. The MRU Ecosystem Conservation and International Water Resources Management (IWRM) Project (2017-2020), was implemented in partnership with the IUCN with the goal of conserving the transboundary Upper Guinea forest ecosystem through the coordinated management of biodiversity, natural resources, and sustainable land use at a global scale (IUCN, 2016). Site-specific efforts for the "Mont Nimba WHR (World Heritage Reserve) - Diécké NF (National Forest) complex" included plans for promoting income-generating activities based on the sustainable use of natural resources and the formulation of community-led management plans and integrated food production systems (IUCN, 2016).

At a national level, grassroots organisations such as the collective "Touche pas à ma forêt" ("Don't touch my forest") are promoting environmental education and conservation awareness through outreach events in local communities (Sylla, 2018). Together with other local groups, they are giving local communities a platform and voice to lobby against current and prospective commercial activities in the area (e.g. logging operations in Diécké and Ziama) that are putting public and ecosystem health under severe threat (Akobi & Poissonnier, 2021; H. K. Guilavogui, 2018).

Human Impact

Guinea is among the 10 countries in the world most affected by deforestation, and like many parts of Guinea, the forests of Guinée Forestiére have been victims of escalating anthropogenic disturbance, such as agriculture, logging, and hunting, since the beginning of the colonial era in 1905 (Akobi & Poissonnier, 2021), although archaeological evidence indicates that small scale land use practices, including food production, have occurred in the area since 200 BCE (Kay et al., 2019). While the establishment of Classified Forests has, in theory, offered some protection against human activities and forest degradation, accelerated population growth and development of commercial ventures in response to international resource demand in the last 30 years is posing new threats to the Diécké Forest and other natural reserves (Figure 2; Akobi and Poissonnier, 2021). In a survey by the Wild Chimpanzee Foundation in 2012, Diécké was the third protected chimpanzee site most affected by human pressure, after the Nimba Mountains and Ziama which are also located in Guinée Forestiére (Wild Chimpanzee Foundation, 2012).

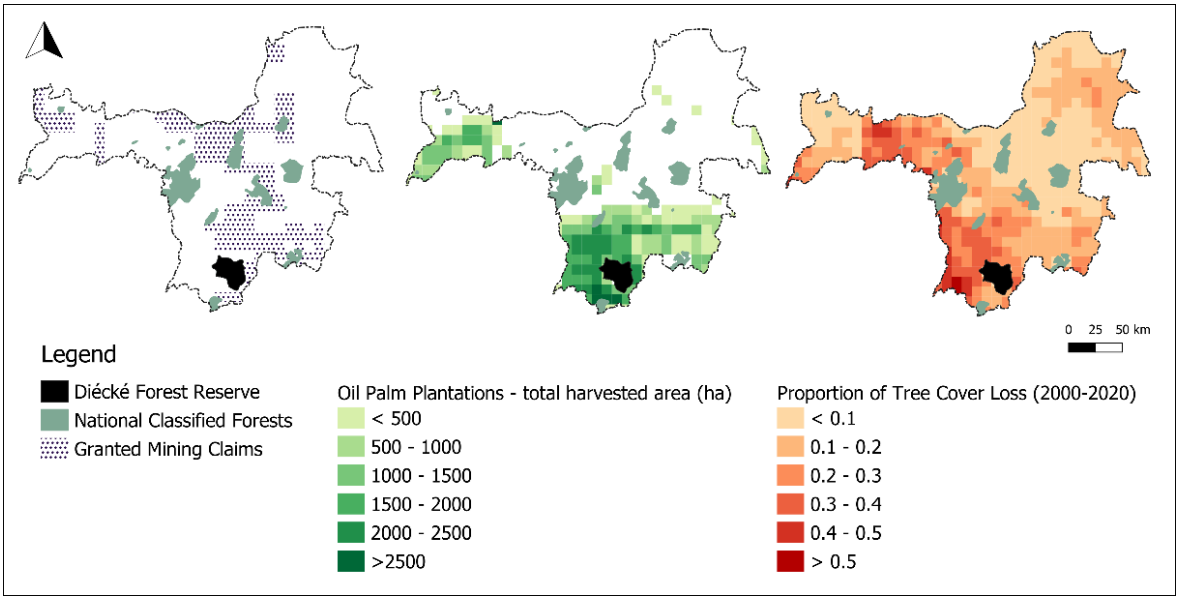


Figure 6.2. Distribution of main commercial activities and tree cover loss in the Guinée Forestiére Region. The map for mining claims is an approximate rendering of the areas where mining exploration and/or extraction has been approved. This includes past, current and future activities. The information was sourced from a publicly available dataset where no interrogation of the data is possible (SNL Metals & Mining, an offering of S&P Global Market Intelligence, 2020; Online source: https://panda.maps.arcgis.com/home/item.html?id=6f8e17219c354878af009a6cc9a9f571). The map of oil palm plantations is presented as the total area harvested (in hectares) during 2017, with white areas indicating locations where commercial oil palm activities are absent. The original data is available from the Harvard Dataverse, under a CC-by-4.0 license (Online source: International Food Policy Research Institute, 2020; https://doi.org/10.7910/DVN/FSSKBW). The proportion of tree cover loss between 2000 and 2020 is calculated from the gross forest cover loss event (lossyear) available online under a CC-by-4.0 license (Hansen et al. 2013; Online source: http://earthenginepartners.appspot.com/science-2013-global-forest) Credit: Hansen/ UMD/Google/USGS/NASA.

RUBBER AND PALM OIL INDUSTRY

The Diécké Forest is surrounded by industrial rubber and oil palm plantations that are controlled by the Société Guinéenne de Palmiers à Huile et d'Hévéa (SOGUIPAH) – the

largest rubber and palm oil producer in the country (Balde et al., 2019; Fauna & Flora International, 2021). SOGUIPAH is an agro-industrial public company that was founded in 1987 to support the development of industrial and family-owned plantations and promote local development and food security (Fauna & Flora International, 2021; The World Bank, 2016). Over the years it has received financial support from multiple donors including the African Development Bank, the Arab Bank for Economic Development in Africa, and the European Investment Bank (López-Cálix, 2020). Today, SOGUIPAH's land holdings extend across ~230 km^2, employing over 3,500 workers on its plantations and in its own factories for processing rubber, palm oil and soap (Thompson et al., 2021). The company also purchases natural rubber and palm fruits from around 3,000 local smallholders and farmers, and supports them by providing training, planting material and technical assistance (Balde et al., 2019; Fauna & Flora International, 2021).

While SOGUIPAH has also contributed towards social infrastructure in the region such as health clinics, schools, roads, and access to water (López-Cálix, 2020), its operations have been associated with substantial negative environmental and socioeconomic impacts (Balde et al., 2019). Between 2011 and 2016, SOGUIPAH's oil palm and rubber exports increased by 900% and 50% respectively (López-Cálix, 2020), yet the income of their workers and small-hold suppliers is increasingly insufficient (Balde et al., 2019). Income from rubber and palm oil can be precarious because the company imposes its own pricing system and does not always respect the agreed price, while smallholders are contractually obliged to sell exclusively to SOGUIPAH (Balde et al., 2019). In February 2020, workers protested against their employer due to wages in arrears of 2-3 months, an issue that has been recurring since 2013 (Z. E. Guilavogui, 2020).

The quality of life in the region remains very poor, with the majority of Guinée Forestiére inhabitants living on less than $850 per year and suffering from malnutrition (Akobi & Poissonnier, 2021). While a preliminary study has indicated that a somewhat stable income from the rubber and palm oil industry can provide a greater level of food security, the dietary diversity is lower when compared to subsistence farmers (Balde et al., 2019).

LOGGING

Timber is one of the most sought-after natural resources in Guinea. Logging activity in Guinea Forestière has been controlled by Forêt Forte, a subsidiary of the Taiwanese company Coujy Corporation, since 2002 when it was granted exclusive concessionary rights by the Guinean government to exploit the regions surviving forests, including the protected reserves of Diécké and Ziama (Akobi & Poissonnier, 2021; Fauna & Flora International, 2021). While operations in these two reserves have been dormant due to setbacks imposed by the Ministry of the Environment (Fauna & Flora International, 2021), recent reports and local media coverage indicate that this could change very soon (Akobi & Poissonnier, 2021; Baldé, 2018a; Camara, 2017).

Forêt Forte is already exploiting classified forests in other parts of Guinea (Akobi & Poissonnier, 2021; Foret Forte, 2021b). While it claims to be committed to sustainable and ethical development (Foret Forte, 2021a; Nydegger, 2021), the company has been repeatedly accused of abusive logging that could lead to the decimation and irreversible deforestation of the last pristine forests in Guinea (Akobi & Poissonnier, 2021; Baldé, 2018b; Camara, 2017; H. K. Guilavogui, 2018). It has also failed to comply with its reforestation and infrastructure development commitments and did not consult with local communities regarding the proposed operations nor their traditions with respect to the sacred areas of the forests

(Akobi & Poissonnier, 2021). Beyond the forest and into production, news articles from 2018 report that workers at the Forêt Forte factory in N'Zerekore were on strike for over 6 months due to poor living and working conditions, which often demand excessive use of physical force (Baldé, 2018a, 2018b).

The local NGO "Touche pas à ma foret", the national green party (Parti Écologique de Guinée - PEG), and the local youth centre (Maison des jeunes et de la culture de N'Zerekore) are amongst those that have strongly criticised and opposed the latest Forêt Forte agenda (Akobi & Poissonnier, 2021). However, while the Guinean government upholds its support for the project, Forêt Forte will continue to pose a serious threat to the Diécké forest which is already in an extremely fragile condition.

MINING

Guinea harbours the largest bauxite reserves and untapped iron ore deposits in the world (Ministry of Mines and Geology, 2021a, 2021b). Historically, the exploitation of mineral resources has been constrained by political conflicts and poor transport infrastructure throughout the country. In recent years, however, the mining operations in Guinea, enabled by increased stability in the West African region, have expanded dramatically in response to the growing global demand for rare metals and minerals (Fauna & Flora International, 2021). The national economy has benefitted greatly from these developments, ranking fifth in the International Council of Mining and Metals (ICMM) Mining Contribution Index of 2020 (ICMM, 2020).

Large-scale mining as well as artisanal and small-scale mining (ASM) are now conspicuous across the Guinean landscape, with many mining claims intersecting areas of high

biodiversity and carbon value, including regions that harbour endemic forests and species that are under threat (Fauna & Flora International, 2021). The largest active mining concessions in Guinea Forestière are located in Mount Nimba (a UNESCO World Heritage Site) and Simandou. Further mining claims have been granted to the South and East of the Diécké forest (Figure 2). Initial prospection of the mineral reserves has estimated a resource potential of approximately 1.2 billion tonnes of iron ore, with the Al Khaldiya Mining Project planning to start production in 2022 (Al Khaldiya Mining, 2021).

The Diécké iron ore mines are the closest mineral reserves to a working railway with access to the coast (Al Khaldiya Mining, 2021), making them attractive extraction sites for quick and direct export of natural resources through Liberia. With the mining industry expected to grow further in the coming years, the region will likely generate a large influx of people which will create a greater demand for food resulting in agricultural expansion. Likewise, increased industrial activities will boost infrastructure developments, particularly transport networks and electricity, providing greater access to the region. While this may bring positives to local communities, it could have serious consequences to public health and the natural environment, if not properly regulated. For example, in the Boké region (Guinée Maritime, western Guinea), decades of bauxite mining, involving the multinational mining corporations Rio Tinto, Alcoa and Dadco, is already having devastating impacts on nearby human settlements and the surrounding environment, such as water contamination, air pollution and soil infertility (Oakes, 2019; Rolando Mazzuca, 2019; Sidiki, 2019; "'What Do We Get Out of It?' The Human Rights Impact of Bauxite Mining in Guinea," 2018). Loss of land and livelihoods, reduced access to clean water, and other threats to public health are amongst the damaging consequences highlighted in the latest Human Rights Watch (2018) report concerning bauxite mining in Guinea. Coupled with the environmental degradation

and biodiversity loss in the region, including the plight of chimpanzees (Bergen, 2020; O'Mahony, 2019), this is a worrying prospect for the future of other mining localities such as Diécké.

POACHING

In addition to the growing levels of agricultural and industrial activity in the areas surrounding the Diécké Forest, illegal hunting within the protected forest has remained high throughout the last three decades (Carvalho, 2011; Ham, 1998; Kormos et al., 2003; Sangbalamou, 2020). In a survey conducted by the Wild Chimpanzee Foundation in 2011, poaching was the highest documented human activity in the area, representing almost 50% of all recorded anthropogenic traces (Wild Chimpanzee Foundation, 2012). It is also the third chimpanzee site in Guinea most affected by hunting pressures with an average of 1.45 traces/km (Wild Chimpanzee Foundation, 2012).

Poachers, often not local, are known to set up camps within the reserve, where they will spend several days trapping and hunting wild animals for bushmeat and other products to sell in larger cities such as N'Zérékoré (Akobi & Poissonnier, 2021; Kormos et al., 2003). In the past, chimpanzees inhabiting the forest have also fallen victim to this exploitation, with three killings reported by the Centre Forestier de N'Zérékoré in 2001 (Kormos et al., 2003).

Currently, the Guinean government has several preventative measures in place such as the deployment of rangers and ecoguards to track down poachers, monitor illegal hunting activities, and raise awareness in local communities. In the Diécké forest, patrols take place once a month, covering eight sectors of the reserve (Sangbalamou, 2020). However, the forest guards have reported that these missions are constrained by the lack of crucial

resources, such as means of transportation, camping equipment, and weapons (Sangbalamou, 2020).

Other parts of Guinée Forestiére, such as Ziama and Mount Nimba, have benefitted from financial support from the EU/UNOPS Projet d'Appui à l'Opérationnalisation d'un Corps Paramilitaire des Conservateurs de la Nature (PAOCPCN), which offered equipment and training to paramilitary units in a pilot scheme (IUCN, 2016). However, these projects are often short-term, and do not always have funding continuity. An assessment presented at CoP18 reports that Guinea has no government budget allocated for protected areas, with efforts supported exclusively by foreign governments and international NGOs (Convention on International Trade in Endangered Species of Wild Fauna and Flora, 2019). Thus, while the establishment of a more permanent presence would help greatly reduce hunting pressure (Kormos et al., 2003), this can only be achievable with adequate provisioning and reliable long-term funds.

Chimpanzee Status and Tool Use

To date, there have been a total of 6 published chimpanzee surveys and research expeditions in the Diécké Forest (Table 6.1; Figure 6.3). An initial national census in 1988, based on questionnaires, estimated the existence of around 50 chimpanzees in the area (Sugiyama & Soumah, 1988). Subsequent transect-based surveys using the number of chimpanzee nests as a proxy for population size, estimated between 209-307 individuals in 1997 (Ham, 1998), and 25-253 individuals in 2011 (Wild Chimpanzee Foundation, 2012). These are, however, rough estimates, and the number of chimpanzee communities in the area still remains unknown. Direct observations of chimpanzees have so far only been confirmed by Ham

(1998), Humle and Matsuzawa (2001), and Carvalho (2011), who also recorded chimpanzee presence through motion-trigger cameras.

It was during the 1997 census in the Yossono area (Figure 6.3) that evidence of nut-cracking activity was first encountered (Ham, 1998) – a collection of stones surrounded by scatters of broken nuts in the vicinity of a *Panda oleosa* tree. Further surveys in the Nonah and Yossono areas specifically targeting technological and cultural traces, found additional nut-cracking sites of both *Panda* and *Coula* nuts, confirming cultural divergence relative to the nearby site of Bossou, where chimpanzees only crack oil palm nuts (Humle & Matsuzawa, 2001; Matsuzawa et al., 1999).

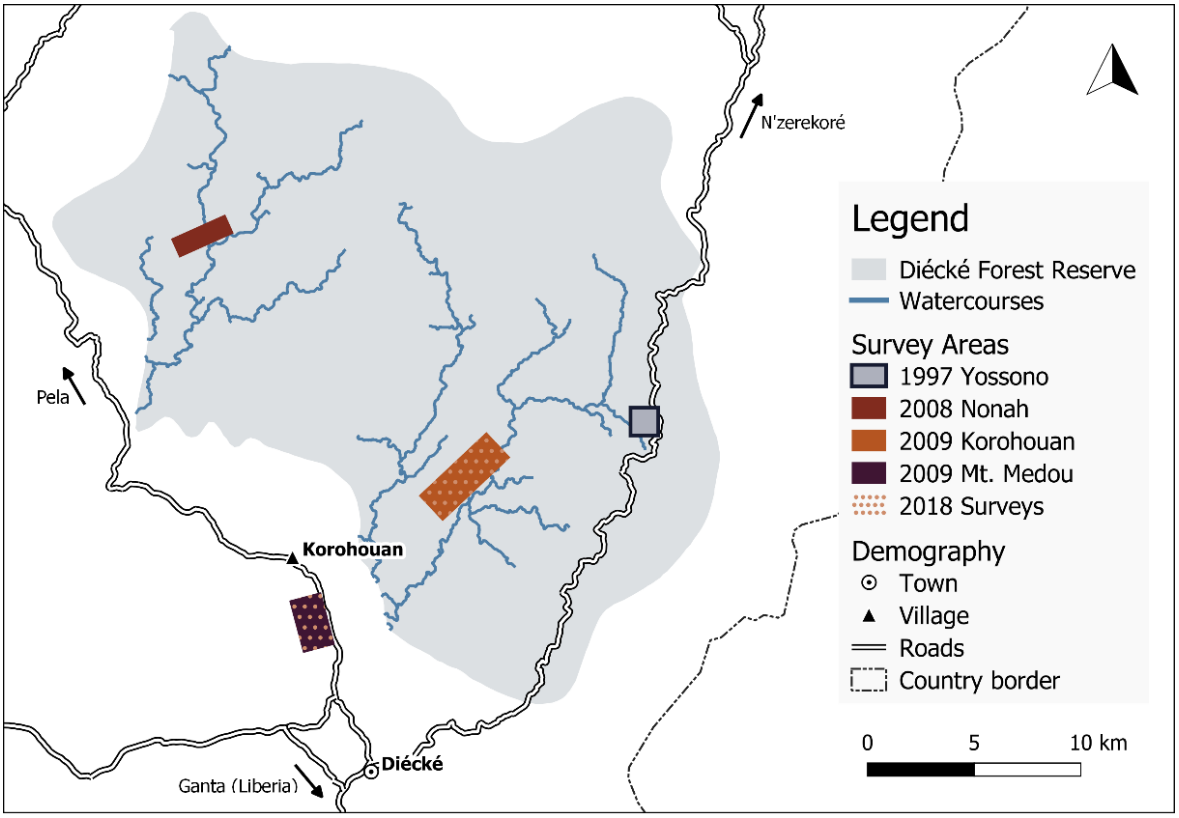


Figure 6.3. Map of the Diécké Forest highlighting the locations of known survey areas and nearby villages.

Table 6.1. Summary of the survey activities that have taken place in the Diécké Forest Reserve. Empty cells represent unknown or unavailable information.

Year	Survey goals[a]	Method[b]	Forest region[c]	Duration[d]	Distance surveyed[e]	Reference
1988	CP	I				Sugiyama & Soumah, 1988
1997	CP, W, H	LT, I	E	1	5.2	Ham, 1998
1999	CTU	ES	NE, NW	3		Matsuzawa et al., 1999
2000	CTU	ES	NE, NW	10		Humle & Matsuzawa, 2001
2006	CNC, CP	ES, TSM	NW, S	19 (NW: 3 + 8 + 4; S: 4)		Carvalho et al., 2007
2008	CNC, CP	ES, TSM	NW	12 (8 + 4)		Carvalho, 2009
2009	CNC, CP	LT, ES, TSM	S	21 (10 + 11 + 10)	14.7	Carvalho, 2009
2011	CP, W, H	LT	AR		144.8	WCF, 2012
2018	CP, CNC, W, H	LT, ES	S	5	21.7	This study

[a] CP = chimpanzee presence; CNC = chimpanzee nut-cracking; CTU = chimpanzee tool use; H = human activity; W = wildlife
[b] ES = exploratory surveys; I = interviews; LT = line transects; TSM = tool site monitoring
[c] AR = All regions; NE = North-East; NW = North-West; S = South
[d] values indicate total duration (in days) of each survey effort. Values in parentheses represent the duration of individual trips
[e] values reported in km

The most recent and longest expedition focusing on the nut-cracking behaviours of the Diécké chimpanzees took place between 2006 and 2009 in the Nonah and Korohouan areas (Carvalho et al., 2007; Carvalho, 2011). This research aimed to investigate, within a primate archaeology framework, the direct and indirect evidence of nut-cracking and to compare with research being conducted in parallel in Bossou (Carvalho et al., 2008, 2011). This was the first archaeological investigation of chimpanzee tool use conducted in the Diécké forest, making it the third chimpanzee habitat to host research of this kind, following Taï and Bossou (Carvalho et al., 2008; Mercader et al., 2002).

Six trips occurred during the two year period, lasting a total of 51 days (Carvalho, 2011). These trips included: the mapping and monitoring of chimpanzee nut-cracking sites; transect surveys of raw materials, nut species, and chimpanzee traces (e.g. nests, faeces, tracks); and the archaeological excavation of an abandoned chimpanzee nut-cracking site – the third of its kind (Carvalho, 2011). A total of eight nut-cracking sites were documented, along with traces of chimpanzee feeding, nests, and tracks (Carvalho et al., 2007). Comparisons with the Bossou data revealed that the chimpanzees of Diécké used larger tools to crack open nuts and exclusively used fixed outcropping stones as anvils, while Bossou chimpanzees always used smaller, movable tools (Carvalho et al., 2008). These differences are likely connected to differences in the number of movable stones available, as well as in properties of the target foods (e.g., Panda nuts are larger and harder to crack), and demonstrate that chimpanzees are able to adapt and optimize their tool use to their current environment (Carvalho et al., 2008). Although there were plans to establish longer term research presence in the area and continue primate archaeological work, no further chimpanzee expeditions took place in Diécké until 2018, except for the Wild Chimpanzee Foundation (WCF) survey of 2012 (Wild Chimpanzee Foundation, 2012).

Korohouan: revisited a decade later

In 2018, nearly a decade after the last primate archaeological research in the area, we returned to the Korohouan locality on a reconnaissance expedition to follow-up on previous work and check the current status of chimpanzee presence and technological activity. This included revisiting known nut-cracking sites, searching for new ones, documenting traces of chimpanzee presence, and recording the availability of resources and raw materials targeted

by chimpanzees. An additional goal was to document the presence of other wildlife and traces of human activities (e.g., fishing; hunting) to compare with earlier surveys.

Study site

Korohouan (7º 26' N; 8º 59' W) is a small village located near the southern border of the Diécké Forest, around 12 km north-west of Diécké town, along the Diécké-Pela road. It is approximately 150 km by road from Bossou via N'Zérékoré and Pela (Figure 6.3). The human population is around 3000 strong and largely lives off subsistence farming and employment by SOGUIPAH.

The Korohouan survey area includes a section to the north-east of the village within the classified area of the Diécké Forest (Figure 6.3). To facilitate surveys in this area, we set up a temporary camp at the former site of Camp Lethou (7° 27' N; 8° 54' W), located on the border of the Gbin river, around 18 km from the Korohouan village. Camp Lethou was originally established in 2008 during previous research activities in the area (Carvalho, 2009). The survey area also extends to Mont Medou (7º 24' N; 8º 59' W) - a small patch of forest surrounded by cultivation fields to the south of the village (Figure 3), where local people have frequently observed chimpanzees in the past (Carvalho, 2006).

Previous research: the 2006-2009 surveys

The Korohouan surveys of 2006-2009, led by SC, took place over 4 separate field trips, totalling 41 days: 14Apr2006 - 19Apr2006; 04Mar2009 - 16MAR09; 01Apr2009 - 14Apr2009; 30Apr09 - 10May2009. The research team identified total of four nut-cracking sites in the forest area. Two of the sites (SB4, SB5) had month-old traces of nut-cracking, and one other

site (SB3) appeared to have been inactive for several years as a number of tools were buried under soil (Carvalho et al., 2007). This abandoned site comprised of a large lithic assemblage (n = 40) and was the target of an archaeological excavation in 2009 (Carvalho, 2006, 2009).

Several chimpanzee traces were also found, including 21 arboreal nests, two faecal remains, five feeding traces, and three trails (Carvalho, 2006, 2009) (Table 6.2). In 2008, six chimpanzees were encountered while feeding on a *Landolphia owarensis* tree – the first and only direct sighting of chimpanzees during the entire survey period. Unpublished data also documented feeding traces of a monkey of unknown species, and tracks from a leopard (*Panthera pardus*), which is now facing rapid decline throughout West Africa, with only a few small remnant populations reported for Guinea (Stein et al., 2020). SC also noted that the hunting frequency in the forest was extremely high and found evidence that Camp Lethou was once used by illegal hunters in between research visits.

In the Mont Medou area, the team found an additional nut-cracking site (SB6), as well as 34 chimpanzee nests (Table 6.2). In March and April 2009, the team also deployed two camera traps in the Mont Medou area (Carvalho, 2009). Conversations with local community members in 2006, revealed that chimpanzees frequently visited the banana plantations around Mont Medou in search of food (Carvalho, 2006). Carvalho (2006) considered that the prevalence of chimpanzees in this comparatively small forest fragment could be an indication that chimpanzees in the Korohouan area were shifting their activity patterns (and perhaps even home range) away from the classified forest areas where hunting pressure was high, towards villages and plantations, where they could access high energy foods in relative safely. However, this remains to be formally investigated. Regarding commercial activities,

SOGHIPAH was already operating in the Korohouan area at the time of the surveys (Carvalho, 2011). SC was also informed of diamond mining in the vicinity.

Table 6.2. Chimpanzee traces documented in the Korohouan area during the 2006-2009 and the 2018 surveys. Values in brackets represent observations recorded by motion-trigger cameras.

	Classified area				Mont Medou			
Trace type	04/06	03/09	04/09	11/18	04/06	03/09	04/09	11/18
direct observation			1 (+1)				(+1)	
nut-cracking	3	1		2	1			
nests	6	8	7	1	25	3	6	
feeding	2		3					
tracks	1		2			1		4?
faeces			2			1		

Current research: 2018 survey

In 2018, KAW and MF organised a reconnaissance expedition between 25Nov2018 - 01Dec2018. The research team spent 5 days in the core area (25Nov2018 - 29Nov2018) and one day surveying Mont Medou (01DEC18). Fieldwork was conducted collaboratively with KAW leading the nut-cracking surveys, and MF coordinating the collection of wildlife and human presence data.

Surveys were initially conducted by navigating towards the four known locations of nut-cracking sites and to other features of interest documented between 2006-2009 (e.g. chimpanzee nests, traces of other primates, camera trap locations). We also carried out a 1.3 km line transect intersecting the two nut-cracking sites with the most recent traces of activity. All evidence of wildlife and human presence encountered during travel within the

forest reserve was logged on a hand-held GPS device and described by source (i.e., taxa), type of trace (e.g., footprint, feeding, snare, hunting camp, shotgun shells), as well as approximate age.

To enable comparisons with earlier records we calculated our total travel distance from live tracks recorded during fieldwork, after overlapping segments and stationary logs had been removed during post-processing in QGIS. We also recoded any concurrent traces of the same source and age as one observation, as these were likely to be the product of the same event.

All four previously recorded nut-cracking sites of the 2006-2009 surveys were found, a few of which still bearing traces of previous work such as white ink numbers on the nut trees or tools, and remnants of the test pits dug during the excavation at SB3. Two additional nut-cracking sites were encountered in the forest area. However, only two out of the 6 sites showed comparatively recent (~ 1 month old) traces of nut-cracking, including the excavated site that was inactive at the time of the 2006-2009 surveys and a newly discovered site nearby (~200 m South; Table 6.3). Based on the state of decay of cracked nuts and clarity of traces on the tools, we estimate that these two sites were last active around one year earlier. The remaining four sites showed very few traces, with distinctive pitting on tools becoming obscured by natural weathering, suggesting these sites have been inactive for several years.

No further chimpanzee traces were found, except for one decayed nest (~ 1 year old) in the core area, and 4 potential chimpanzee trails in Mont Medou (Table 6.2). Evidence of other wildlife (n = 23; Table 6.4) included footprints of mongoose (*Herpestes sanguineus*), duiker

(*Cephalophus* sp.), pangolin (Phataginus tricuspis), suids (*Hylochoerus meinertzhageni*; *Potamochorus porcus*), and forest buffalo (Syncerus caffer nanus), as well as feeding traces of a warthog and a monkey of unknown species (See Table E.1 and Table E.2 for a full list of fauna and flora encountered). All other traces encountered were of anthropogenic origin (n = 149; Table 6.5), and largely associated to hunting activity (e.g., snares, bullet casings, abandoned hunting camps; Figure 6.4). During the time spent at Camp Lethou, we also heard 6 gunshots over two consecutive nights.

Table 6.3. Data recorded for nut-cracking sites surveyed in 2006-2009 and 2018.

			2006-2009			2018		
ID	Year found	Species	Status[a]	Age of traces[b]	Tools (n)	Status[a]	Age of traces[b]	Tools (n)
TS42/SB4	2006	*Coula*	A	~ 1 mo	6	I		4
TS43/SB5	2006	*Coula*	A	~ 1 mo	11	I		7
TS44	2018	*Panda*				I		2
TS45/SB3	2006	*Panda*	I		40	A	~ 1 yr	37
TS46	2018	*Coula*				A	~ 1 yr	7
TS47/SB6	2006	*Panda*	U		10	I	> 1 yr	3

[a] = active; I = inactive; U = unknown
[b] mo = month; yr = year

Table 6.4. Summary of mammalian traces documented in 2011 by the WCF (144.8 km), compared with traces encountered during the 2018 survey in the Korohouan core area (21.7 km).

	2011 – Diécké Forest		2018 – Korohouan	
Taxa	n	n/km	n	n/km
Carnivores	3	0.02	0	0.00
Chimpanzees	44	0.3	1	0.05
Other primates	41	0.29	1	0.05
Bovids	420	2.9	2	0.09
Suids	23	0.16	4	0.18
Small mammals	21	0.14	14	0.65

Near the Korohouan village and *en route* towards the Diécké Forest, we encountered SOGHIPAH rubber and oil palm plantations, and crossed a large rice field adjoining the boundary to the protected area. We also found evidence of logging in the forest periphery, including a red timber species, likely *Lophira alata* – which is currently classified as vulnerable in the IUCN red list (Haba & Couch, 2018).The short survey of Mont Medou revealed that the surviving patch of forest has been further reduced by the expansion of new cultivation fields. Areas previously surveyed in 2006-2009 were deforested, and the tree upon which one of the camera traps was set up had been cut down. Hunting traces found in the area included two bullet casings and a snare that was likely intended for cane rats (*Thryonomys swinderianus*).

Table 6.5. Summary of traces of anthropogenic origin collected in 2011 by the WCF (144.8 km), compared with traces collected during the 2018 survey in the Korohouan core area (21.7 km). Blank cells indicate data that was unavailable/not collected.

		2011 – Diécké Forest		2018 – Korohouan	
		n	n/km	n	n/km
Hunting	Total	210	1.45	137	6.31
	Bullets			118	5.44
	Snares/traps			18	0.83
	Camps			3	0.14
Fishing				2	0.09
Trails		182	1.26	4	0.18
Agriculture		43	0.3	1	0.05
Logging		7	0.05		
Other traces			0.02	5	0.23

Discussion

Only two tool sites in the core area showed traces of relatively recent nut-cracking activity. The two sites were within 250 metres of each other, and all traces were around 1 year old.

This pattern is not much different from the 2006 records which documented two, albeit different, active sites with month-old traces that were around 50 metres apart. While new activity was observed at a site that was thought to be permanently abandoned in previous surveys, the fact that traces on tools at other previously recorded nut-cracking sites were becoming inconspicuous strongly suggests that nut-cracking activity in the area is in decline. This is likely a result of decreased chimpanzee presence as evidenced by the absence of other traces, except for one nest with a high level of decay, relative to the surveys conducted a decade earlier. While no formal data on human activity was collected during the 2006-2009 surveys, comparisons with data collected by the WCF in 2011 across the Diécké reserve indicate that the forest around Camp Lethou is suffering from a comparatively higher incidence of hunting when adjusted for distance surveyed, while signs of agricultural activity were much lower both per kilometre and relative to other anthropogenic traces. Whether



Figure 6.4. Material traces of human presence collected during surveys in the classified area: one shoe, a plastic bottle, dozens of wires used for snares, and >100 shotgun shells.

this difference reflects a historical trend across the entire Diécké forest or a local phenomenon remains to be determined. Nevertheless, it is clear that hunting activities are a major threat to chimpanzees in the Korohouan core area. Other taxa that appear to be dwindling in numbers relative to the 2012 census include other primates and bovids, while suids and other small mammals appear largely stable (Table 6.4).

In reports of the 2006-2009 surveys it was suggested that chimpanzees in the Korohouan area were favouring forest fragments outside the protected area, such as those around Mont Medou to avoid threats from hunting activities. Studies involving other chimpanzee populations have also documented increased use of buffer zones relative to neighbouring protected areas (Tweh et al., 2018), while orangutan research has highlighted the importance of forest fragments to the survival of metapopulations (Ancrenaz et al., 2021). Such studies are bringing to light the value of human-modified landscapes to primate conservation, although knowledge remains limited due to lack of data from unprotected areas (Galán-Acedo et al., 2019).

Approximately 25% of the total land area of the Guinée Forestière region has suffered from tree cover loss between 2000-2018, with agriculture identified as the primary driver (Fitzgerald et al., 2021). Our observations are consistent with this trend, suggesting that further agricultural expansion and deforestation in forest periphery are rendering this area increasingly less hospitable for chimpanzees. Added to the high levels of hunting pressure in the protected area, this is an indication that viable areas for chimpanzee habitation in the Korohouan vicinity are rapidly shrinking. While these findings suggest that the Korohouan area may no longer be a feasible site for studying chimpanzees and their nut-cracking behaviours, except perhaps in terms of archaeological investigations *sensu stricto* (e.g.,

excavations to uncover past behaviour and historical changes), further research seeking to understand the causes of chimpanzee decline both in the Diécké reserve and the forest periphery should provide valuable insights as to the thresholds of habitability by chimpanzees (and other wildlife). Diécké is now one of the many landscapes at the protected-anthropogenic interface and further research on the ground is crucial to inform conservation practices that support human-wildlife coexistence (as per Leblan and Soiret, 2021).

The WCF (2012) report indicates that different parts of the Diécké forest are affected by different types of anthropogenic disturbance to different degrees. This is likely due to the degree of accessibility of different regions of the forest, as well as topographic and hydrological variations in topography throughout the reserve (Robertson, 2001; Wild Chimpanzee Foundation, 2012). However, this has yet to be formally investigated. The spatial distribution of chimpanzees and other wildlife as of 2011 was equally heterogenous. Given that the evidence from Korohouan points to an overall lower biodiversity and an intensification of human activity relative to the 2012 assessment, it would be important to conduct follow-up forest-wide surveys to monitor changes in human activities and biodiversity in other parts of the forest and assess whether this reflects a localized or global trend. Critically, such surveys should also extend to buffer zones, as these may constitute important strongholds to the surviving chimpanzee populations (Galán-Acedo et al., 2019; Leblan & Soiret, 2021), especially considering that over 80% of western chimpanzees are estimated to live outside protected areas (Heinicke, Mundry, Boesch, Amarasekaran, et al., 2019). It would also be paramount to investigate how humans, chimpanzees and other animals use different habitat types to help better understand where conservation efforts are most needed and will be most effective.

During our surveys it was apparent that the Korohouan area continues to attract a high degree of commercial activity, particularly from the palm oil and rubber industry. Recent reports also allude to the commencement of logging operations in the Diécké forest, as well as iron ore mining to the South of the reserve. With convenient access to Liberia and transport routes to the coast and international trade, industrial operations in Diécké, as well as in other areas Guinée Forestiére rich in highly sought-after natural resources, are likely to proliferate for decades to come. Future investigations into community perceptions of industrial activities and how they are currently affecting local livelihoods at the interface of biodiversity and resource richness, such as Korohouan, will generate much-needed empirical evidence of their impact beyond the environmental sphere. This will be paramount for driving prospective economic investments towards concerted action between industry, conservation and human development that recognizes the needs of the local populations, ensures financial and food security, and empowers community-led, sustainable conservation efforts that build on indigenous knowledge and foster human-chimpanzee coexistence.

Acknowledgments

We are grateful to the people of Korohouan village for their support and hospitality. We thank our research teams: Cê Kanou Loua, Cê Koti Mamy, Honoré Mamy, Péh Fromo Mamy, Paquilé Cherif, Albert Kpomou (2006-2009); Clément Mamy, Justin Kpomi, Jules Doré, Henry Camara, Pascal Goumy, Guano Zogbila (2006-2009; 2018); and Jean Maomy (2018). We also thank the Direction Nationale de la Recherche Scientifique (Guinea), the Centre Forestier de N'Zérékoré (Guinea), the Institut de Recherche Environmentale de Bossou (Guinea), and the Kyoto University Primate Research Institute (Japan), for research permissions and logistical support.

This work was funded by the Fundação para a Ciência e Tecnologia (FCT) [grant number: SFRH/BD/115085/2016] to KAW, with support from the Programa Operacional Capital Humano (POCH) and the European Union; the Boise Trust Fund (University of Oxford) to KAW; the National Geographic Society [grant number: EC-399R-18] to KAW.

Chapter 7

Conclusion

Summary

Since the 1960's, human origins studies have benefitted greatly from research into the lives of one of our closest living relatives, the chimpanzee. This has been further enriched by the burgeoning field of primate archaeology which is providing new perspectives on the technical behaviours of our earliest ancestors. Nevertheless, this research is still overwhelmingly biased towards stone tools with a focus on typological characteristics, assemblage composition, raw material acquisition, raw material transport, and cultural variation. Its scope has also been partially curtailed by differences in field methods and spatial resolutions that limit comparisons between non-human primate and hominin archaeological records.

The overarching objective of this thesis was to provide further insights into how the environment may have shaped the behaviours of our earliest ancestors by advancing three key areas of primate archaeology:

I. **Mapping methods** through the development of a new approach that would enable standardized spatial resolution across primate records (Chapter 2);

II. **Perishable archaeology** by investigating the diversity and drivers of plant material procurement strategies in chimpanzee termite-fishing in order to expand our knowledge of perishable technology (Chapter 3);

III. **Landscape archaeology** by conducting the first landscape-scale study of the ecological and behavioural correlates of chimpanzee stone tool-use to gain a better understanding of the relationship between technological landscapes and patterns of landscape use (Chapters 4 and 5).

Negotiating the inherent differences between non-human primate and hominin archaeological contexts has been one of the biggest challenges that primate archaeology has faced since its inception. Rigorous empirical comparisons can only be achieved when data collection methods and sample sizes are equally comparable. While this is easily achievable under controlled laboratory settings, reproducing the same methods and achieving equal levels of success in two distinct field environments — e.g., the dense forests typical of most chimpanzee habitats and the arid rocky outcrops of the East African Rift — is no simple task.

Developing the new method for spatial mapping presented in Chapter 2 constituted one important step towards achieving this goal. This involved adapting the DistoX2 survey method, employed in speleological mapping, for use in above-ground archaeological settings. A custom tripod adapter was designed to enable setup in line with standard archaeological protocols and the system was tested extensively at both chimpanzee and hominin field sites to assess its performance relative to other methods. This new methodology proved to be a more reliable and accurate alternative to the current methods employed in primate archaeology, enabling, for the first time, standardised spatial resolution across the primate order.

Selection and transport of materials for stone tools was ubiquitous throughout our evolutionary history, but little is known about the behaviours associated with the use of plant technologies, which likely predated the first stone tools. Chapter 3 sought to address this gap by investigating the environmental determinants of raw material procurement strategies employed by chimpanzees for the manufacture of termite-fishing tools. It also sought to uncover potential intra-specific variations by comparing three chimpanzee populations in Tanzania: Gombe, Issa, and Mahale. The results showed that procedures of raw material acquisition differed between the three communities according to the local environment. Issa chimpanzees, who live in a more open and drier habitat, used sources more intensively, with frequency of removals per source decreasing with distance to the target termite mount. It was also found that, despite similar raw materials available at all sites, Issa and Mahale chimpanzees only used bark to manufacture tools, while at Gombe various materials were employed, indicating that raw material selection is yet another aspect of chimpanzee termite-fishing that is shaped by cultural processes, in addition to manufacture/modification and technique (e.g., Sanz et al., 2009; Sanz & Morgan, 2011). The

techno-cultural variation and flexible exploitation strategies revealed by this study parallel the behaviours associated to the use of stone tools by our earliest ancestors, suggesting these behaviours have a much deeper origin than originally thought.

Chapter 4 investigated the ecological conditions required for chimpanzee stone tool use to occur and persist over time in discrete locations. This was achieved through a landscape-scale study of the drivers of site selection, re-use, and abandonment in wild chimpanzee nut-cracking in Bossou (Guinea), with a focus on the role of three key resources: food, water, and shelter. The results showed that in addition to *proximity to a nut tree* and *availability of raw materials*, *abundance of food-providing trees* and *proximity to nesting locations* were significant predictors of nut-cracking activity in Bossou. This implies that the establishment of nut-cracking sites is spatially mediated by the broader foraging and behavioural context, such as feeding on tree foods and nocturnal sleeping. It was also found that the lower the number of usable tools present, the less likely a tool site remained in use. In contrast, the number of raw materials (stones) had no significant effect on site inactivity. This evidence combined provides compelling evidence of stigmergy, whereby visual traces of activity stimulate further activity in a self-perpetuating cycle.

The spatial relationship between nut-cracking sites, proximity to nest sites, and food availability, suggesting the presence of *activity hotspots*, is reminiscent of the '*favoured places' model* for the formation of hominin assemblages proposed by Schick (1987). As such, these findings present the first empirical evidence that chimpanzee stone tool use shares affinities with the patterns of landscape-use that have been proposed for our earliest tool-using ancestors.

The empirical data collected in Chapter 4 was used to develop an agent-based model that would allow a controlled experimental investigation of how variations in the distribution of key resources may shape landscape-scale patterns of stone tool use (Chapter 5). Following from Chapter 4, this research also focused on chimpanzee nut-cracking and its relationships to wild food distribution, water availability, and nesting sites. It was found that variations in the spatial patterning and availability of these key resources did not affect overall spatial patterning of nut cracking sites, nor frequency of nut-cracking events. However, it was also found that *variations in wild food distribution* and *water availability* had significant effects on other measures such as daily caloric intake, distance travelled per day, and rates of fission fusion. When examined as a whole, these results indicate that material traces of tool use may only be able to reveal one part of the behavioural multiplex of chimpanzee, and likely hominin, landscape use. While findings from Chapter 4 point to clear spatial relationships between ecological variables and where nut-cracking sites occur, these results suggest that the dynamic relationship between the environment, behaviour and the spatial patterning of stone tool use may be even more complex than originally thought.

The thesis concludes with a brief report on the conservation status and major threats to the Diécké Forest — the second largest forest in Guinea and home to another population of nut-cracking chimpanzees. Survey efforts were concentrated in the Korohouan area where research on chimpanzee nut-cracking had previously been conducted. The report found that the chimpanzee presence in the area continues to decline with no recent evidence of nut-cracking or other activities. Hunting was identified as one of the major threats to wildlife, but small-scale agriculture as well as commercial activities in the region are also having an impact on forest fragments outside the protected area, where chimpanzee presence had been documented in previous studies. To contextualise these findings, the report provided

the first extensive overview of the historical, socio-political, environmental, and scientific developments around Diécké. With industrial activity expected to proliferate in the region for decades to come, it is hoped that this chapter will serve testimony of the imposing threats to biodiversity in Diécké and provide empirical support towards future conservation efforts in Guinée Forestiére and elsewhere.

Challenges and limitations

One of the original goals of this thesis was to investigate whether early hominin lithic assemblages could have resulted from chimpanzee-like patterns of behaviour and whether diachronic changes in the spatial patterning of stone artefacts reflected changes in hominin behaviour and their relationship with the ecological landscape. To achieve this, archaeological and paleo-ecological data from Plio-Pleistocene deposits in Koobi Fora (Kenya) were collected using the same baseline methods employed at the chimpanzee field-site of Bossou. This involved targeting areas where archaeological sites had previously been identified and recorded and conducting transect and quadrat surveys of the surrounding landscape. Equally, all artefacts and features were mapped using the same spatial methods as Bossou.

As a proxy for ecological data, I collected and documented fossilized bone and wood to build a paleo-ecological profile of the surveyed areas. This was complemented by hydrological reconstructions available for the Koobi Fora region. Given the high level of post-depositional disturbance characteristic of surface assemblages (Isaac et al., 1997), it was also necessary to document a series of measures (e.g., depositional environment, degree

of winnowing, and patination on artefact surfaces) to evaluate the likelihood that the artefacts were found in their original locations.

Despite these additional considerations, application of this methodological protocol revealed some issues. The first, was that the quadrat area (a 5-metre radius circle) was too small to capture ecological parameters. Often the sample area would only contain stone artefacts, even though there were several fossils nearby. Secondly, in the absence of *in situ* deposits eroding out of the substrate, it was near impossible to assess with certainty whether the materials encountered belonged to the period, and associated stratigraphic deposit, of interest.

There were also additional logistical limitations. Fieldwork was facilitated through the Koobi Fora Field School who generously provided all research support, including transport and accommodation. The Field School is a large operation involving many researchers who are conducting fieldwork in different parts of the Koobi Fora region, while simultaneously teaching and training a cohort of undergraduate students. As there were not enough vehicles or drivers to get research teams out to the various sites every day, each researcher had a limited number of days to collect data. Consequently, the resulting dataset (32 quadrats between 4 temporal horizons) was much smaller than what was achieved in Bossou (195 quadrats) and was deemed insufficient for pursuing this line of enquiry. Brief reports of the two field trips to Koobi Fora can be found in Appendix F1.

In addition to the research presented for the chimpanzee nut-cracking site of Bossou (Chapter 5), an investigation of the distance and frequency of tool transport by chimpanzees was planned to gain further insights into the spatial displacement of artefacts over larger

timescales. This formed part of a larger National Geographic funded project led by Prof. Susana Carvalho – *Stones on the Move: The real life of a chimpanzee tool*. This ambitious project sought to adapt micro-GPS animal tracking technology to track the movement of chimpanzee nut-cracking tools over one year. While the devices were assembled and deployed successfully, and the chimpanzees used the modified tools despite the inconspicuous antennas attached to them, the resulting data revealed that the accuracy and the resolution of the micro-GPSs was insufficient for the study we hoped to conduct. This was likely due to canopy cover, and the fact that the chimpanzees often placed the devices face-down after manipulation, which limited the detection of GNSS satellites. Additionally, one of the devices stopped working shortly after deployment due to percussive impacts caused during nut-cracking. The battery-life was also lower than expected, so the study was only able to run for 6 months, instead of the planned 12. The small population (n = 7) also meant that nut-cracking occurrence, and, therefore, the displacement of tools was infrequent. It was therefore decided not to include this component in the main body of the thesis. Instead, a brief report is included in Appendix F2. Nevertheless, renewed efforts with smaller, more accurate devices and an upgraded GPS system may be commencing soon at nearby field sites where the chimpanzee populations are larger.

Finally, an analysis on the types of stones Bossou chimpanzees used for nut-cracking was also planned to better understand the role of raw material properties on the selection of stones and locations for nut-cracking activities. A series of stone samples were collected for X-Ray Diffraction (XRD) analysis and optical mineralogy with assistance from the University of Oxford Earth Sciences Department. This work commenced in February 2020 but was interrupted in March 2020 due to the imposition of COVID-19 restrictions and closure of the Earth Sciences labs. Attempts were made to resume work in November 2020, but new

restrictions in early 2021 led to the decision to reprioritize research efforts to other components of the DPhil. The results that were obtained are summarised in Appendix F3.

Future directions

PERISHABLE ARCHAEOLOGY[1]

The archaeology of the perishable, even at its infancy, is providing a new framework for reconstructing archaeologically invisible aspects of early human behaviour and our own technological origins (Almeida-Warren et al., 2017; Hernandez-Aguilar, 2009; Koops et al., 2015; Pascual-Garrido, 2018; Sanz & Morgan, 2007; Sept, 1992; Stewart et al., 2011). Future efforts should concentrate in providing information that will help contextualize the current archaeological record and aid investigations into potential, yet currently unknown, hominin sites and behaviours (Carvalho & Almeida-Warren, 2019). Current research in this direction includes using long-term records of chimpanzee nesting sites to model ranging patterns in early hominins (Haslam et al., 2009; Sept, 1992; Stewart et al., 2011), primate archaeological analysis of chimpanzee artefacts to enable comparisons with implements employed for similar purposes in the archaeological record (Backwell & D'Errico, 2001; Heaton & Pickering, 2006), and the identification of termite evidence at early human sites (Lesnik et al., 2019).

Still, much is yet to be done regarding archaeological investigations of chimpanzee and other non-human primate, perishable technology. Studying the mechanical properties of different plant materials (e.g., durability and flexibility), would help gain a better

[1] This section is modified after the *Future Directions* published originally in Pascual-Garrido and Almeida-Warren (2021)

understanding of chimpanzee material selection both in terms of type and plant species. This could be complemented by investigations of the physical properties of the tools themselves (e.g., shape, length, modifications) and experimental studies to explore how tool design might affect foraging and harvesting efficiency. Beyond providing insights into the cognitive abilities of the tool users, such studies will be instrumental in advancing our still limited knowledge about the behaviour of termites and other prey and their influence on tool typology (Möbius et al., 2008; Schöning et al., 2008).

Furthermore, archaeological studies of use wear, such as fraying on tool ends, can help to distinguish the diagnostic features of a tool and develop a framework for identifying, in the absence of direct observations, materials that have been used as tools from those that have not (Carvalho & Almeida-Warren, 2019; Heaton & Pickering, 2006). Finally, while this study focused on chimpanzee termite-fishing, this archaeology of the perishable can and should be applied to other plant-based technologies. With 21 types of plant tool use recorded for Bossou chimpanzees alone (Humle, 2011c; Whiten et al., 2001), we have only just scratched the surface of this exciting new direction of primate archaeological enquiry. The archaeology of the perishable, even within the challenges of long-term preservation, may contribute to a comprehensive understanding of primate technology as a whole, including the origins of human technology.

FORMATION OF CHIMPANZEE AND HOMININ TECHNOLOGICAL LANDSCAPES

The studies on landscape-scale patterns of chimpanzee technology (Chapter 4; Chapter 5) focused exclusively on stone tool use. This was a necessary choice to enable comparison with the hominin archaeological record, which is almost entirely composed of stone tools.

Nevertheless, chimpanzees, including the population of Bossou, also engage in a variety of activities that require the use of plant tools. Given their prevalence in present-day chimpanzee and hunter-gatherer tool kits, it is likely that they played an equally important role in the lives of early hominins, likely shaping their patterns of landscape use, and by consequence, the formation of lithic assemblages. Now that a first step has been established regarding stone tool use, future efforts should seek to expand this research towards perishable technology both to understand its role in the formation of archaeological landscapes, as well as investigate differences between landscape-scale patterns of plant and stone tool use and the potential environmental and behavioural mechanisms behind them. For the latter, termite-fishing offers exciting research potential as, like nut-cracking, this activity occurs in spatially discrete locations.

Likewise, research should be expanded to other chimpanzee communities to enable a broader perspective of site-specific, subspecies-specific, and universal patterns of tool site formation. These data could also be employed to further improve and refine the agent-based model presented in Chapter 5, so that it is empirically relevant to a wide range of landscapes.

One major research gap that became evident during the development of this project is the scarcity of data pertaining to the energetic value of different plant food types, the daily energetic intake across different seasons, as well as the frequency of drinking bouts. This information is well documented only for a few sites, namely Kanyawara in Kibale, Uganda (and Fongoli, Senegal regarding water intake). Efforts to collect such data from other sites would be invaluable to building a clearer picture of the affordances of different chimpanzee habitats, and how they may affect patterns of behaviour.

With a larger and more comprehensive empirical dataset, the model complexity could be gradually expanded to integrate more refined ecological characteristics, such as the spatial distribution and seasonality of different food species, life cycles of oil palms, and longevity of tools (e.g., the length of time they can be used for). Some of these features have been successfully integrated in other ABMs (Griffith et al., 2010; Reeves, Proffitt, et al., 2021), however, these have overlooked many of elements and interactions considered in the present model. Equally, given that chimpanzees (and hominins) are selective of the raw materials they use for tools (see Chapter 3), it would be relevant to factor in preferences for raw material type, as well as additional characteristics such as size and durability. As mentioned in the previous section, work towards achieving this was initiated during this project, and will be revisited in the future.

The focus of this research was to explore the role of critical resources – water, food, and shelter – on patterns of landscape use and the formation of tool sites. Nevertheless, these are not the only ecological factors that may shape patterns of primate landscape use. The presence or absence of predators, and even resource competition with neighbouring or sympatric groups (whether of the same or different species), can also affect how primates navigate their home-ranges and where they choose to engage in different activities (Basabose & Yamagiwa, 2002; Coleman & Hill, 2014; D. B. Morgan & Sanz, 2006). Other factors worthy of integration of topology and human-made pathways, which have recently been shown to shape chimpanzee travel routes (Green, Boruff, & Grueter, 2020; Green, Boruff, Bonnell, et al., 2020). Such considerations were beyond the scope of the present project, but future efforts to bring together all these different elements, will ultimately help produce an ever more accurate representation of the dynamic and complex relationships

between chimpanzees, the habitats they live in, and the behavioural traces they leave across the landscape.

Above all, it will be paramount to apply these models to hominin contexts, using ecological data drawn from paleoenvironmental reconstructions to explore what sets of conditions may have generated the observed spatial patterns of hominin stone artefacts. More and more detailed large-scale paleo-reconstructions of hominin environment are becoming available. However, there is still insufficient standardized data available regarding landscape-scale distributions of hominin lithic assemblages. Despite Isaac's seminal work on investigating the "scatters-between-the-patches", archaeological research has continued to focus primarily on the ~10% of the archaeological record found at larger sites. During this project, renewed attempts to collect these data proved unsuccessful, highlighting yet another method that was unable to surmount the prevailing challenges of studying surface materials. Further efforts are needed to explore and test novel data collection methods that can quickly sample artefact and fossil distributions over a large surface area, while minimizing chronostratigraphic uncertainties.

CONSERVING CHIMPANZEES AND THEIR CULTURAL HERITAGE

The research conducted in Bossou and Diécké (Chapter 4; Chapter 6) has provided important insights into the fragility of West African chimpanzee populations and their habitats. The Bossou chimpanzees, like the infamous chimpanzees of Gombe, captivated the public's imagination and curiosity about the rich lives of one of our closest living relatives, through features in several news and popular science articles. Decades of research have provided invaluable knowledge and understanding of their social behaviours, learning processes, technology, ingenuity, as well as adaptations to anthropogenic change (Matsuzawa et al.,

2011). Yet this once 23-strong community has now dwindled to a mere seven individuals, with fading behavioural traditions and meagre prospects of recovery.

While the Bossou chimpanzees demise may be inevitable, we can safeguard their legacy and cultural heritage through documenting and preserving the material (as well as immaterial) traces they leave behind. Primate archaeology and ethnographic approaches are well suited for this task and continued investigations will help ensure that the story of the Bossou chimpanzees is kept alive for generations to come.

The present study has provided further evidence that spatial patterns of chimpanzee behaviour are not random, and that their environment influences their behaviour and where they might practice certain activities (Chapter 4; Chapter 5). Additionally, some of these patterns may be culturally driven, as was found regarding the selection of raw materials for tools (Chapter 3). While chimpanzees are capable of adapting to change (Dijk et al., 2021; Hockings et al., 2015; Kalan et al., 2020; McCarthy et al., 2017), these adaptations may come at a high cost (Kühl et al., 2019). As such, conservation efforts can no longer be just about preserving a population, but must also extend towards the landscapes and cultures they depend on (Carvalho et al., 2022). Further landscape-scale research into the complex relationships between ecology and behaviour will be crucial to the development of holistic conservation strategies.

The Diécké forest bears witness that even protected areas are insufficient for preserving chimpanzees and other wildlife. With large scale industrial activity expected to continue in the region, it may only be a matter of time before the second largest forest of Guinea loses its chimpanzees. Many of these industries promise much needed infrastructure,

development, and employment to the region, potentially encroaching on biodiversity and conflicting with conservation objectives. However, increasing evidence suggests that local communities may not always benefit from these commercial ventures, reporting poor working conditions, and negative impacts of industrial refuse on health (Chapter 6). Further research is needed to understand the impacts of industry not only on biodiversity, but also human welfare. This can be achieved by conducting interviews with local communities in tandem with more regular biodiversity surveys (Bersacola et al., 2021; Staddon et al., 2021). Importantly, this is needed not only from Diécké, but also from other protected and unprotected forests elsewhere in Guinea to get a better sense of global and site-specific impacts. This will be critical to ensure the development of tailored strategies that put conservation hand-in-hand with human needs (Carvalho et al., 2022; Junker et al., 2017).

Bibliography

Abwe, E. E., & Morgan, B. J. (2008). The Ebo forest: Four years of preliminary research and conservation of the Nigeria-Cameroon chimpanzee (*Pan troglodytes vellerosus*). *Pan Africa News*, *15*(2).

Akobi, B., & Poissonnier, G. (2021). Les dernières forêts primaires de Guinée, un patrimoine mondial en danger. *Revue Internationale et Stratégique*, *N° 121*(1), 51–61. https://doi.org/https://doi.org/10.3917/ris.121.0051

Al Khaldiya Mining. (2021). *Al Khaldiya Mining Projects - Diecké*. https://www.akm-brasil.com/projects

Alden, E. S., & Choi, J.-K. (2007). The emergence of inequality in small-scale societies: simple scenarios and agent-based simulations. In T. Kohler & S. van der Leeuw (Eds.), *Modeling Socioecological Systems*. SAR Press.

Allsop, K. A., & Miller, J. B. (1996). Honey revisited: a reappraisal of honey in pre-industrial diets. *British Journal of Nutrition*, *75*(4), 513–520. https://doi.org/10.1079/BJN19960155

Almeida-Warren, K., Braun, D. R., & Carvalho, S. (2021). The DistoX2: A methodological solution to archaeological mapping in poorly accessible environments. *Journal of Archaeological Science: Reports*, *35*, 102688. https://doi.org/10.1016/J.JASREP.2020.102688

Almeida-Warren, K., Braun, D. R., Matsuzawa, T., & Carvalho, S. (2018). Mapping primate archaeology: New tools for standardizing spatial data collection across the primate

order. *Proceedings of the XXVIIth Congress of the International Primatological Society, 19-15 August.*

Almeida-Warren, K., Matsuzawa, T., & Carvalho, S. (2021). Landscaping the behavioural ecology of primate stone tool use. *BioRxiv*, 2021.08.24.457369. https://doi.org/10.1101/2021.08.24.457369

Almeida-Warren, K., Sommer, V., Piel, A. K., & Pascual-Garrido, A. (2017). Raw material procurement for termite fishing tools by wild chimpanzees in the Issa valley, Western Tanzania. *American Journal of Physical Anthropology*, *164*(2), 292–304. https://doi.org/10.1002/ajpa.23269

Ancrenaz, M., Oram, F., Nardiyono, N., Silmi, M., Jopony, M. E. M., Voigt, M., Seaman, D. J. I., Sherman, J., Lackman, I., Traeholt, C., Wich, S. A., Santika, T., Struebig, M. J., & Meijaard, E. (2021). Importance of small forest fragments in agricultural landscapes for maintaining orangutan metapopulations. *Frontiers in Forests and Global Change*, *4*, 5. https://doi.org/10.3389/ffgc.2021.560944

Anderson, D. P., Nordheim, E. V., Boesch, C., & Moermond, T. C. (2002). Factors influencing fission–fusion grouping in chimpanzees in the Taï National Park, Côte d'Ivoire. *Behavioural Diversity in Chimpanzees and Bonobos*, 90–101. https://doi.org/10.1017/CBO9780511606397.010

Andrefsky, W. (1994). Raw-Material Availability and the Organization of Technology. *American Antiquity*, *59*(1), 21–34. https://doi.org/10.2307/3085499

Arroyo, A., & de la Torre, I. (2016). Assessing the function of pounding tools in the Early Stone Age: A microscopic approach to the analysis of percussive artefacts from Beds I and II, Olduvai Gorge (Tanzania). *Journal of Archaeological Science*, *74*, 23–34. https://doi.org/10.1016/j.jas.2016.08.003

Arroyo, A., Harmand, S., Ene Roche, H., & Taylor, N. (2020). Searching for hidden activities:

Percussive tools from the Oldowan and Acheulean of West Turkana, Kenya (2.3-1.76 Ma). *Journal of Archaeological Science*, *123*, 105238. https://doi.org/10.1016/j.jas.2020.105238

Backwell, L. R., & D'Errico, F. (2001). Evidence of termite foraging by Swartkrans early hominids. *Proceedings of the National Academy of Sciences of the United States of America*, *98*(4), 1358–1363. https://doi.org/10.1073/pnas.98.4.1358

Badji, L., Ndiaye, P. I., Lindshield, S. M., Ba, C. T., & Pruetz, J. D. (2018). Savanna chimpanzee (*Pan troglodytes verus*) nesting ecology at Bagnomba (Kedougou, Senegal). *Primates*, *59*(3), 235–241. https://doi.org/10.1007/s10329-017-0647-2

Baldé, A. O. (2018a, January 5). *N'Zérékoré: la Forêt forte obtient l'exploitation de la grandes forêts de Ziama et de Diécké*. Aminata. https://aminata.com/nzerekore-foret-forte-obtient-lexploitation-de-grandes-forets-de-ziama-de-diecke/

Baldé, A. O. (2018b, March 16). *Nzérékoré: la Société Forêt Forte abuse la coupe des bois*. Aminata. https://aminata.com/nzerekore-la-societe-foret-forte-abuse-la-coupe-des-bois/

Balde, B. S., Diawara, M., Rossignoli, C. M., & Gasparatos, A. (2019). Smallholder-Based Oil Palm and Rubber Production in the Forest Region of Guinea: An Exploratory Analysis of Household Food Security Outcomes. *Agriculture*, *9*(41). https://doi.org/10.3390/AGRICULTURE9020041

Ballesteros, D., Domínguez-Cuesta, M. J., Jiménez-Sánchez, M., & González- Pumariega, P. (2013). Tape-compass-clinometer, DistoX or total station, what is the best method to elaborate a cave survey? A case study in El Pindal Cave, Spain. *8th International Conference (AIG) on Geomorphology, 27-31 August, Paris*.

Ban, S. D., Boesch, C., & Janmaat, K. R. L. (2014). Taï chimpanzees anticipate revisiting high-valued fruit trees from further distances. *Animal Cognition*, *17*(6), 1353–1364.

https://doi.org/10.1007/s10071-014-0771-y

Barceló, J. A., & Del Castillo, F. (2016). Simulating the Past for Understanding the Present. A Critical Review. In J. A. Barceló & F. Del Castillo (Eds.), *Simulating Prehistoric and Ancient Worlds. Computational Social Sciences* (pp. 1–140). Springer. https://doi.org/10.1007/978-3-319-31481-5_1

Barratt, C. D., Lester, J. D., Gratton, P., Onstein, R. E., Kalan, A. K., McCarthy, M. S., Bocksberger, G., White, L. C., Vigilant, L., Dieguez, P., Abdulai, B., Aebischer, T., Agbor, A., Assumang, A. K., Bailey, E., Bessone, M., Buys, B., Carvalho, J. S., Chancellor, R., … Kühl, H. (2021). Quantitative estimates of glacial refugia for chimpanzees (*Pan troglodytes*) since the Last Interglacial (120,000 BP). *American Journal of Primatology*, *83*(10), e23320. https://doi.org/10.1002/AJP.23320

Barrett, B. J., Monteza-Moreno, C. M., Dogandžić, T., Zwyns, N., Ibáñez, A., & Crofoot, M. C. (2018). Habitual stone-tool-aided extractive foraging in white-faced capuchins, *Cebus capucinus*. *Royal Society: Open Science*, *5*(181002). https://doi.org/10.1098/rsos.181002

Barsky, D. (2009). An Overview of Some African and Eurasian Oldowan Sites: Evaluation of Hominin Cognition Levels, Technological Advancement and Adaptive Skills. In E. Hovers & D. R. Braun (Eds.), *Interdisciplinary Approaches to the Oldowan. Vertebrate Paleobiology and Paleoanthropology.* (pp. 39–47). Springer. https://doi.org/10.1007/978-1-4020-9060-8_4

Bartón, K. (2020). *MuMIn: Multi-Model Inference. R package version 1.43.17.*

Barton, R. A., Whiten, A., Strum, S. C., Byrne, R. W., & Simpson, A. J. (1992). Habitat use and resource availability in baboons. *Animal Behaviour*, *43*(5), 831–844. https://doi.org/10.1016/S0003-3472(05)80206-4

Basabose, A. K., & Yamagiwa, J. (2002). Factors affecting nesting site choice in chimpanzees

at Tshibati, Kahuzi-Biega national park: Influence of sympatric gorillas. *International Journal of Primatology*, *23*(2), 263–282. https://doi.org/10.1023/A:1013879427335

Behrensmeyer, A. K. (2011). Conversations with Glynn's ghost: the evolution of paleolandscape research at East Turkana. In J. M. Sept & D. Pilbeam (Eds.), *Casting the Net Wide: Papers in Honor of Glynn Isaac and His Approach to Human Origins Research* (pp. 21–40). Oxbow Books.

Bergen, M. (2020, October 23). *Mining Threatens Largest Population of Western Chimpanzees*. Global Wildlife Conservation. https://www.rewild.org/news/mining-threatens-largest-population-of-western-chimpanzees

Bermejo, M., & Illera, G. (1999). Tool-set for termite-fishing and honey extraction by wild chimpanzees in the Lossi Forest, Congo. *Primates*, *40*(4), 619–627. https://doi.org/10.1007/BF02574837

Bersacola, E., Parathian, H., Frazão-Moreira, A., Jaló, M., Sanhá, A., Regalla, A., Saíd, A. R., Quecuta, Q., Camará, S. T., Quade, S. M. F. F., Jaquite, S. M., Lopes, A. G., Patrono, L. V., Ramon, M., Bessa, J., Godley, B. J., Bonneaud, C., Leendertz, F. H., & Hockings, K. J. (2021). Developing an Evidence-Based Coexistence Strategy to Promote Human and Wildlife Health in a Biodiverse Agroforest Landscape. *Frontiers in Conservation Science*, *0*, 85. https://doi.org/10.3389/FCOSC.2021.735367

Bertolani, P. (2013). *Ranging and travelling patterns of wild chimpanzees at Kibale, Uganda: a GIS approach*. PhD Thesis. University of Cambridge.

Binford, L. R. (1980). Willow Smoke and Dogs' Tails: Hunter-Gatherer Settlement Systems and Archaeological Site Formation. *American Antiquity*, *45*(1), 4–20.

Binford, L. R. (1981). *Bones: Ancient Men and Modern Myths. Studies in Archaeology.* Elsevier. https://doi.org/10.1016/C2013-0-07180-0

Binford, L. R. (1983). *In pursuit of the past : decoding the archaeological record* (2nd ed.).

University of California Press.

Bluff, L. A., Troscianko, J., Weir, A. A. S., Kacelnik, A., & Rutz, C. (2010). Tool use by wild New Caledonian crows *Corvus moneduloides* at natural foraging sites. *Proceedings of the Royal Society B: Biological Sciences*, *277*(1686), 1377–1385. https://doi.org/10.1098/rspb.2009.1953

Blumenschine, R. J. (1987). Characteristics of an Early Hominid Scavenging Niche. *Current Anthropology*, *28*(4), 383–407.

Blumenschine, R. J., & Masao, F. T. (1991). Living sites at Olduvai Gorge, Tanzania? Preliminary landscape archaeology results in the basal Bed II lake margin zone. *Journal of Human Evolution*, *21*(6), 451–462. https://doi.org/10.1016/0047-2484(91)90095-D

Blumenschine, R. J., Masao, F. T., Tactikos, J. C., & Ebert, J. I. (2008). Effects of distance from stone source on landscape-scale variation in Oldowan artifact assemblages in the Paleo-Olduvai Basin, Tanzania. *Journal of Archaeological Science*, *35*(1), 76–86. https://doi.org/10.1016/j.jas.2007.02.009

Blumenschine, R. J., Stanistreet, I. G., & Masao, F. T. (2012). Olduvai Gorge and the Olduvai Landscape Paleoanthropology Project. *Journal of Human Evolution*, *63*(2), 247–250. https://doi.org/10.1016/j.jhevol.2012.05.005

Bobe, R., Behrensmeyer, A. K., & Chapman, R. E. (2002). Faunal change, environmental variability and late Pliocene hominin evolution. *Journal of Human Evolution*, *42*(4), 475–497. https://doi.org/10.1006/jhev.2001.0535

Bobe, R., & Carvalho, S. (2019). Hominin diversity and high environmental variability in the Okote Member, Koobi Fora Formation, Kenya. *Journal of Human Evolution*, *126*, 91–105. https://doi.org/10.1016/j.jhevol.2018.10.012

Boero, R., Bravo, G., Castellani, M., & Squazzoni, F. (2010). Why Bother with What Others Tell You? An Experimental Data-Driven Agent-Based Model. *Journal of Artificial Societies*

and Social Simulation, *13*(3). https://doi.org/10.18564/jasss.1620

Boesch, C., & Boesch-Achermann, H. (2000). *The chimpanzees of the Taï Forest: behavioural ecology and evolution*. Oxford University Press.

Boesch, C., & Boesch, H. (1984a). Mental map in wild chimpanzees: An analysis of hammer transports for nut cracking. *Primates*, *25*(2), 160–170. https://doi.org/10.1007/BF02382388

Boesch, C., & Boesch, H. (1984b). Possible causes of sex differences in the use of natural hammers by wild chimpanzees. *Journal of Human Evolution*, *13*(5), 415–440. https://doi.org/10.1016/S0047-2484(84)80055-X

Boesch, C., & Boesch, H. (1990). Tool Use and Tool Making in Wild Chimpanzees. *Folia Primatologica*, *54*(1–2), 86–99. https://doi.org/10.1159/000156428

Boesch, C., Head, J. S., & Robbins, M. M. (2009). Complex tool sets for honey extraction among chimpanzees in Loango National Park, Gabon. *Journal of Human Evolution*, *56*(6), 560–569. https://doi.org/10.1016/j.jhevol.2009.04.001

Boesch, C., Kalan, A. K., Agbor, A., Arandjelovic, M., Dieguez, P., Lapeyre, V., & Kühl, H. S. (2017). Chimpanzees routinely fish for algae with tools during the dry season in Bakoun, Guinea. *American Journal of Primatology*, *79*(3), 1–7. https://doi.org/10.1002/ajp.22613

Boesch, C., Kalan, A. K., Mundry, R., Arandjelovic, M., Pika, S., Dieguez, P., Ayimisin, A. E., Barciela, A., Coupland, C., Egbe, V. E., Eno-Nku, M., Michael Fay, J., Fine, D., Hernandez-Aguilar, R. A., Hermans, V., Kadam, P., Kambi, M., Llana, M., Maretti, G., … Kühl, H. S. (2020). Chimpanzee ethnography reveals unexpected cultural diversity. *Nature Human Behaviour*, *4*(9), 910–916. https://doi.org/10.1038/s41562-020-0890-1

Bogart, S. L., & Pruetz, J. D. (2008). Ecological context of savanna chimpanzee (*Pan troglodytes verus*) termite fishing at Fongoli, Senegal. *American Journal of Primatology*, *70*(6), 605–612. https://doi.org/10.1002/ajp.20530

Bogart, S. L., & Pruetz, J. D. (2011). Insectivory of savanna chimpanzees (*Pan troglodytes verus*) at Fongoli, Senegal. *American Journal of Physical Anthropology*, *145*(1), 11–20. https://doi.org/10.1002/ajpa.21452

Brain, C. K. (1983). *The hunters or the hunted? An introduction to African cave taphonomy*. University of Chicago Press.

Brantingham, P. J. (2003). A neutral model of stone raw material procurement. *American Antiquity*, *68*(3), 487–509. https://doi.org/10.2307/3557105

Braun, D. R. (2012). What does Oldowan technology represent in terms of hominin behavior? In M. Domínguez-Rodrigo (Ed.), *Stone Tools and Fossil Bones: Debates in the Archaeology of Human Orgins* (pp. 222–244). Cambridge University Press.

Braun, D. R. (2013). The behavior of plio-pleistocene hominins: archaeological perspectives. In M. Sponheimer, J. Lee-Torp, & K. Reed (Eds.), *Early Hominin Paleoecology* (pp. 325–351). University Press of Colorado.

Braun, D. R., Aldeias, V., Archer, W., Arrowsmith, J. R., Baraki, N., Campisano, C. J., Deino, A. L., DiMaggio, E. N., Dupont-Nivet, G., Engda, B., Feary, D. A., Garello, D. I., Kerfelew, Z., McPherron, S., Patterson, D. B., Reeves, J. S., Thompson, J. C., & Reed, K. E. (2019). Earliest known Oldowan artifacts at >2.58 Ma from Ledi-Geraru, Ethiopia, highlight early technological diversity. *Proceedings of the National Academy of Sciences of the United States of America*, *116*(24), 11712–11717. https://doi.org/10.1073/pnas.1820177116

Braun, D. R., Plummer, T., Ditchfield, P., Ferraro, J. V, Maina, D., Bishop, L. C., & Potts, R. (2008). Oldowan behavior and raw material transport: perspectives from the Kanjera Formation. *Journal of Archaeological Science*, *35*(8), 2329–2345. https://doi.org/10.1016/j.jas.2008.03.004

Braun, D. R., Plummer, T., Ferraro, J. V, Ditchfield, P., & Bishop, L. C. (2009). Raw material quality and Oldowan hominin toolstone preferences: evidence from Kanjera South,

Kenya. *Journal of Archaeological Science*, *36*(7), 1605–1614. https://doi.org/10.1016/j.jas.2009.03.025

Braun, D. R., Rogers, M. J., Harris, J. W. K., & Walker, S. J. (2008). Landscape-scale variation in hominin tool use: Evidence from the Developed Oldowan. *Journal of Human Evolution*, *55*(6), 1053–1063. https://doi.org/10.1016/j.jhevol.2008.05.020

Braun, D. R., Tactikos, J. C., Ferraro, J. V, Arnow, S. L., & Harris, J. W. K. (2008). Oldowan reduction sequences: methodological considerations. *Journal of Archaeological Science*, *35*(8), 2153–2163. https://doi.org/10.1016/j.jas.2008.01.015

Brugière, D., & Kormos, R. (2008). Review of the protected area network in Guinea, West Africa, and recommendations for new sites for biodiversity conservation. *Biodiversity and Conservation*, *18*(4), 847–868. https://doi.org/10.1007/S10531-008-9508-Z

Bryson-Morrison, N., Beer, A., Gaspard Soumah, A., Matsuzawa, T., & Humle, T. (2020). The macronutrient composition of wild and cultivated plant foods of West African chimpanzees (*Pan troglodytes verus*) inhabiting an anthropogenic landscape. *American Journal of Primatology*, *82*(3). https://doi.org/10.1002/ajp.23102

Bryson-Morrison, N., Matsuzawa, T., & Humle, T. (2016). Chimpanzees in an anthropogenic landscape: Examining food resources across habitat types at Bossou, Guinea, West Africa. *American Journal of Primatology*, *78*(12), 1237–1249. https://doi.org/10.1002/ajp.22578

Bryson-Morrison, N., Tzanopoulos, J., Matsuzawa, T., & Humle, T. (2017). Activity and Habitat Use of Chimpanzees (*Pan troglodytes verus*) in the Anthropogenic Landscape of Bossou, Guinea, West Africa. *International Journal of Primatology*, *38*(2), 282–302. https://doi.org/10.1007/s10764-016-9947-4

Burkill, H. M. (1985). Panda oleosa Pierre [family PANDACEAE]. In *The useful plants of west tropical Africa, Vol 4*. Royal Botanic Gardens, Kew. University Press of Virginia.

Burnham, K. P., & Anderson, D. R. (Eds.). (2004). *Model Selection and Multimodel Inference* (2nd ed). Springer. https://doi.org/10.1007/b97636

Camara, M. (2017, April 11). *Forêt forte: Accusé de détruire les forêts classées de Ziama et Diécké, le directeur général de Forêt forte donne des précisions*. Le Courrier de Conakry. https://lecourrierdeconakry.com/foret-forte-accuse-de-detruire-les-forets-classees-de-ziama-et-diecke-le-directeur-general-de-foret-forte-donne-des-precisions/

Carrella, E. (2021). No Free Lunch when Estimating Simulation Parameters. *Journal of Artificial Societies and Social Simulation*, *24*(2). https://doi.org/10.18564/jasss.4572

Carvalho, J. S., Meyer, C. F. J., Vicente, L., & Marques, T. A. (2015). Where to nest? Ecological determinants of chimpanzee nest abundance and distribution at the habitat and tree species scale. *American Journal of Primatology*, *77*(2), 186–199. https://doi.org/10.1002/ajp.22321

Carvalho, S. (2006). Report of Research Activities at Bossou-Diecké for the Periods of 07/Jan/2006-10/May/2006 and 25/Nov/2006-14/Dec/2006. In *Unpublished report*.

Carvalho, S. (2009). KUPRI International: Research Activities from April 2008 to April 2009. In *Unpublished report*.

Carvalho, S. (2011). Diécké Forest, Guinea: Delving into Chimpanzee Behavior Using Stone Tool Surveys. In T. Matsuzawa, T. Humle, & Y. Sugiyama (Eds.), *The Chimpanzees of Bossou and Nimba* (pp. 301–312). Springer Japan.

Carvalho, S., & Almeida-Warren, K. (2019). Primate Archaeology. In J. Chun Choe (Ed.), *Encyclopedia of Animal Behavior* (2nd ed., Vol. 1, pp. 397–407). Elsevier. https://doi.org/10.1016/B978-0-12-809633-8.90156-0

Carvalho, S., & Beardmore-Herd, M. (2019). Technological Origins: Primate Perspectives and Early Hominin Tool Use in Africa. In *Oxford Research Encyclopedia of African History*. Oxford University Press. https://doi.org/10.1093/acrefore/9780190277734.013.75

Carvalho, S., Biro, D., McGrew, W. C., & Matsuzawa, T. (2009). Tool-composite reuse in wild chimpanzees (*Pan troglodytes*): archaeologically invisible steps in the technological evolution of early hominins? *Animal Cognition*, *12*(S1), 103–114. https://doi.org/10.1007/s10071-009-0271-7

Carvalho, S., Cunha, E., Sousa, C., & Matsuzawa, T. (2008). Chaînes opératoires and resource-exploitation strategies in chimpanzee (*Pan troglodytes*) nut cracking. *Journal of Human Evolution*, *55*(1), 148–163. https://doi.org/10.1016/j.jhevol.2008.02.005

Carvalho, S., Cunha, E., Sousa, C., & Matsuzawa, T. (2011). Extensive surveys of chimpanzee stone tools: from the telescope to the magnifying glass. In T. Matsuzawa, T. Humle, & Y. Sugiyama (Eds.), *The Chimpanzees of Bossou and Nimba* (pp. 145–155). Springer Japan.

Carvalho, S., Matsuzawa, T., & McGrew, W. C. (2013). From pounding to knapping: How chimpanzees can help us to model hominin lithics. In C. M. Sanz, J. Call, & C. Boesch (Eds.), *Tool Use in Animals* (pp. 225–241). Cambridge University Press. https://doi.org/10.1017/CBO9780511894800.015

Carvalho, S., & McGrew, W. C. (2012). The origins of the Oldowan: Why chimpanzees (*Pan troglodytes*) still are good models for technological evolution in Africa. In M. Domínguez-Rodrigo (Ed.), *Stone Tools and Fossil Bones: Debates in the Archaeology of Human Origins* (pp. 201–221). Cambridge University Press. https://doi.org/10.1017/CBO9781139149327.010

Carvalho, S., Sousa, C., & Matsuzawa, T. (2007). New Nut-Cracking Sites in Diecké Forest, Guinea: An Overview of the Surveys. *Pan Africa News*, *14*(1), 11–13.

Carvalho, S., Wessling, E. G., Abwe, E. E., Almeida-Warren, K., Arandjelovic, M., Boesch, C., Danquah, E., Diallo, M. S., Hobaiter, C., Hockings, K. J., Humle, T., Ikemeh, R. A., Kalan, A. K., Luncz, L. V, Ohashi, G., Pascual-Garrido, A., Piel, A. K., Samuni, L., Soiret, S., … Koops,

K. (2022). Using nonhuman culture in conservation requires careful and concerted action. *Conservation Letters*, e12860. https://doi.org/10.1111/CONL.12860

Cegielski, W. H., & Rogers, J. D. (2016). Rethinking the role of Agent-Based Modeling in archaeology. *Journal of Anthropological Archaeology*, *41*, 283–298. https://doi.org/10.1016/j.jaa.2016.01.009

Coleman, B. T., & Hill, R. A. (2014). Living in a landscape of fear: The impact of predation, resource availability and habitat structure on primate range use. *Animal Behaviour*, *88*, 165–173. https://doi.org/10.1016/j.anbehav.2013.11.027

Collins, D. A., & McGrew, W. C. (1987). Termite fauna related to differences in tool-use between groups of chimpanzees (*Pan troglodytes*). *Primates*, *28*(4), 457–471. https://doi.org/10.1007/BF02380861

Collins, D. A., & McGrew, W. C. (1988). Habitats of three groups of chimpanzees (Pan troglodytes) in western Tanzania compared. *Journal of Human Evolution*, *17*(6), 553–574. https://doi.org/10.1016/0047-2484(88)90084-X

Conard, N. J., Serangeli, J., Böhner, U., Starkovich, B. M., Miller, C. E., Urban, B., & Van Kolfschoten, T. (2015). Excavations at Schöningen and paradigm shifts in human evolution. *Journal of Human Evolution*, *89*, 1–17. https://doi.org/10.1016/j.jhevol.2015.10.003

Conklin-Brittain, N. L., Knott, C. D., & Wrangham, R. W. (2006). Energy intake by wild chimpanzees and orangutans: methodological considerations and a preliminary companson. In G. Hohmann, M. M. Robbins, & C. Boesch (Eds.), *Feeding Ecology in Apes and Other Primates. Ecological, Physical and Behavioral Aspects* (pp. 445–463). Cambridge University Press.

Convention on International Trade in Endangered Species of Wild Fauna and Flora. (2019). West and Central Africa Wildlife Crime Threat Assessment. *CITES CoP18*.

Copeland, S. R. (2007). Vegetation and plant food reconstruction of lowermost Bed II, Olduvai Gorge, using modern analogs. *Journal of Human Evolution*, *53*(2), 146–175. https://doi.org/10.1016/j.jhevol.2007.03.002

Corvi, M. (2016). *TopoDroid* (2.7).

Couch, C., & Haba, P. M. (2018). TIPA assessment: Dièckè Classified Forest, Yomou Préfecture. *Royal Botanic Gardens, Kew*.

Crabtree, S. A., Millington, J., & Wainwright, J. (2016). Simulating Littoral Trade: Modeling the Trade of Wine in the Bronze to Iron Age Transition in Southern France. *Land 2016, Vol. 5, Page 5*, *5*(1), 5. https://doi.org/10.3390/LAND5010005

Darlington, J. P. E. C. (2005). Distinctive fossilised termite nests at Laetoli, Tanzania. *Insectes Sociaux*, *52*(4), 408–409. https://doi.org/10.1007/s00040-005-0830-0

Davidson, I., & McGrew, W. C. (2005). Stone tools and the uniqueness of human culture. *Journal of the Royal Anthropological Institute*, *11*(4), 793–817. https://doi.org/10.1111/j.1467-9655.2005.00262.x

Davies, B., Romanowska, I., Harris, K., & Crabtree, S. A. (2019). Combining Geographic Information Systems and Agent-Based Models in Archaeology: Part 2 of 3. *Advances in Archaeological Practice*, *7*(2), 185–193. https://doi.org/10.1017/aap.2019.5

Davies, R. M. (2012). Physical and mechanical properties of palm fruit, kernel and nut. *Journal of Agricultural Technology*, *8*(7), 2147–2156.

de la Torre, I. (2004). Omo Revisited. *Current Anthropology*, *45*(4), 439–465.

de la Torre, I., Mora, R., Domínguez-Rodrigo, M., de Luque, L., & Alcalá, L. (2003). The Oldowan industry of Peninj and its bearing on the reconstruction of the technological skills of LowerPleistocene hominids. *Journal of Human Evolution*, *44*(2), 203–224. https://doi.org/10.1016/S0047-2484(02)00206-3

Deblauwe, I. (2009). Temporal Variation in Insect-eating by Chimpanzees and Gorillas in

Southeast Cameroon: Extension of Niche Differentiation. *International Journal of Primatology*, *30*(2), 229–252. https://doi.org/10.1007/s10764-009-9337-2

Delagnes, A., & Roche, H. (2005). Late Pliocene hominid knapping skills: The case of Lokalalei 2C, West Turkana, Kenya. *Journal of Human Evolution*, *48*(5), 435–472. https://doi.org/10.1016/j.jhevol.2004.12.005

Diallo, T. O. (1996). L'amenagement des reserves forestieres et la gestion des terres agricoles des zones peripheriques: Cas de Diécké - Ziama. In The World Bank (Ed.), *African Forest Policy Form, August 29-30* (pp. 125–135).

Dibble, H. L. (1987). Measurement of Artifact Provenience with an Electronic Theodolite. *Journal of Field Archaeology*, *14*(2), 249–254. https://doi.org/10.1179/009346987792208457

Dibble, H. L., Holdaway, S. J., Lin, S. C., Braun, D. R., Douglass, M. J., Iovita, R., McPherron, S., Olszewski, D. I., & Sandgathe, D. (2016). Major Fallacies Surrounding Stone Artifacts and Assemblages. *Journal of Archaeological Method and Theory*, *33*(1), 1–39. https://doi.org/10.1007/s10816-016-9297-8

Dijk, K. van, Cibot, M., & McLennan, M. R. (2021). Chimpanzees (*Pan troglodytes*) adapt their nesting behavior after large-scale forest clearance and community decline. *American Journal of Primatology*, e23323. https://doi.org/10.1002/AJP.23323

Dobson, A. J. (2002). *An introduction to generalized linear models*. Chapman & Hall/CRC.

Domínguez-Rodrigo, M. (2012a). Introduction. In M. Domínguez-Rodrigo (Ed.), *Stone tools and fossil bones : debates in the archaeology of human origins* (pp. 1–10). Cambridge University Press.

Domínguez-Rodrigo, M. (2012b). *Stone tools and fossil bones: debates in the archaeology of human origins*. Cambridge University Press.

Domínguez-Rodrigo, M., Serrallonga, J., Juan-Tresserras, J., Alcala, L., & Luque, L. (2001).

Woodworking activities by early humans: a plant residue analysis on Acheulian stone tools from Peninj (Tanzania). *Journal of Human Evolution*, *40*(4), 289–299. https://doi.org/10.1006/jhev.2000.0466

Douglass, M. J., Lin, S. C., Braun, D. R., & Plummer, T. W. (2018). Core Use-Life Distributions in Lithic Assemblages as a Means for Reconstructing Behavioral Patterns. *Journal of Archaeological Method and Theory*, *25*(1), 254–288. https://doi.org/10.1007/S10816-017-9334-2/TABLES/3

EOS Positioning Systems Inc. (2017). *Arrow Gold*. https://eos-gnss.com/wp-content/uploads/2017/11/eos-arrow-gold-revC-v4.pdf

Faith, J. T., Du, A., Behrensmeyer, A. K., Davies, B., Patterson, D. B., Rowan, J., & Wood, B. (2021). Rethinking the ecological drivers of hominin evolution. *Trends in Ecology & Evolution*, *36*(9), 797–807. https://doi.org/10.1016/j.tree.2021.04.011

Faith, J. T., Rowan, J., & Du, A. (2019). Early hominins evolved within non-analog ecosystems. *Proceedings of the National Academy of Sciences*, *116*(43), 21478–21483. https://doi.org/10.1073/pnas.1909284116

Falótico, T., Proffitt, T., Ottoni, E. B., Staff, R. A., & Haslam, M. (2019). Three thousand years of wild capuchin stone tool use. *Nature Ecology & Evolution*, *3*(7), 1034–1038. https://doi.org/10.1038/s41559-019-0904-4

Fauna & Flora International. (2021). *Coordinated and collaborative application of the mitigation hierarchy in complex multi-use landscapes in Africa: Upper Guinean Forest transboundary landscape. Opportunities and challenges for maintaining a connected forest landscape in the face of develop*. Fauna & Flora International.

Fay, J. M., & Carroll, R. W. (1994). Chimpanzee tool use for honey and termite extraction in Central Africa. *American Journal of Primatology*, *34*(4), 309–317. https://doi.org/10.1002/ajp.1350340403

Fitzgerald, M., Nackoney, J., Potapov, P., & Turubanova, S. (2021). Agriculture is the primary driver of tree cover loss across the Forestière region of the Republic of Guinea, Africa. *Environmental Research Communications*, *3*(12), 121004. https://doi.org/10.1088/2515-7620/AC4278

Foret Forte. (2021a). *Pour ou contre l'exploitation industrielle dans ziama et diecke*. Foret Forte. http://foretforte.net/index.php/actualites/1-pour-ou-contre-l-exploitation-industrielle-dans-ziama-et-diecke

Foret Forte. (2021b). *Qui sommes nous*. Foret Forte. http://foretforte.net/index.php/qui-sommes-nous

Fox, C. (1932). *The personality of Britain: its influence on inhabitant and invader in prehistoric and early historic times*. National Museum of Wales.

Fox, C. (2010). *The Archaeology of the Cambridge Region*. Cambridge University Press. https://doi.org/10.1017/CBO9780511697739

Fox, J. (2002). *An R and S-Plus companion to applied regression*. Sage Publications.

Fox, J., & Weisberg, S. (2011). *An R Companion to Applied Regression* (2nd ed.). Sage.

Furuichi, T. (2009). Factors underlying party size differences between chimpanzees and bonobos: A review and hypotheses for future study. *Primates*, *50*(3), 197–209. https://doi.org/10.1007/S10329-009-0141-6/FIGURES/2

Furuichi, T., & Hashimoto, C. (2004). Botanical and Topographical Factors Influencing Nesting-Site Selection by Chimpanzees in Kalinzu Forest, Uganda. *International Journal of Primatology 2004 25:4*, *25*(4), 755–765. https://doi.org/10.1023/B:IJOP.0000029121.25284.7F

Galán-Acedo, C., Arroyo-Rodríguez, V., Andresen, E., Verde Arregoitia, L., Vega, E., Peres, C. A., & Ewers, R. M. (2019). The conservation value of human-modified landscapes for the world's primates. *Nature Communications 2019 10:1*, *10*(1), 1–8.

https://doi.org/10.1038/s41467-018-08139-0

Gerwing, J. J., Schnitzer, S. A., Burnham, R. J., Bongers, F., Chave, J., Dewalt, S. J., Ewango, C. E. N., Foster, R., Kenfack, D., Martínez-Ramos, M., Parren, M., Parthasarathy, N., Pérez-Salicrup, D. R., Putz, F. E., & Thomas, D. W. (2006). A Standard Protocol for Liana Censuses. *Biotropica*, *38*(2), 256–261. https://doi.org/10.1111/j.1744-7429.2006.00134.x

Gilbert, G. N. (2019). *Agent-based models. Quantitative Applications in the Social Sciences*. SAGE Publications.

Goldman-Neuman, T., & Hovers, E. (2009). Methodological considerations in the study of Oldowan raw material selectivity: insights from A. L. 894 (Hadar, Ethiopia). In E. Hovers & D. R. Braun (Eds.), *Interdisciplinary Approaches to the Oldowan* (pp. 71–84). Springer.

Goldman-Neuman, T., & Hovers, E. (2012). Raw material selectivity in Late Pliocene Oldowan sites in the Makaamitalu Basin, Hadar, Ethiopia. *Journal of Human Evolution*, *62*(3), 353–366. https://doi.org/10.1016/j.jhevol.2011.05.006

González-Ruibal, A., Hernando, A., & Politis, G. (2011). Ontology of the self and material culture: Arrow-making among the Awá hunter–gatherers (Brazil). *Journal of Anthropological Archaeology*, *30*(1), 1–16. https://doi.org/10.1016/j.jaa.2010.10.001

Goodall, J. (1962). Nest building behavior in the free ranging chimpanzee. *Annals of the New York Academy of Sciences*, *102*(2), 455–467. https://doi.org/10.1111/j.1749-6632.1962.tb13652.x

Goodall, J. (1963). Feeding behaviour of wild chimpanzees: a preliminary report. *Symposium of the Zoological Society of London*, *10*, 39–48.

Goodall, J. (1964). Tool-using and aimed throwing in a community of free-living chimpanzees. *Nature*, *201,* 1264–1266. https://doi.org/10.1038/2011264a0

Goodall, J. (1986). *The Chimpanzees of Gombe: Patterns of Behavior*. Belknap Press.

Goodchild, M. F. (1986). *Spatial autocorrelation: Concepts and Techniques in Modern Geography* (Vol. 47). Geo Books.

Green, S. J., Boruff, B. J., Bonnell, T. R., & Grueter, C. C. (2020). Chimpanzees Use Least-Cost Routes to Out-of-Sight Goals. *Current Biology*, *30*(22), 4528-4533.e5. https://doi.org/10.1016/J.CUB.2020.08.076

Green, S. J., Boruff, B. J., & Grueter, C. C. (2020). From ridge tops to ravines: landscape drivers of chimpanzee ranging patterns. *Animal Behaviour*, *163*, 51–60. https://doi.org/10.1016/J.ANBEHAV.2020.02.016

Griffith, C. S., Long, B. L., & Sept, J. M. (2010). HOMINIDS: An agent-based spatial simulation model to evaluate behavioral patterns of early Pleistocene hominids. *Ecological Modelling*, *221*(5), 738–760. https://doi.org/10.1016/j.ecolmodel.2009.11.009

Grimm, V., Berger, U., DeAngelis, D. L., Polhill, J. G., Giske, J., & Railsback, S. F. (2010). The ODD protocol: A review and first update. *Ecological Modelling*, *221*(23), 2760–2768. https://doi.org/10.1016/j.ecolmodel.2010.08.019

Gruber, T., Potts, K. B., Krupenye, C., Byrne, M. R., Mackworth-Young, C., McGrew, W. C., Reynolds, V., & Zuberbühler, K. (2012). The influence of ecology on chimpanzee (*Pan troglodytes*) cultural behavior: A case study of five ugandan chimpanzee communities. *Journal of Comparative Psychology*, *126*(4), 446–457. https://doi.org/10.1037/a0028702

Grund, C., Neumann, C., Zuberbühler, K., & Gruber, T. (2019). Necessity creates opportunities for chimpanzee tool use. *Behavioral Ecology*, *30*(4), 1136–1144. https://doi.org/10.1093/beheco/arz062

Guilavogui, H. K. (2018). *Collectif Touche Pas A Ma Foret - Note d'Information*. Collectif Touche Pas A Ma Foret. https://www.arguifausa.org/wp-content/uploads/2018/09/Memorandum-final.pdf

Guilavogui, Z. E. (2020, February 21). *Affaire SOGUIPAH: le nerf de la guerre c'est la transparence*. Aminata. https://aminata.com/affaire-soguipah-le-nerf-de-la-guerre-cest-la-transparence/

Gumert, M. D., Kluck, M., & Malaivijitnond, S. (2009). The Physical Characteristics and Usage Patterns of Stone Axe and Pounding Hammers Used by Long-Tailed Macaques in the Andaman Sea Region of Thailand. *American Journal of Primatology*, *608*(71), 594–608. https://doi.org/10.1002/ajp.20694

Gürbüz, R. B., & Lycett, S. J. (2021). Could woodworking have driven lithic tool selection? *Journal of Human Evolution*, *156*, 102999. https://doi.org/10.1016/J.JHEVOL.2021.102999

Haba, P. M., & Couch, C. (2018). Evaluation de ZTIP: Forêt Classée de Dièckè, Préfecture de Yomou. *Royal Botanic Gardens, Kew*.

Haba, P. M., Sékou, K. S., Delamou, R., & Bouamou, D. (2018). *Rapport de terrain du projet Darwin Initiative en Guinée: Forêt Classée de Diécké: Villages-Guêpa-Yonsono*. Guinée-Biodiversité.

Hallett, E. Y., Marean, C. W., Steele, T. E., Álvarez-Fernández, E., Jacobs, Z., Cerasoni, J. N., Aldeias, V., Scerri, E. M. L., Olszewski, D. I., El Hajraoui, M. A., & Dibble, H. L. (2021). A worked bone assemblage from 120,000–90,000 year old deposits at Contrebandiers Cave, Atlantic Coast, Morocco. *IScience*, *24*(9), 102988. https://doi.org/10.1016/j.isci.2021.102988

Ham, R. (1998). Nationwide chimpanzee sensus and large mammal survey of the republic of guinea. *Report to the European Union, Guinea-Conakry*.

Hardy, B. L., Moncel, M. H., Kerfant, C., Lebon, M., Bellot-Gurlet, L., & Mélard, N. (2020). Direct evidence of Neanderthal fibre technology and its cognitive and behavioral implications. *Scientific Reports*, *10*(1), 75005. https://doi.org/10.1038/s41598-020-61839-w

Harmand, S. (2009). Variability in Raw Material Selectivity at the Late Pliocene sites of Lokalalei, West Turkana, Kenya. In E. Hovers & D. Braun (Eds.), *Interdisciplinary Approaches to the Oldowan* (pp. 85–97). Springer. https://doi.org/10.1007/978-1-4020-9059-2

Harmand, S., Lewis, J. E., Feibel, C. S., Lepre, C. J., Prat, S., Lenoble, A., Boës, X., Quinn, R. L., Brenet, M., Arroyo, A., Taylor, N., Clément, S., Daver, G., Brugal, J.-P., Leakey, L., Mortlock, R. A., Wright, J. D., Lokorodi, S., Kirwa, C., … Roche, H. (2015). 3.3-million-year-old stone tools from Lomekwi 3, West Turkana, Kenya. *Nature*, *521*(7552), 310–315. https://doi.org/10.1038/nature14464

Harrison, X. A. (2014). Using observation-level random effects to model overdispersion in count data in ecology and evolution. *PeerJ*, *2*(1), e616. https://doi.org/10.7717/peerj.616

Haslam, M. (2012). Towards a prehistory of primates. *Antiquity*, *86,* 299–315.

Haslam, M., Hernandez-Aguilar, R. A., Ling, V., Carvalho, S., De La Torre, I., Destefano, A., Du, A., Hardy, B. L., Harris, J., Marchant, L., Matsuzawa, T., McGrew, W. C., Mercader, J., Mora, R., Petraglia, M., Roche, H., Visalberghi, E., & Warren, R. (2009). Primate archaeology. *Nature*, *460*(7253), 339–344. https://doi.org/10.1038/nature08188

Haslam, M., Hernandez-Aguilar, R. A., Proffitt, T., Arroyo, A., Falótico, T., Fragaszy, D. M., Gumert, M. D., Harris, J. W. K., Huffman, M. A., Kalan, A. K., Malaivijitnond, S., Matsuzawa, T., McGrew, W. C., Ottoni, E. B., Pascual-Garrido, A., Piel, A. K., Pruetz, J. D., Schuppli, C., Stewart, F. A., … Luncz, L. V. (2017). Primate archaeology evolves. *Nature Ecology and Evolution*, *1*(10), 1431–1437. https://doi.org/10.1038/s41559-017-0286-4

Haslam, M., Luncz, L. V, Pascual-Garrido, A., Falótico, T., Malaivijitnond, S., & Gumert, M. D. (2016). Archaeological excavation of wild macaque stone tools. *Journal of Human Evolution*, *96*, 134–138. https://doi.org/10.1016/j.jhevol.2016.05.002

Haslam, M., Luncz, L. V, Staff, R. A., Bradshaw, F., Ottoni, E. B., & Falótico, T. (2016). Pre-Columbian monkey tools. *Current Biology*, *26*(13), R521–R522. https://doi.org/10.1016/j.cub.2016.05.046

Heaton, J. L., & Pickering, T. R. (2006). Archaeological analysis does not support intentionality in the production of brushed ends on chimpanzee termiting tools. *International Journal of Primatology*, *27*(6), 1619–1633. https://doi.org/10.1007/s10764-006-9091-7

Heeb, B. (2008). Paperless Caving - An Electronic Cave Surveying System. *Proceedings of the IV European Speleological Congress, 23-30 August*, 130–133.

Heeb, B. (2013). *DistoX2 Calibration Manual*. https://paperless.bheeb.ch/download/DistoX2_CalibrationManual.pdf

Heeb, B. (2014). The Next Generation of the DistoX Cave Surveying Instrument. *Cave Radio & Electronics Group Journal*, *88*, 5–8.

Heinicke, S., Mundry, R., Boesch, C., Amarasekaran, B., Barrie, A., Brncic, T. M., Brugière, D., Campbell, G., Carvalho, J., Danquah, E., Dowd, D., Eshuis, H., Fleury-Brugière, M.-C., Gamys, J., Ganas, J., Gatti, S., Ginn, L., Goedmakers, A., Granier, N., … Kühl, H. S. (2019). Advancing conservation planning for western chimpanzees using IUCN SSC A.P.E.S.—the case of a taxon-specific database. *Environmental Research Letters*, *14*(6), 064001. https://doi.org/10.1088/1748-9326/AB1379

Heinicke, S., Mundry, R., Boesch, C., Hockings, K. J., Kormos, R., Ndiaye, P. I., Tweh, C. G., Williamson, E. A., & Kühl, H. S. (2019). Towards systematic and evidence-based conservation planning for western chimpanzees. *American Journal of Primatology*, *81*(9), e23042. https://doi.org/10.1002/AJP.23042

Hernandez-Aguilar, R. A. (2009). Chimpanzee nest distribution and site reuse in a dry habitat: implications for early hominin ranging. *Journal of Human Evolution*, *57*(4), 350–364. https://doi.org/10.1016/j.jhevol.2009.03.007

Hernandez-Aguilar, R. A., Moore, J., & Pickering, T. R. (2007). Savanna chimpanzees use tools to harvest the underground storage organs of plants. *Proceedings of the National Academy of Sciences of the United States of America*, *104*(49), 19210–19213. https://doi.org/10.1073/pnas.0707929104

Hernandez-Aguilar, R. A., Moore, J., & Stanford, C. B. (2013). Chimpanzee nesting patterns in savanna habitat: Environmental influences and preferences. *American Journal of Primatology*, *75*(10), 979–994. https://doi.org/10.1002/ajp.22163

Hernandez-Aguilar, R. A., & Reitan, T. (2020). Deciding Where to Sleep: Spatial Levels of Nesting Selection in Chimpanzees (*Pan troglodytes*) Living in Savanna at Issa, Tanzania. *International Journal of Primatology*, *41*(6), 870–900. https://doi.org/10.1007/s10764-020-00186-z

Hicks, T. C., Kühl, H. S., Boesch, C., Dieguez, P., Ayimisin, A. E., Fernandez, R. M., Zungawa, D. B., Kambere, M., Swinkels, J., Menken, S. B. J., Hart, J., Mundry, R., & Roessingh, P. (2019). Bili-Uéré: A Chimpanzee Behavioural Realm in Northern Democratic Republic of Congo. *Folia Primatologica*, *90*(1), 3–64. https://doi.org/10.1159/000492998

Historic England. (2017). *Understanding the Archaeology of Landscapes: A Guide to Good Recording Practice* (2nd ed.). Historic England.

Hobaiter, C., Poisot, T., Zuberbühler, K., Hoppitt, W., & Gruber, T. (2014). Social Network Analysis Shows Direct Evidence for Social Transmission of Tool Use in Wild Chimpanzees. *PLoS Biology*, *12*(9). https://doi.org/10.1371/journal.pbio.1001960

Hockings, K. J. (2011). The crop-raiders of the sacred hill. In T. Matsuzawa, T. Humle, & Y. Sugiyama (Eds.), *The Chimpanzees of Bossou and Nimba* (pp. 211–220). Springer Japan.

Hockings, K. J., Anderson, J. R., & Matsuzawa, T. (2006). Road crossing in chimpanzees: A risky business. *Current Biology*, *16*(17), R668–R670. https://doi.org/10.1016/j.cub.2006.08.019

Hockings, K. J., Anderson, J. R., & Matsuzawa, T. (2009). Use of wild and cultivated foods by chimpanzees at Bossou, Republic of Guinea: feeding dynamics in a human-influenced environment. *American Journal of Primatology*, *71*(8), 636–646. https://doi.org/10.1002/ajp.20698

Hockings, K. J., Anderson, J. R., & Matsuzawa, T. (2012). Socioecological adaptations by chimpanzees, *Pan troglodytes verus*, inhabiting an anthropogenically impacted habitat. *Animal Behaviour*, *83*(3), 801–810. https://doi.org/10.1016/j.anbehav.2012.01.002

Hockings, K. J., McLennan, M. R., Carvalho, S., Ancrenaz, M., Bobe, R., Byrne, R. W., Dunbar, R. I. M., Matsuzawa, T., McGrew, W. C., Williamson, E. A., Wilson, M. L., Wood, B., Wrangham, R. W., & Hill, C. M. (2015). Apes in the Anthropocene: Flexibility and survival. *Trends in Ecology and Evolution*, *30*(4), 215–222. https://doi.org/10.1016/j.tree.2015.02.002

Hodder, I. (Ed.). (1978). *Simulation studies in archaeology*. Cambridge University Press.

Hoffecker, J. F., & Hoffecker, I. T. (2018). The Structural and Functional Complexity of Hunter-Gatherer Technology. *Journal of Archaeological Method and Theory*, *25*(1), 202–225. https://doi.org/10.1007/s10816-017-9332-4

Holdaway, S. J., & Davies, B. (2020). Surface Stone Artifact Scatters, Settlement Patterns, and New Methods for Stone Artifact Analysis. *Journal of Paleolithic Archaeology 2019 3:4*, *3*(4), 612–632. https://doi.org/10.1007/S41982-019-00030-8

Humle, T. (2003). *Culture and Variation in Wild Chimpanzee Behaviour: a Study of Three Communities in West Africa*. PhD Thesis. University of Stirling.

Humle, T. (2011a). Location and Ecology. In T. Matsuzawa, T. Humle, & Y. Sugiyama (Eds.), *The Chimpanzees of Bossou and Nimba* (pp. 13–22). Springer Japan.

Humle, T. (2011b). The 2003 Epidemic of a Flu-Like Respiratory Disease at Bossou. In T. Matsuzawa, T. Humle, & Y. Sugiyama (Eds.), *The Chimpanzees of Bossou and Nimba* (pp. 325–333). Springer Japan.

Humle, T. (2011c). The Tool Repertoire of Bossou Chimpanzees. In T. Matsuzawa, T. Humle, & Y. Sugiyama (Eds.), *The Chimpanzees of Bossou and Nimba* (pp. 61–72). Springer Japan.

Humle, T., Boesch, C., Campbell, G., Junker, J., Koops, K., Kuehl, H., & Sop, T. (2016). *Pan troglodytes ssp. verus*. The IUCN Red List of Threatened Species. https://doi.org/http://dx.doi.org/10.2305/IUCN.UK.2016-2.RLTS.T15935A17989872.en

Humle, T., Maisels, F., Oates, J. F., Plumptre, A., & Williamson, E. A. (2016). Pan troglodytes (errata version published in 2018). *The IUCN Red List of Threatened Species*, e.T15933A129038584. https://doi.org/10.2305/IUCN.UK.2016-2.RLTS.T15933A17964454.en

Humle, T., & Matsuzawa, T. (2001). Behavioural Diversity among the Wild Chimpanzee Populations of Bossou and Neighbouring Areas, Guinea and Côte d'Ivoire, West Africa. *Folia Primatologica*, *72*(2), 57–68. https://doi.org/10.1159/000049924

Humle, T., & Matsuzawa, T. (2002). Ant-dipping among the chimpanzees of Bossou, Guinea, and some comparisons with other sites. *American Journal of Primatology*, *58*(3), 133–148. https://doi.org/10.1002/AJP.10055

Humle, T., & Matsuzawa, T. (2004). Oil palm use by adjacent communities of chimpanzees at Bossou and Nimba Mountains, West Africa. *International Journal of Primatology*, *25*(3), 551–581. https://doi.org/10.1023/B:IJOP.0000023575.93644.f4

Humle, T., & Matsuzawa, T. (2009). Laterality in hand use across four tool-use behaviors among the wild chimpanzees of Bossou, Guinea, West Africa. *American Journal of Primatology*, *71*(1), 40–48. https://doi.org/10.1002/ajp.20616

Humle, T., Snowdon, C. T., & Matsuzawa, T. (2009). Social influences on ant-dipping acquisition in the wild chimpanzees (*Pan troglodytes verus*) of Bossou, Guinea, West Africa. *Animal Cognition*, *12*, 37–48. https://doi.org/10.1007/S10071-009-0272-

6/TABLES/2

Hundley, M. H. (1963). Notes on Methods of Feeding and the Use of Tools in the Geospizinae. *The Auk*, *80*(3), 372–373. https://doi.org/10.2307/4082901

Hunt, G. R. (1996). Manufacture and use of hook-tools by New Caledonian crows. *Nature*, *379*(6562), 249–251. https://doi.org/10.1038/379249a0

Hunt, K. D. (1994). The evolution of human bipedality: Ecology and functional morphology. *Journal of Human Evolution*, *26*(3), 183–202. https://doi.org/10.1006/JHEV.1994.1011

Hussain, S. T., & Soressi, M. (2021). The Technological Condition of Human Evolution: Lithic Studies as Basic Science. *Journal of Paleolithic Archaeology 2021 4:3*, *4*(3), 1–17. https://doi.org/10.1007/S41982-021-00098-1

ICMM. (2020). *Role of Mining in National Economies: Mining Contribution Index (MCI)* (5th Editio). International Council on Mining & Metals.

Ihobe, H. (2005). Life Span of Chimpanzee Beds at the Mahale Mountains National Park, Tanzania. *Pan Africa News*, *12*(1), 10–12.

Inoue, E., Tashiro, Y., Ogawa, H., Inoue-Murayama, M., Nishida, T., & Takenaka, O. (2013). Gene Flow and Genetic Diversity of Chimpanzees in Tanzanian Habitats. *Primate Conservation*, *26*(1), 67–74. https://doi.org/10.1896/052.026.0105

Isaac, G. L. (1976). Plio-Pleistocene artifact assemblages from east Rudolf, Kenya. In Y. Coppens, C. F. Howel, G. L. Isaac, & R. E. F. Leakey (Eds.), *Early Man and Environments in the Lake Rudolf Basin: Stratigraphy, Paleoecology and Evolution.* (pp. 552–564). University of Chicago Press.

Isaac, G. L. (1981a). Archaeological tests of alternative models of early hominid behaviour: excavations and experiments. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *292*, 177–188.

Isaac, G. L. (1981b). Stone Age visiting cards: approaches to the study of early land use

patterns. In I. Hodder, G. L. Isaac, & N. Hammond (Eds.), *Pattern of the past: studies in honour of David Clarke* (pp. 131–155). Cambridge University Press.

Isaac, G. L. (1983). *Early Stages in the Evolution of Human Behaviour: The Adaptive Significance of Stone Tools*. Stichting Nederlands Museum voor Anthropologie en Prehistorie.

Isaac, G. L. (1989). Early phases of human behaviour: models in Lower Palaeolithic archaeology. In G. L. Isaac & B. Isaac (Eds.), *The Archaeology of Human Origins: Papers by Glynn Isaac* (p. 447). Cambridge University Press.

Isaac, G. L., & Harris, J. W. K. (1980). A method for determining the characteristics of artefacts between sites in the Upper Member of the Koobi Fora Formation, East Lake Turkana. In R. E. F. Leakey & B. A. Ogot (Eds.), *Proceedings of the 8th Panafrican Congress on Prehistory and Quaternary Studies* (pp. 19–22).

Isaac, G. L., Harris, J. W. K., Kaufulu, Z. M., & Schick, K. D. (1997). Site formation processes: application of the observations and experiments to Koobi Fora. In G. L. Isaac & B. Isaac (Eds.), *Koobi Fora Research Project, Volume 5: Plio-Pleistocene Archaeology* (pp. 256–261). Oxford University Press.

Isaac, G. L., Harris, J. W. K., & Marshall, F. (1981). Small is informative: the application of the study of mini-sites and least effort criteria in the interpretation of the Early Pleistocene archaeological record at Koobi Fora, Kenya. In B. Isaac (Ed.), *The Archaeology of Human Origins: Papers by Glynn Isaac* (pp. 101–119). Cambridge University Press.

Itani, J., & Suzuki, A. (1967). The social unit of chimpanzees. *Primates 1967 8:4*, *8*(4), 355–381. https://doi.org/10.1007/BF01792020

IUCN. (2016). *Mano River Ecosystem Conservation and International Water Resources Management (IWRM)*. IUCN, International Union for Conservation of Nature.

Jang, H., Boesch, C., Mundry, R., Ban, S. D., & Janmaat, K. R. L. (2019). Travel linearity and

speed of human foragers and chimpanzees during their daily search for food in tropical rainforests. *Scientific Reports*, *9*(1), 11066. https://doi.org/10.1038/s41598-019-47247-9

Janmaat, K. R. L., Boesch, C., Byrne, R. W., Chapman, C. A., Gon, Z. B., Bi, E., Head, J. S., Robbins, M. M., Wrangham, R. W., & Polansky, L. (2016). Spatio-temporal complexity of chimpanzee food: How cognitive adaptations can counteract the ephemeral nature of ripe fruit; Spatio-temporal complexity of chimpanzee food: How cognitive adaptations can counteract the ephemeral nature of ripe fruit. *American Journal of Primatology*, *78*, 626–645. https://doi.org/10.1002/ajp.22527

Janmaat, K. R. L., de Guinea, M., Collet, J., Byrne, R. W., Robira, B., van Loon, E., Jang, H., Biro, D., Ramos-Fernández, G., Ross, C., Presotto, A., Allritz, M., Alavi, S., & Van Belle, S. (2021). Using natural travel paths to infer and compare primate cognition in the wild. *IScience*, *24*(4), 102343. https://doi.org/10.1016/j.isci.2021.102343

Janmaat, K. R. L., Polansky, L., Ban, S. D., & Boesch, C. (2014). Wild chimpanzees plan their breakfast time, type, and location. *Proceedings of the National Academy of Sciences of the United States of America*, *111*(46), 16343–16348. https://doi.org/10.1073/pnas.1407524111

Jo, Y., & Hong, S. (2019). Three-dimensional digital documentation of cultural heritage site based on the convergence of terrestrial laser scanning and unmanned aerial vehicle photogrammetry. *ISPRS International Journal of Geo-Information*, *8*(2), 53. https://doi.org/10.3390/ijgi8020053

Joordens, J. C. A., Feibel, C. S., Vonhof, H. B., Schulp, A. S., & Kroon, D. (2019). Relevance of the eastern African coastal forest for early hominin biogeography. *Journal of Human Evolution*, *131*, 176–202. https://doi.org/10.1016/J.JHEVOL.2019.03.012

Junker, J., Kühl, J. S., Orth, H. S., Smith, L. K., Petrovan, R. K., & Sutherland, S. O. (2017). *Primate*

conservation: Global evidence for the effects of interventions. University of Cambridge.

Kalan, A. K., Kulik, L., Arandjelovic, M., Boesch, C., Haas, F., Dieguez, P., Barratt, C. D., Abwe, E. E., Agbor, A., Angedakin, S., Aubert, F., Ayimisin, A. E., Bailey, E., Bessone, M., Brazzola, G., Buh, V. E., Chancellor, R., Cohen, H., Coupland, C., … Kühl, H. S. (2020). Environmental variability supports chimpanzee behavioural diversity. *Nature Communications*, *11*(1), 4451. https://doi.org/10.1038/s41467-020-18176-3

Kalan, A. K., Piel, A. K., Mundry, R., Wittig, R. M., Boesch, C., & Kühl, H. S. (2016). Passive acoustic monitoring reveals group ranging and territory use: A case study of wild chimpanzees (*Pan troglodytes*). *Frontiers in Zoology*, *13*(1), 34. https://doi.org/10.1186/s12983-016-0167-8

Kamgang, S. A., Carme, T. C., Bobo, K. S., Abwe, E. E., Gonder, M. K., & Sinsin, B. (2020). Assessment of in situ nest decay rate for chimpanzees (Pan troglodytes ellioti Matschie, 1914) in Mbam-Djerem National Park, Cameroon: implications for long-term monitoring. *Primates*, *61*(2), 189–200. https://doi.org/10.1007/s10329-019-00768-3

Kaplan, R. S. (2012). *Quantifying Selection in Chimpanzee Composite Tool Use at Bossou, Guinea: Novel Material Property Tests of the Archaeological Record*. MSc Thesis. The George Washington University.

Kaufulu, Z. M. (1997). The implications of sedimentology. In G. L. Isaac & B. Isaac (Eds.), *Koobi Fora Research Project, Volume 5: Plio-Pleistocene Archaeology*. Oxford University Press.

Kay, A. U., Fuller, D. Q., Neumann, K., Eichhorn, B., Höhn, A., Morin-Rivat, J., Champion, L., Linseele, V., Huysecom, E., Ozainne, S., Lespez, L., Biagetti, S., Madella, M., Salzmann, U., & Kaplan, J. O. (2019). Diversification, Intensification and Specialization: Changing Land Use in Western Africa from 1800 BC to AD 1500. *Journal of World Prehistory*, *32*(2), 179–228. https://doi.org/10.1007/S10963-019-09131-2

Kimura, Y. (1999). Tool-using strategies by early hominids at Bed II, Olduvai Gorge, Tanzania.

Journal of Human Evolution, *37*(6), 807–831. https://doi.org/10.1006/jhev.1999.0316

Kingsland, S. E. (1985). *Modeling Nature: Episodes in the History of Population Ecology*. University of Chicago Press.

Kjellman, E. (2012). *From 2D to 3D: a photogrammetric revolution in archaeology?* MSc Thesis. University of Tromsø.

Klump, B. C., Cantat, M., & Rutz, C. (2019). Raw-material selectivity in hook-tool-crafting New Caledonian crows. *Biology Letters*, *15*(2), 20180836. https://doi.org/10.1098/rsbl.2018.0836

Koops, K., McGrew, W. C., de Vries, H., & Matsuzawa, T. (2012). Nest-Building by Chimpanzees (*Pan troglodytes verus*) at Seringbara, Nimba Mountains: Antipredation, Thermoregulation, and Antivector Hypotheses. *International Journal of Primatology*, *33*(2), 356–380. https://doi.org/10.1007/s10764-012-9585-4

Koops, K., McGrew, W. C., & Matsuzawa, T. (2013). Ecology of culture: do environmental factors influence foraging tool use in wild chimpanzees, *Pan troglodytes verus*? *Animal Behaviour*, *85*(1), 175–185. https://doi.org/10.1016/j.anbehav.2012.10.022

Koops, K., Schöning, C., Isaji, M., & Hashimoto, C. (2015). Cultural differences in ant-dipping tool length between neighbouring chimpanzee communities at Kalinzu, Uganda. *Scientific Reports*, *5*(1), 12456. https://doi.org/10.1038/srep12456

Koops, K., Schuppli, C., & Van Schaik, C. P. (2018). Cultural primatology. In *The International Encyclopedia of Biological Anthropology* (pp. 1–7). John Wiley & Sons, Inc. https://doi.org/10.1002/9781118584538.ieba0114

Koops, K., Visalberghi, E., & van Schaik, C. P. (2014). The ecology of primate material culture. *Biology Letters*, *10*(11), 20140508. https://doi.org/10.1098/rsbl.2014.0508

Koops, K., Wrangham, R. W., Cumberlidge, N., Fitzgerald, M. A., Van Leeuwen, K. L., Rothman, J. M., & Matsuzawa, T. (2019). Crab-fishing by chimpanzees in the Nimba Mountains,

Guinea. *Journal of Human Evolution*, *133*, 230–241. https://doi.org/10.1016/J.JHEVOL.2019.05.002

Kopps, A. M., & Sherwin, W. B. (2012). Modelling the emergence and stability of a vertically transmitted cultural trait in bottlenose dolphins. *Animal Behaviour*, *84*(6), 1347–1362. https://doi.org/10.1016/j.anbehav.2012.08.029

Kormos, R., Boesch, C., Bakarr, M. I., & Butynski, T. M. (2003). *West African Chimpanzees Status Survey and Conservation Action Plan*. IUCN/SSC Primate Specialist Group. IUCN, Gland, Switzerland and Cambridge, UK.

Kouakou, C. Y., Boesch, C., & Kuehl, H. (2009). Estimating chimpanzee population size with nest counts: validating methods in Taï National Park. *American Journal of Primatology*, *71*(6), 447–457. https://doi.org/10.1002/ajp.20673

Kühl, H. S., Boesch, C., Kulik, L., Haas, F., Arandjelovic, M., Dieguez, P., Bocksberger, G., McElreath, M. B., Agbor, A., Angedakin, S., Ayimisin, A. E., Bailey, E., Barubiyo, D., Bessone, M., Brazzola, G., Chancellor, R., Cohen, H., Coupland, C., Danquah, E., … Kalan, A. K. (2019). Human impact erodes chimpanzee behavioral diversity. *Science*, *363*(6434), 1453–1455. https://doi.org/10.1126/science.aau4532

Lake, M. W. (2015). Explaining the Past with ABM: On Modelling Philosophy. In G. Wurzer, K. Kowarik, & H. Reschreiter (Eds.), *Agent-based Modeling and Simulation in Archaeology. Advances in Geographic Information Science* (pp. 3–35). Springer. https://doi.org/10.1007/978-3-319-00008-4_1

Lamon, N., Neumann, C., Gier, J., Zuberbühler, K., & Gruber, T. (2018). Wild chimpanzees select tool material based on efficiency and knowledge. *Proceedings of the Royal Society B: Biological Sciences*, *285*(1888), 20181715. https://doi.org/10.1098/rspb.2018.1715

Langergraber, K. E., Prüfer, K., Rowney, C., Boesch, C., Crockford, C., Fawcett, K., Inoue, E.,

Inoue-Muruyama, M., Mitani, J. C., Muller, M. N., Robbins, M. M., Schubert, G., Stoinski, T. S., Viola, B., Watts, D., Wittig, R. M., Wrangham, R. W., Zuberbühler, K., Pääbo, S., & Vigilant, L. (2012). Generation times in wild chimpanzees and gorillas suggest earlier divergence times in great ape and human evolution. *Proceedings of the National Academy of Sciences*, *109*(39), 15716–15721. https://doi.org/10.1073/pnas.1211740109

Langergraber, K. E., Rowney, C., Schubert, G., Crockford, C., Hobaiter, C., Wittig, R., Wrangham, R. W., Zuberbühler, K., & Vigilant, L. (2014). How old are chimpanzee communities? Time to the most recent common ancestor of the Y-chromosome in highly patrilocal societies. *Journal of Human Evolution*, *69*(1), 1–7. https://doi.org/10.1016/j.jhevol.2013.12.005

Lapuente, J., Hicks, T. C., & Linsenmair, K. E. (2017). Fluid dipping technology of chimpanzees in Comoé National Park, Ivory Coast. *American Journal of Primatology*, *79*(5), e22628. https://doi.org/10.1002/ajp.22628

Leach, M. (2008). Pathways to sustainability in the forest? Misunderstood dynamics and the negotiation of knowledge, power, and policy. *Environment and Planning*, *40*(8), 1783–1795. https://doi.org/10.1068/a40215

Leakey, M. D. (1971). *Olduvai Gorge, Vol. III: Excavations in Beds I and II, 1960-1963*. Cambridge University Press.

Leakey, M. D., & Hay, R. L. (1979). Pliocene footprints in the Laetolil Beds at Laetoli, northern Tanzania. *Nature*, *278*(5702), 317–323. https://doi.org/10.1038/278317a0

Leakey, M. D., Hay, R. L., Curtis, G. H., Drake, R. E., Jackes, M. K., & White, T. D. (1976). Fossil hominids from the Laetolil Beds. *Nature*, *262*(5568), 460–466. https://doi.org/10.1038/262460a0

Leblan, V., & Soiret, S. P. K. (2021). The future of human-chimpanzee coexistence in West Africa: Reconsidering the role of shifting agriculture in chimpanzee (*Pan troglodytes*

verus) conservation planning. *Conservation Science and Practice*, *3*(9). https://doi.org/10.1111/csp2.496

Lee, J.-S., Filatova, T., Ligmann-Zielinska, A., Hassani-Mahmooei, B., Stonedahl, F., Lorscheid, I., Voinov, A., Polhill, G., Sun, Z., & Parker, D. C. (2015). The Complexities of Agent-Based Modeling Output Analysis. *Journal of Artificial Societies and Social Simulation*, *18*(4). https://doi.org/10.18564/jasss.2897

Lee, R. B., & DeVore, I. (1976). *Kalahari Hunter-Gatherers: Studies of the !Kung San and Their Neighbors* (R. B. Lee & I. DeVore (Eds.)). Harvard University Press.

Lehmann, J., Korstjens, A. H., & Dunbar, R. I. M. (2007). Fission-fusion social systems as a strategy for coping with ecological constraints: A primate case. *Evolutionary Ecology*, *21*(5), 613–634. https://doi.org/10.1007/S10682-006-9141-9/FIGURES/7

Lesnik, J. J. (2011). Bone Tool Texture Analysis and the Role of Termites in the Diet of South African Hominids. *PaleoAnthropology*, 268–281. https://doi.org/10.4207/PA.2011.ART57

Lesnik, J. J. (2014). Termites in the hominin diet: A meta-analysis of termite genera, species and castes as a dietary supplement for South African robust australopithecines. *Journal of Human Evolution*, *71*, 94–104. https://doi.org/10.1016/j.jhevol.2013.07.015

Lesnik, J. J. (2018). *Edible Insects and Human Evolution*. University Press of Florida. https://doi.org/10.2307/j.ctvx07bbr

Lesnik, J. J., O'Malley, R., Mabulla, A., Baquedano, E., Domínguez-Rodrigo, M., & Magill, C. (2019). Evidence of *Macrotermes* termites within the *Zinjanthropus* horizon at Olduvai Gorge, Tanzania. *Proceedings of the the 88th Annual Meeting of the American Association of Physical Anthropologists, March 27-30.*

Lewis, J. E., & Harmand, S. (2016). An earlier origin for stone tool making: implications for cognitive evolution and the transition to Homo. *Philosophical Transactions of the Royal*

Society B: Biological Sciences, *371*(1698), 20150233. https://doi.org/10.1098/rstb.2015.0233

Lindshield, S., Hernandez-Aguilar, R. A., Korstjens, A. H., Marchant, L. F., Narat, V., Ndiaye, P. I., Ogawa, H., Piel, A. K., Pruetz, J. D., Stewart, F. A., Leeuwen, K. L. van, Wessling, E. G., & Yoshikawa, M. (2021). Chimpanzees (*Pan troglodytes*) in savanna landscapes. *Evolutionary Anthropology: Issues, News, and Reviews*. https://doi.org/10.1002/EVAN.21924

Lonsdorf, E. V. (2005). Sex differences in the development of termite-fishing skills in the wild chimpanzees, *Pan troglodytes schweinfurthii*, of Gombe National Park, Tanzania. *Animal Behaviour*, *70*(3), 673–683. https://doi.org/10.1016/j.anbehav.2004.12.014

Lonsdorf, E. V. (2006). What is the role of mothers in the acquisition of termite-fishing behaviors in wild chimpanzees (*Pan troglodytes schweinfurthii*)? *Animal Cognition*, *9*(1), 36–46. https://doi.org/10.1007/s10071-005-0002-7

Lonsdorf, E. V, Eberly, L. E., & Pusey, A. E. (2004). Sex differences in learning in chimpanzees. *Nature*, *428*(6984), 715–716. https://doi.org/10.1038/428715a

López-Cálix, J. (2020). *Leveraging Export Diversification in Fragile Countries: The Emerging Value Chains of Mali, Chad, Niger, and Guinea*. The World Bank. https://doi.org/10.1596/978-1-4648-1490-7

Lucas, J. R. (1979). Wilberforce And Huxley: A Legendary Encounter. *The Historical Journal*, *22*(2), 313–330. https://doi.org/10.1017/S0018246X00016848

Luncz, L. V, Proffitt, T., Kulik, L., Haslam, M., & Wittig, R. M. (2016). Distance-decay effect in stone tool transport by wild chimpanzees. *Proceedings of the Royal Society B: Biological Sciences*, *283*(1845), 20161607. https://doi.org/10.1098/rspb.2016.1607

Luncz, L. V, Wittig, R. M., & Boesch, C. (2015). Primate archaeology reveals cultural transmission in wild chimpanzees (*Pan troglodytes verus*). *Philosophical Transactions*

of the Royal Society B: Biological Sciences, *370*(1682). https://doi.org/10.1098/rstb.2014.0348

Maier, M. J. (2015). *Package "REdaS". R package version 0.9.3* (0.9.3).

Malaivijitnond, S., Lekprayoon, C., Tandavanittj, N., Panha, S., Cheewatham, C., & Hamda, Y. (2007). Stone-tool usage by Thai long-tailed macaques (*Macaca fascicularis*). *American Journal of Primatology*, *69*(2007), 227–233. https://doi.org/10.1002/ajp

Mano River Union. (2018). *Rapport de mise en place de la plate-forme consultative de la Foret Classee de Diecke*. MRU/IUCN/GEF/GIRE/PROJET N°4953 GUI. http://mru.int/wp-content/uploads/2020/04/RAPPORT-DE-MISE-EN-PLACE-PF-DIECKE-1.pdf

Martínez-Fernández, A., Benito-Calvo, A., Campaña, I., Ortega, A. I., Karampaglidis, T., Bermúdez de Castro, J. M., & Carbonell, E. (2020). 3D monitoring of Paleolithic archaeological excavations using terrestrial laser scanner systems (Sierra de Atapuerca, Railway Trench sites, Burgos, N Spain). *Digital Applications in Archaeology and Cultural Heritage*, *19*, e00156. https://doi.org/10.1016/j.daach.2020.e00156

Martins-Junior, A. M. G., Carneiro, J., Sampaio, I., Ferrari, S. F., & Schneider, H. (2018). Phylogenetic relationships among Capuchin (Cebidae, Platyrrhini) lineages: An old event of sympatry explains the current distribution of *Cebus* and *Sapajus*. *Genetics and Molecular Biology*, *41*(3), 699. https://doi.org/10.1590/1678-4685-GMB-2017-0012

Matsuzawa, T. (2011). Field Experiments of Tool-Use. In T. Matsuzawa, T. Humle, & Y. Sugiyama (Eds.), *The Chimpanzees of Bossou and Nimba* (pp. 157–164). Springer Japan.

Matsuzawa, T., Humle, T., & Sugiyama, Y. (Eds.). (2011). *The Chimpanzees of Bossou and Nimba*. Springer Japan.

Matsuzawa, T., Takemoto, H., Hayakawa, S., & Shimada, M. (1999). Diecke Forest in Guinea. *Pan Africa News*, *6*(1), 10–11. https://doi.org/10.5134/143391

Mcbeath, N. M., & McGrew, W. C. (1982). Tools used by wild chimpanzees to obtain termites

at Mt Assirik, Senegal: The influence of habitat. *Journal of Human Evolution*, *11*(1), 65–72. https://doi.org/10.1016/S0047-2484(82)80032-8

McCarthy, M. S., Lester, J. D., & Stanford, C. B. (2017). Chimpanzees (*Pan troglodytes*) Flexibly Use Introduced Species for Nesting and Bark Feeding in a Human-Dominated Habitat. *International Journal of Primatology*, *38*(2), 321–337. https://doi.org/10.1007/s10764-016-9916-y

McGrew, W. C. (1979). Evolutionary implications of sex differences in chimpanzee predation and tool use. In D. A. Hamburg & E. R. McCown (Eds.), *The Great Apes* (pp. 441–463). Benjamin/Cummings.

McGrew, W. C. (1992). *Chimpanzee Material Culture: Implications for Human Evolution*. Cambridge University Press. https://doi.org/10.1017/CBO9780511565519

McGrew, W. C. (2010a). Chimpanzee Technology. *Science*, *328*(5978), 579–580. https://doi.org/10.1126/SCIENCE.1187921

McGrew, W. C. (2010b). In search of the last common ancestor: new findings on wild chimpanzees. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365*(1556), 3267–3276. https://doi.org/10.1098/rstb.2010.0067

McGrew, W. C. (2014). The "other faunivory" revisited: Insectivory in human and non-human primates and the evolution of human diet. *Journal of Human Evolution*, *71*, 4–11. https://doi.org/10.1016/j.jhevol.2013.07.016

McGrew, W. C. (2021). Sheltering Chimpanzees. *Primates*, *62*(3), 445–455. https://doi.org/10.1007/s10329-021-00903-z

McGrew, W. C., & Collins, D. A. (1985). Tool use by wild chimpanzees (*Pan troglodytes*) to obtain termites (*Macrotermes herus*) in the Mahale Mountains, Tanzania. *American Journal of Primatology*, *9*(1), 47–62. https://doi.org/10.1002/ajp.1350090106

McGrew, W. C., Falótico, T., Gumert, M. D., & Ottoni, E. B. (2019). A Simian View of the

Oldowan. In K. A. Overmann & F. L. Coolidge (Eds.), *Squeezing Minds From Stones* (pp. 13–41). Oxford University Press. https://doi.org/10.1093/oso/9780190854614.003.0002

McGrew, W. C., Marchant, L. F., Beuerlein, M. M., Vrancken, D., Fruth, B., & Hohmann, G. (2007). Prospects for bonobo insectivory: Lui Kotal, Democratic Republic of Congo. *International Journal of Primatology*, *28*(6), 1237–1252. https://doi.org/10.1007/s10764-007-9215-8

McGrew, W. C., Pruetz, J. D., & Fulton, S. J. (2005). Chimpanzees use tools to harvest social insects at Fongoli, Senegal. *Folia Primatologica*, *76*(4), 222–226. https://doi.org/10.1159/000086023

McGrew, W. C., Tutin, C. E. G., & Baldwin, P. J. (1979). Chimpanzees, Tools, and Termites: Cross-Cultural Comparisons of Senegal, Tanzania, and Rio Muni. *Man*, *14*(2), 185. https://doi.org/10.2307/2801563

McPherron, S. (2013). Perspectives on stone tools and cognition in the early Paleolithic record. In C. M. Sanz, J. Call, & C. Boesch (Eds.), *Tool Use in Animals: Cognition and Ecology*. Cambridge University Press.

McPherron, S. J. P. (2005). Artifact orientations and site formation processes from total station proveniences. *Journal of Archaeological Science*, *32*, 1003–1014. https://doi.org/10.1016/j.jas.2005.01.015

Meijaard, E. (2016). The role of multifunctional landscapes in primate conservation. In S. A. Wich & A. J. Marshall (Eds.), *An Introduction to Primate Conservation*. Oxford University Press. https://doi.org/10.1093/ACPROF:OSO/9780198703389.003.0013

Mercader, J. (Ed.). (2002). *Under the canopy: the archaeology of tropical rain forests*. Rutgers University Press.

Mercader, J., Barton, H., Gillespie, J., Harris, J., Kuhn, S., Tyler, R., & Boesch, C. (2007). 4,300-year-old chimpanzee sites and the origins of percussive stone technology. *Proceedings*

of the National Academy of Sciences of the United States of America, *104*(9), 3043–3048. https://doi.org/10.1073/pnas.0607909104

Mercader, J., Panger, M., & Boesch, C. (2002). Excavation of a Chimpanzee Stone Tool Site in the African Rainforest. *Science*, *296*(5572), 1452–1455. https://doi.org/10.1126/science.1070268

Ministère de l'Environnement, des E. et F. (2019a). *Centre Forestier de N'Zérékoré (CFZ)*. https://meef-guinee.org/centre-forestier-de-nzerekore-cfz/

Ministère de l'Environnement, des E. et F. (2019b). *Monographie Nationale la Diversité Biologique*. https://meef-guinee.org/monographie-nationale-la-diversite-biologique/

Ministry of Mines and Geology. (2021a). *Bauxite: becoming a world leading producer*. https://mines.gov.gn/en/resources/bauxite/

Ministry of Mines and Geology. (2021b). *Iron ore: the world's largest untapped deposits*. https://mines.gov.gn/en/resources/iron-ore/

Mitani, J. C. (2013). Chimpanzee models of human behavioral evolution. In M. Sponheimer, J. Lee-Torp, & K. Reed (Eds.), *Early Hominin Paleoecology* (pp. 397–436). University Press Colorado. https://doi.org/10.5876/9781607322252:C11

Mobile GIS Services. (2019). *GeoGrafi-M - MGISS*. https://mgiss.co.uk/product/geografi-m/

Möbius, Y., Boesch, C., Koops, K., Matsuzawa, T., & Humle, T. (2008). Cultural differences in army ant predation by West African chimpanzees? A comparative study of microecological variables. *Animal Behaviour*, *76*(1), 37–45. https://doi.org/10.1016/J.ANBEHAV.2008.01.008

Morell, V. (1993). Called "Trimates," three bold women shaped their field. *Science*, *260*(5106), 420–425.

Morgan, B. J., & Abwe, E. E. (2006). Chimpanzees use stone hammers in Cameroon. *Current Biology*, *16*(16), 632–633. https://doi.org/10.1016/j.cub.2006.07.045

Morgan, D. B., & Sanz, C. M. (2006). Chimpanzee feeding ecology and comparisons with sympatric gorillas in the Goualougo Triangle, Republic of Congo. In G. Hohmann, M. M. Robbins, & C. Boesch (Eds.), *Feeding Ecology in Apes and Other Primates* (pp. 97–122). Cambridge University Press.

Moupela, C., Doucet, J.-L., Daïnou, K., Brostaux, Y., Fayolle, A., & Vermeulen, C. (2014). Reproductive ecology of *Coula edulis* Baill., source of a valuable non-timber forest product. *Tropical Ecology*, *55*(3), 327–338.

Musgrave, S., Lonsdorf, E., Morgan, D., Prestipino, M., Bernstein-Kurtycz, L., Mundry, R., & Sanz, C. M. (2020). Teaching varies with task complexity in wild chimpanzees. *Proceedings of the National Academy of Sciences of the United States of America*, *117*(2), 969–976. https://doi.org/10.1073/pnas.1907476116

Musgrave, S., Lonsdorf, E., Morgan, D., & Sanz, C. M. (2021). The ontogeny of termite gathering among chimpanzees in the Goualougo Triangle, Republic of Congo. *American Journal of Physical Anthropology*, *174*(2), 187–200. https://doi.org/10.1002/ajpa.24125

Musgrave, S., Morgan, D., Lonsdorf, E., Mundry, R., & Sanz, C. M. (2016). Tool transfers are a form of teaching among chimpanzees. *Scientific Reports*, *6*(1), 34783. https://doi.org/10.1038/srep34783

Nakamura, M., Corp, N., Fujimoto, M., Fujita, S., Hanamura, S., Hayaki, H., Hosaka, K., Huffman, M. A., Inaba, A., Inoue, E., Itoh, N., Kutsukake, N., Kiyono-Fuse, M., Kooriyama, T., Marchant, L. F., Matsumoto-Oda, A., Matsusaka, T., McGrew, W. C., Mitani, J. C., … Zamma, K. (2013). Ranging behavior of Mahale chimpanzees: A 16 year study. *Primates*, *54*(2), 171–182. https://doi.org/10.1007/s10329-012-0337-z

Ndiaye, P. I., Badji, L., Lindshield, S. M., & Pruetz, J. D. (2018). Nest-Building Behaviour by Chimpanzees (*Pan troglodytes verus*) in the Non-Protected Area of Diaguiri (Kedougou,

Senegal): Implications for Conservation. *Folia Primatologica*, *89*(5), 316–326. https://doi.org/10.1159/000490945

Nishida, T., & Uehara, S. (1980). Chimpanzees, tools, and termites: another example from Tanzania. *Curr. Anthropol.*, *21*(5), 671–672.

Nonaka, K. (1996). Ethnoentomology of the Central Kalahari San. *African Study Monographs, Supplementary Issue*, *22*, 29–46.

Nydegger, E. (2021). *Seule une gestion forestière durable peut protéger les forêts de Ziama et de Diécké*. Foret Forte. http://foretforte.net/index.php/actualites/2-seule-une-gestion-forestiere-durable-peut-proteger-les-forets-de-ziama-et-de-diecke

O'Connell, J. F., Hawkes, K., & Jones, N. B. (1988). Hadza Hunting, Butchering, and Bone Transport and Their Archaeological Implications. *Journal of Anthropological Research*, *44*(2), 113–161.

O'Mahony, J. (2019, May 21). *Bauxite mining and Chinese dam push Guinea's chimpanzees to the brink*. Mongabay. https://news.mongabay.com/2019/05/bauxite-mining-and-chinese-dam-push-guineas-chimpanzees-to-the-brink/

O'Malley, R. C., & McGrew, W. C. (2014). Primates, insects and insect resources. *Journal of Human Evolution*, *71*, 1–3. https://doi.org/10.1016/j.jhevol.2014.02.010

Oakes, D. (2019, November 11). *Mine joint-owned by Australian mining giant Rio Tinto is polluting community in Guinea, villagers say - ABC News*. ABC Investigations. https://www.abc.net.au/news/2019-11-12/villagers-in-guinea-say-australian-part-owned-mine-polluting/11685412

Oates, J. F., Tutin, C. E. G., Humle, T., Wilson, M. L., Baillie, J. E. M., Balmforth, Z., Blom, A., Boesch, C., Cox, D., Davenport, T., Dunn, A., Dupain, J., Duvall, C. S., Ellis, C. M., Farmer, K. H., Gatti, S., Greengrass, E., Hart, J., Herbinger, I., … Walsh, P. D. (2015). *Pan troglodytes*. The IUCN Red List of Threatened Species. Version 2015.2.

www.iucnredlist.org

Oestmo, S., Janssen, M. A., & Cawthra, H. C. (2020). Applying Brantingham's neutral model of stone raw material procurement to the Pinnacle Point Middle Stone Age record, Western Cape, South Africa. *Quaternary Science Reviews*, *235*, 105901. https://doi.org/10.1016/j.quascirev.2019.105901

Ogawa, H., Idani, G., Moore, J., Pintea, L., & Hernandez-Aguilar, R. A. (2007). Sleeping Parties and nest distribution of chimpanzees in the Savanna woodland, Ugalla, Tanzania. *International Journal of Primatology*, *28*(6), 1397–1412. https://doi.org/10.1007/s10764-007-9210-0

Ohashi, G. (2015). Pestle-pounding and nut-cracking by wild chimpanzees at Kpala, Liberia. *Primates*, *56*(2), 113–117. https://doi.org/10.1007/s10329-015-0459-1

Ottoni, E. B., & Izar, P. (2008). Capuchin monkey tool use: Overview and implications. *Evolutionary Anthropology*, *17*(4), 171–178. https://doi.org/10.1002/evan.20185

Pal, A., Kumara, H. N., Mishra, P. S., Velankar, A. D., & Singh, M. (2018). Extractive foraging and tool-aided behaviors in the wild Nicobar long-tailed macaque (*Macaca fascicularis umbrosus*). *Primates*, *59*(2), 173–183. https://doi.org/10.1007/s10329-017-0635-6

Panger, M. A., Brooks, A. S., Richmond, B. G., & Wood, B. (2002). Older than the Oldowan? Rethinking the emergence of hominin tool use. *Evolutionary Anthropology*, *11*(6), 235–245. https://doi.org/10.1002/evan.10094

Pascual-Garrido, A. (2017). Termite Fishing by Mahale Chimpanzees: Revisited, Decades Later. *Pan Africa News*, *24*(2), 15–19. https://doi.org/10.5134/228897

Pascual-Garrido, A. (2018). Scars on plants sourced for termite fishing tools by chimpanzees: Towards an archaeology of the perishable. *American Journal of Primatology*, *80*(9), e22921. https://doi.org/10.1002/ajp.22921

Pascual-Garrido, A. (2019). Cultural variation between neighbouring communities of

chimpanzees at Gombe, Tanzania. *Scientific Reports*, *9*(1), 8260. https://doi.org/10.1038/s41598-019-44703-4

Pascual-Garrido, A., & Almeida-Warren, K. (2021). Archaeology of the Perishable. *Current Anthropology*, *62*(3), 333–362. https://doi.org/10.1086/713766

Pascual-Garrido, A., Buba, U., Nodza, G., & Sommer, V. (2012). Obtaining Raw Material: Plants as Tool Sources for Nigerian Chimpanzees. *Folia Primatologica*, *83*(1), 24–44. https://doi.org/10.1159/000338898

Pascual-Garrido, A., & Scheffrahn, R. H. (2020). Cultural dietary stasis? Four decades on, Mahale chimpanzees still favour Macrotermes. *Pan Africa News*, *27*(1), 6–9.

Pascual-Garrido, A., Umaru, B., Allon, O., & Sommer, V. (2013). Apes finding ants: Predator-prey dynamics in a chimpanzee habitat in Nigeria. *American Journal of Primatology*, *75*(12), 1231–1244. https://doi.org/10.1002/ajp.22187

Patterson, E. M., & Mann, J. (2011). The Ecological Conditions That Favor Tool Use and Innovation in Wild Bottlenose Dolphins (*Tursiops sp.*). *PLoS ONE*, *6*(7), e22243. https://doi.org/10.1371/journal.pone.0022243

Pearson, T., Ainsworth, S., & Thomason, B. (2015). *Where on Earth Are We? The Role of Global Navigation Satellite Systems (GNSS) in Archaeological Field Survey*. Historic England.

Piel, A. K. (2014). *Savanna Sounds: Using Remote Acoustic Sensing to Study Spatiotemporal Patterns in Wild Chimpanzee Loud Vocalizations in the Issa Valley, Ugalla, Western Tanzania*. PhD Thesis. University of California, San Diego.

Piel, A. K., Stewart, F. A., Pintea, L., Li, Y., Ramirez, M. A., Loy, D. E., Crystal, P. A., Learn, G. H., Knapp, L. A., Sharp, P. M., & Hahn, B. H. (2013). The Malagarasi River Does Not Form an Absolute Barrier to Chimpanzee Movement in Western Tanzania. *PLoS ONE*, *8*(3), e58965. https://doi.org/10.1371/journal.pone.0058965

Plummer, T. (2004). Flaked stones and old bones: biological and cultural evolution at the

dawn of technology. *Yearbook of Physical Anthropology*, *47*, 118–164. https://doi.org/10.1016/S0047-2484(86)80004-5

Pontzer, H., Brown, M. H., Wood, B. M., Raichlen, D. A., Mabulla, A. Z. P., Harris, J. A., Dunsworth, H. M., Hare, B., Walker, K., Luke, A., Dugas, L. R., Schoeller, D., Plange-Rhule, J., Bovet, P., Forrester, T. E., Thompson, M. E., Shumaker, R. W., Rothman, J. M., Vogel, E., … Ross, S. R. (2021). Evolution of water conservation in humans. *Current Biology*, *31*, 1–7. https://doi.org/10.1016/j.cub.2021.02.045

Pontzer, H., & Wrangham, R. W. (2004). Climbing and the daily energy cost of locomotion in wild chimpanzees: Implications for hominoid locomotor evolution. *Journal of Human Evolution*, *46*(3), 315–333. https://doi.org/10.1016/j.jhevol.2003.12.006

Pope, M. (2017). Thresholds in behaviour, thresholds of visibility: landscape processes, asymmetries in landscape records and niche construction in the formation of the Palaeolithic record. In M. Pope, C. Gamble, & J. McNabb (Eds.), *Crossing the Human Threshold Dynamic Transformation and Persistent Places During the Late Middle Pleistocene*. Routledge.

Pope, M., Russel, K., & Watson, K. (2006). Biface form and structured behaviour in the Acheulean. *Lithics*, *27*, 44–57.

Popkin, B. M., D'Anci, K. E., & Rosenberg, I. H. (2010). Water, hydration, and health. *Nutrition Reviews*, *68*(8), 439–458. https://doi.org/10.1111/J.1753-4887.2010.00304.X

Potts, K. B., Baken, E., Levang, A., & Watts, D. P. (2016). Ecological factors influencing habitat use by chimpanzees at Ngogo, Kibale National Park, Uganda. *American Journal of Primatology*, *78*(4), 432–440. https://doi.org/10.1002/AJP.22513

Potts, R. (1984). Home Bases and Early Hominids: Reevaluation of the fossil record at Olduvai Gorge suggests that the concentrations of bones and stone tools do not represent fully formed campsites but an antecedent to them. *American Scientist*, *72*(4), 338–347.

https://doi.org/10.2307/27828530

Potts, R. (1994). Variables versus models of early Pleistocene hominid land use. *Journal of Human Evolution*, *27*(1–3), 7–24. https://doi.org/10.1006/jhev.1994.1033

Potts, R. (1998). Environmental hypotheses of hominin evolution. *American Journal of Physical Anthropology*, *107*, 93–136. https://doi.org/10.1002/(SICI)1096-8644(1998)107:27+<93::AID-AJPA5>3.0.CO;2-X

Potts, R., Dommain, R., Moerman, J. W., Behrensmeyer, A. K., Deino, A. L., Riedl, S., Beverly, E. J., Brown, E. T., Deocampo, D., Kinyanjui, R., Lupien, R., Owen, R. B., Rabideaux, N., Russell, J. M., Stockhecke, M., DeMenocal, P., Faith, J. T., Garcin, Y., Noren, A., … Uno, K. (2020). Increased ecological resource variability during a critical transition in hominin evolution. *Science Advances*, *6*(43), eabc8975. https://doi.org/10.1126/sciadv.abc8975

Premo, L. S. (2006). Agent-based models as behavioral laboratories for evolutionary anthropological research. *Arizona Anthropologist*, *17*, 91–113.

Premo, L. S. (2015). Mobility and Cultural Diversity in Central-Place Foragers: Implications for the Emergence of Modern Human Behavior. In A. Mesoudi & K. Aoki (Eds.), *Learning Strategies and Cultural Evolution during the Palaeolithic* (pp. 45–65). Springer Japan. https://doi.org/10.1007/978-4-431-55363-2_5

Proffitt, T., Haslam, M., Mercader, J., Boesch, C., & Luncz, L. V. (2018). Revisiting Panda 100, the first archaeological chimpanzee nut-cracking site. *Journal of Human Evolution*, *124*, 117–139. https://doi.org/10.1016/J.JHEVOL.2018.04.016

Proffitt, T., Luncz, L. V, Falótico, T., Ottoni, E. B., de la Torre, I., & Haslam, M. (2016). Wild monkeys flake stone tools. *Nature*, *539*(7627), 85–88.

Proffitt, T., Luncz, L. V, Malaivijitnond, S., Gumert, M. D., Svensson, M. S., & Haslam, M. (2018). Analysis of wild macaque stone tools used to crack oil palm nuts. *Royal Society: Open Science*, *5*(171904).

Pruetz, J. D., & Bertolani, P. (2007). Savanna chimpanzees, *Pan troglodytes verus*, hunt with tools. *Current Biology*, *17*, 412–417. https://doi.org/10.1016/j.cub.2006.12.042

Pruetz, J. D., & Bertolani, P. (2009). Chimpanzee (*Pan troglodytes verus*) Behavioral Responses to Stresses Associated with Living in a Savannah-Mosaic Environment: Implications for Hominin Adaptations to Open Habitats. *PaleoAnthropology*, *2009*, 252–262. https://doi.org/10.4207/pa.2009.art33

Pruetz, J. D., & Herzog, N. M. (2017). Savanna Chimpanzees at Fongoli, Senegal, Navigate a Fire Landscape. *Current Anthropology*, *58*(16), S337–S350. https://doi.org/10.1086/692112

Quinn, G. P., & Keough, M. J. (2002). *Experimental Design and Data Analysis for Biologists*. Cambridge University Press.

R Core Team. (2017). R: A language and environment for statistical computing. In *R Foundation for Statistical Computing*.

R Core Team. (2021). *R: A language and environment for statistical computing* (4.1.0). R Foundation for Statistical Computing.

R Studio Team. (2016). *RStudio: Integrated Development for R* (1.1.383). RStudio, Inc.

Raubenheimer, D., Rothman, J. M., Pontzer, H., & Simpson, S. J. (2014). Macronutrient contributions of insects to the diets of hunter-gatherers: A geometric analysis. *Journal of Human Evolution*, *71*, 70–76. https://doi.org/10.1016/j.jhevol.2014.02.007

Redovniković, L., Ivković, M., Cetl, V., & Sambunjak, I. (2014). Testing DistoX Device for Measuring in the Unfavourable Conditions. *Proceedings of the 6th International Conference on Engineering Surveying April 3-4, 2014*, 269–274.

Redovniković, L., Stančić, B., & Cetl, V. (2016). Comparison of Different Methods of Underground Survey. *Proceedings of the International Symposium on Engineering Geodesy, 20–22 May 2016*, 465–472.

Reed, K. E. (1997). Early hominid evolution and ecological change through the African Plio-Pleistocene. *Journal of Human Evolution*, *32*(2–3), 289–322. https://doi.org/10.1006/jhev.1996.0106

Reeves, J. S., Braun, D. R., Finestone, E. M., & Plummer, T. W. (2021). Ecological perspectives on technological diversity at Kanjera South. *Journal of Human Evolution*, *158*, 103029. https://doi.org/10.1016/J.JHEVOL.2021.103029

Reeves, J. S., Proffitt, T., & Luncz, L. V. (2021). Modeling a primate technological niche. *Scientific Reports*, *11*(1), 23139. https://doi.org/10.1038/s41598-021-01849-4

Regala, F. T. (2015). AESDA Calib - um calibrador para DistoX/X2. *Proceedings of the 6th National Congress of Speliology*, 77–82. https://doi.org/10.1017/CBO9781107415324.004

Robbins, M. M., & Hohmann, G. (2006). Primate feeding ecology: an integrative approach. In G. Hohmann, M. M. Robbins, & C. Boesch (Eds.), *Feeding Ecology in Apes and Other Primates* (pp. 1–13). Cambridge University Press.

Robertson, P. (2001). Guinea. In L. D. C. Fishpool & M. I. Evans (Eds.), *Important Bird Areas in Africa and associated islands: Priority sites for conservation* (pp. 391–402). Pisces Publications and BirdLife International.

Rogers, M. J., Harris, J. W. K., & Feibel, C. S. (1994). Changing patterns of land use by Plio-Pleistocene hominids in the Lake Turkana Basin. *Journal of Human Evolution*, *27*(1–3), 139–158. https://doi.org/10.1006/jhev.1994.1039

Rolando Mazzuca, C. (2019). *Bauxite Mines on the Sangaredi Plateau & Kamsar port installations, involving the multinationals Alcoa, Rio Tinto and Dadco, Guinea | EJAtlas*. Environmental Justice Atlas. https://ejatlas.org/conflict/bauxite-mining-boke-guinea

Rolian, C., & Carvalho, S. (2017). Tool use and manufacture in the last common ancestor of Pan and Homo. In M. Muller, R. Wrangham, & D. Pilbeam (Eds.), *Chimpanzees and*

Human Evolution (pp. 602– 644). Belknap Press of Harvard University Press.

Romanowska. (2015). So You Think You Can Model? A Guide to Building and Evaluating Archaeological Simulation Models of Dispersals. *Human Biology*, *87*(3), 169. https://doi.org/10.13110/humanbiology.87.3.0169

Romanowska, I., Crabtree, S. A., Harris, K., & Davies, B. (2019). Agent-Based Modeling for Archaeologists: Part 1 of 3. *Advances in Archaeological Practice*, *7*(2), 178–184. https://doi.org/10.1017/aap.2019.6

Roosevelt, C. H. (2014). Mapping site-level microtopography with Real-Time Kinematic Global Navigation Satellite Systems (RTK GNSS) and Unmanned Aerial Vehicle Photogrammetry (UAVP). *Open Archaeology*, *1*, 29–53. https://doi.org/10.2478/opar-2014-0003

Rose, L., & Marshall, F. (1996). Meat Eating, Hominid Sociality, and Home Bases Revisited. *Current Anthropology*, *37*(2), 307. https://doi.org/10.1086/204494

Russak, S. (2013). *Ecological role of dry-habitat chimpanzees (*Pan troglodytes schweinfurthii*)*. PhD Thesis. Arizona State University.

Russon, A. E., Handayani, D. P., Kuncoro, P., & Ferisa, A. (2007). Orangutan leaf-carrying for nest-building: Toward unraveling cultural processes. *Animal Cognition*, *10*(2), 189–202. https://doi.org/10.1007/s10071-006-0058-z

Rutz, C., Bluff, L. A., Weir, A. A. S., & Kacelnik, A. (2007). Video Cameras on Wild Birds. *Science*, *318*(5851), 765–765. https://doi.org/10.1126/science.1146788

Rutz, C., Klump, B. C., Komarczyk, L., Leighton, R., Kramer, J., Wischnewski, S., Sugasawa, S., Morrissey, M. B., James, R., St Clair, J. J. H., Switzer, R. A., & Masuda, B. M. (2016). Discovery of species-wide tool use in the Hawaiian crow. *Nature*, *537*(7620), 403–407. https://doi.org/10.1038/nature19103

Rutz, C., & St Clair, J. J. H. (2012). The evolutionary origins and ecological context of tool use

in New Caledonian crows. *Behavioural Processes*, *89*(2), 153–165. https://doi.org/10.1016/j.beproc.2011.11.005

Samuelson, D. A., & Macal, C. M. (2006). Agent-based simulation comes of age. *OR/MS Today*, *33*(4).

Sangbalamou, J. P. (2020, April 25). *A cause de la forte pression des braconniers et des coupeurs de bois: la forêt classée de Diécké menacée de disparition*. Guinéenews. https://guineenews.org/a-cause-de-la-forte-pression-des-braconniers-et-des-coupeurs-de-bois-la-foret-classee-de-diecke-menacee-de-disparition/

Sanz, C. M., Call, J., & Morgan, D. (2009). Design complexity in termite-fishing tools of chimpanzees (*Pan troglodytes*). *Biology Letters*, *5*(3), 293–296. https://doi.org/10.1098/rsbl.2008.0786

Sanz, C. M., Caspar, S., & Morgan, D. B. (2010). Chimpanzees prey on army ants with specialized tool set. *American Journal of Primatology*, *72*(1), 17–24. https://doi.org/10.1002/ajp.20744

Sanz, C. M., Deblauwe, I., Tagg, N., & Morgan, D. B. (2014). Insect prey characteristics affecting regional variation in chimpanzee tool use. *Journal of Human Evolution*, *71*, 28–37. https://doi.org/10.1016/j.jhevol.2013.07.017

Sanz, C. M., & Morgan, D. (2007). Chimpanzee tool technology in the Goualougo Triangle, Republic of Congo. *Journal of Human Evolution*, *52*(4), 420–433. https://doi.org/10.1016/j.jhevol.2006.11.001

Sanz, C. M., & Morgan, D. B. (2009). Flexible and persistent tool-using strategies in honey-gathering by wild chimpanzees. *International Journal of Primatology*, *30*(3), 411–427. https://doi.org/10.1007/s10764-009-9350-5

Sanz, C. M., & Morgan, D. B. (2010). The complexity of chimpanzee tool-use behaviours. In E. V Lonsdorf, S. R. Ross, T. Matsuzawa, & J. Goodall (Eds.), *The Mind of the Chimpanzee:*

Ecological and Experimental Perspectives (pp. 127–140). University of Chicago Press.

Sanz, C. M., & Morgan, D. B. (2011). Elemental variation in the termite fishing of wild chimpanzees (*Pan troglodytes*). *Biology Letters*, *7*(4), 634–637. https://doi.org/10.1098/rsbl.2011.0088

Sanz, C. M., & Morgan, D. B. (2013). Ecological and social correlates of chimpanzee tool use. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *368*(1630), 20120416. https://doi.org/10.1098/rstb.2012.0416

Sanz, C. M., Morgan, D., & Gulick, S. (2004). New Insights into Chimpanzees, Tools, and Termites from the Congo Basin. *The American Naturalist*, *164*(5), 567–581. https://doi.org/10.1086/424803

Schick, K. D. (1987). Modeling the formation of Early Stone Age artifact concentrations. *Journal of Human Evolution*, *16*(7–8), 789–807. https://doi.org/10.1016/0047-2484(87)90024-8

Schick, K. D. (1997). Experimental studies of site formation processes. In G. L. Isaac & B. Isaac (Eds.), *Koobi Fora Research Project, Volume 5: Plio-Pleistocene Archaeology*. Oxford University Press.

Schick, K. D., & Toth, N. (1993). *Making silent stones speak*. Simon and Schuster.

Schick, K. D., & Toth, N. (2006). An overview of the Oldowan industrial complex: the sites and the nature of their evidence. In N. Toth & K. Schick (Eds.), *The Oldowan: Case Studies into the Earliest Stone Age*. Stone Age Institute Press.

Schielzeth, H., & Forstmeier, W. (2009). Conclusions beyond support: Overconfident estimates in mixed models. *Behavioral Ecology*, *20*(2), 416–420. https://doi.org/10.1093/beheco/arn145

Schlager, S., Jefferis, G., & Dryden, I. (2020). *Package "Morpho". R package version 2.8*.

Schöning, C., Humle, T., Möbius, Y., & McGrew, W. C. (2008). The nature of culture:

Technological variation in chimpanzee predation on army ants revisited. *Journal of Human Evolution*, *55*(1), 48–59. https://doi.org/10.1016/j.jhevol.2007.12.002

Schuppli, C., & van Schaik, C. P. (2019). Animal cultures: how we've only seen the tip of the iceberg. *Evolutionary Human Sciences*, *1*, e2. https://doi.org/10.1017/ehs.2019.1

Semaw, S. (2000). The world's oldest stone artefacts from Gona, Ethiopia: Their implications for understanding stone technology and patterns of human evolution between 2.6–1.5 million years ago. *Journal of Archaeological Science*, *27*, 1197–1214. https://doi.org/10.1006/jasc.1999.0592

Sept, J. M. (1992). Was there no place like home?: A new perspective on early hominid archaeological sites from the mapping of chimpanzee nests. *Current Anthropology*, *33*(2), 187–207. https://doi.org/10.1086/204050

Sept, J. M. (2011). A worm's eye view of primate behavior. In J. M. Sept & D. Pilbeam (Eds.), *Casting the Net Wide: Papers in Honor of Glynn Isaac and His Approach to Human Origins Research* (pp. 169–192). Oxbow Books.

Shaw, A., Bates, M., Conneller, C., Gamble, C., Julien, M.-A., McNabb, J., Pope, M., & Scott, B. (2016). The archaeology of persistent places: the Palaeolithic case of La Cotte de St Brelade, Jersey. *Antiquity*, *90*(354), 1437–1453. https://doi.org/10.15184/aqy.2016.212

Shea, J. J. (2017). Occasional, obligatory, and habitual stone tool use in hominin evolution. *Evolutionary Anthropology*, *26*(5), 200–217. https://doi.org/10.1002/evan.21547

Sidiki, S. (2019). Bauxite Mining in the Boké Region (Western Guinea): Method Used and Impacts on Physical Environment. *European Journal of Sustainable Development Research*, *3*(3), em0087. https://doi.org/10.29333/ejosdr/5735

Smith, C., & Warren, M. (2019). *GLMs in R for Ecology*. Amazon Publishing.

Smolker, R., Richards, A., Connor, R., Mann, J., & Berggren, P. (1997). Sponge Carrying by Dolphins (Delphinidae, *Tursiops* sp.): A Foraging Specialization Involving Tool Use?

Ethology, *103*(6), 454–465. https://doi.org/10.1111/j.1439-0310.1997.tb00160.x

Spalinger, D. E., & Thompson Hobbs, N. (1992). Mechanisms of Foraging in Mammalian Herbivores: New Models of Functional Response. In *The American Naturalist* (Vol. 140, Issue 2).

Staddon, S., Byg, A., Chapman, M., Fish, R., Hague, A., & Horgan, K. (2021). The value of listening and listening for values in conservation. *People and Nature*, *00*, 1–14. https://doi.org/10.1002/PAN3.10232

Stein, A. B., Athreya, V., Gerngross, P., Balme, G., Henschel, P., Karanth, U., Miquelle, D., Rostro-Garcia, S., Kamler, J. F., Laguardia, A., Khorozyan, I., & Ghoddousi, A. (2020). *Panthera pardus* (amended version of 2019 assessment). *The IUCN Red List of Threatened Species 2020*, e.T15954A163991139. https://doi.org/https://dx.doi.org/10.2305/IUCN.UK.2020-1.RLTS.T15954A163991139.en

Stern, N. (1991). *The Scatters-Between-the-Patches: A Study of Early Hominid Land Use Patterns in the Turkana Basin, Kenya*. PhD Thesis. Harvard University.

Stewart, F. A., & Piel, A. K. (2014). Termite fishing by wild chimpanzees: New data from Ugalla, western Tanzania. *Primates*, *55*(1), 35–40. https://doi.org/10.1007/s10329-013-0362-6

Stewart, F. A., Piel, A. K., & McGrew, W. C. (2011). Living archaeology: Artefacts of specific nest site fidelity in wild chimpanzees. *Journal of Human Evolution*, *61*(4), 388–395. https://doi.org/10.1016/j.jhevol.2011.05.005

Stout, D., Quade, J., Semaw, S., Rogers, M. J., & Levin, N. E. (2005). Raw material selectivity of the earliest stone toolmakers at Gona, Afar, Ethiopia. *Journal of Human Evolution*, *48*, 365–380. https://doi.org/10.1016/j.jhevol.2004.10.006

Stout, D., Semaw, S., Rogers, M. J., & Cauche, D. (2010). Technological variation in the earliest Oldowan from Gona, Afar, Ethiopia. *Journal of Human Evolution*, *58*(6), 474–491.

https://doi.org/10.1016/j.jhevol.2010.02.005

Strier, K. B. (2011). *Primate Behavioral Ecology* (4th ed.). Allyn and Bacon.

Sugiyama, Y. (1985). The brush-stick of chimpanzees found in south-west Cameroon and their cultural characteristics. *Primates 1985 26:4*, *26*(4), 361–374. https://doi.org/10.1007/BF02382453

Sugiyama, Y. (2004). Demographic parameters and life history of chimpanzees at Bossou, Guinea. *American Journal of Physical Anthropology*, *124*(2), 154–165. https://doi.org/10.1002/ajpa.10345

Sugiyama, Y., & Fujita, S. (2011). The Demography and Reproductive Parameters of Bossou Chimpanzees. In T. Matsuzawa, T. Humle, & Y. Sugiyama (Eds.), *The Chimpanzees of Bossou and Nimba* (pp. 23–34). Springer Japan.

Sugiyama, Y., & Koman, J. (1979). Tool-using and -making behavior in wild chimpanzees at Bossou, Guinea. *Primates*, *20*(4), 513–524. https://doi.org/10.1007/BF02373433

Sugiyama, Y., & Soumah, A. G. (1988). Preliminary Survey of the Distribution and Population of Chimpanzees in the Republic of Guinea. *Primates*, *29*(4), 569–574.

Sutton, R. S., & Barto, A. G. (2018). *Reinforcement Learning: An Introduction* (Second Edi). MIT Press.

Suzuki, S., Kuroda, S., & Nishihara, T. (1995). Tool-Set for Termite-Fishing By Chimpanzees in the Ndoki Forest, Congo. *Behaviour*, *132*(3–4), 219–235. https://doi.org/10.1163/156853995X00711

Sylla, B. (2018). Environnement: un collectif tente de sauver les forêts de Ziama et Diécké. *Guinée Eco*.

Takemoto, H., Hirata, S., & Sugiyama, Y. (2005). The formation of the brush-sticks: Modification of chimpanzees or the by-product of folding? *Primates*, *46*(3), 183–189. https://doi.org/10.1007/s10329-005-0127-y

Tátá Regala, F. (2016). *AESDA - Calib: a calibrator for DistoX/X2*. https://www.aesda.org/wp-content/uploads/2016/09/Calibrator-EuroSpeleo2016-adapted.pdf

Teleki, G. (1974). Chimpanzee subsistence technology: Materials and skills. *Journal of Human Evolution*, *3*(6), 575,IN13,585--584,IN16,594. https://doi.org/10.1016/0047-2484(74)90018-9

ten Broeke, G., van Voorn, G., & Ligtenberg, A. (2016). Which Sensitivity Analysis Method Should I Use for My Agent-Based Model? *Journal of Artificial Societies and Social Simulation*, *19*(1). https://doi.org/10.18564/jasss.2857

Tennie, C., Bandini, E., van Schaik, C. P., & Hopper, L. M. (2020). The zone of latent solutions and its relevance to understanding ape cultures. *Biology and Philosophy*, *35*(5), 55. https://doi.org/10.1007/s10539-020-09769-9

The World Bank. (1997). *Implementation completion report: Republic of Guinea Forestry and Fisheries Management Project*. The World Bank.

The World Bank. (2016). *Guinea: Diagnostic Trade Integration Study (DTIS) Final Report*. The World Bank.

Thiele, J. C., Kurth, W., & Grimm, V. (2014). Facilitating Parameter Estimation and Sensitivity Analysis of Agent-Based Models: A Cookbook Using NetLogo and "R." *Journal of Artificial Societies and Social Simulation*, *17*(3), 11. https://doi.org/10.18564/jasss.2503

Thompson, J. C., Wright, D. K., Ivory, S. J., Choi, J.-H., Nightingale, S., Mackay, A., Schilt, F., Otárola-Castillo, E., Mercader, J., Forman, S. L., Pietsch, T., Cohen, A. S., Arrowsmith, J. R., Welling, M., Davis, J., Schiery, B., Kaliba, P., Malijani, O., Blome, M. W., … Gomani-Chindebvu, E. (2021). Early human impacts and ecosystem reorganization in southern-central Africa. *Science Advances*, *7*(19), eabf9776. https://doi.org/10.1126/sciadv.abf9776

Tonooka, R. (2001). Leaf-folding behavior for drinking water by wild chimpanzees (*Pan*

troglodytes verus) at Bossou, Guinea. *Animal Cognition*, *4*(3–4), 325–334. https://doi.org/10.1007/s100710100110

Toth, N. (1983). *The Stone Technologies of Early Hominids at Koobi Fora, Kenya: An Experimental Approach*. PhD Thesis. University of California.

Toth, N. (1985). The Oldowan reassessed: A close look at early stone artifacts. *Journal of Archaeological Science*, *12*, 101–120. https://doi.org/10.1016/0305-4403(85)90056-1

Toth, N. (1997). The artefact assemblages in light of experimental studies. In G. L. Isaac & B. Isaac (Eds.), *Koobi Fora Research Project: Vol. 5* (pp. 363–402). Oxford University Press.

Toth, N., & Schick, K. (2009). The Oldowan: The tool making of early hominins and chimpanzees compared. *Annual Review of Anthropology*, *38*(1), 289–305. https://doi.org/10.1146/annurev-anthro-091908-164521

Toth, N., Schick, K. D., & Semaw, S. (2006). A comparative study of the stone tool-making skills of *Pan*, *Australopithecus*, and *Homo sapiens*. In N. Toth & K. Schick (Eds.), *The Oldowan: case studies into the earliest Stone Age* (pp. 155–222). Stone Age Institute Press.

Trapanese, C., Meunier, H., & Masi, S. (2019). What, where and when: spatial foraging decisions in primates. *Biological Reviews*, *94*(2), 483–502. https://doi.org/10.1111/brv.12462

Trimmis, K. P. (2015). Fear of the Light: Mapping Modern Cave Use Strategies in Kythera Island Caves. *Ethnoarchaeology*, *7*(2), 141–156. https://doi.org/10.1179/1944289015Z.00000000031

Trimmis, K. P. (2018). Paperless mapping and cave archaeology: a review on the application of DistoX survey method in archaeological cave sites. *Journal of Archaeological Science: Reports*, *18*, 399–407. https://doi.org/10.1016/j.jasrep.2018.01.022

Tweh, C. G., Kouakou, C. Y., Chira, R., Freeman, B., Githaiga, J. M., Kerwillain, S., Molokwu-

Odozi, M., Varney, M., & Junker, J. (2018). Nest Counts Reveal a Stable Chimpanzee Population in Sapo National Park, Liberia. *Primate Conservation*, *32*, 141–152.

Uehara, S. (1982). Seasonal changes in the techniques employed by wild chimpanzees in the Mahale Mountains, Tanzania, to feed on termites (*Pseudocanthotermes spiniger*). *Folia Primatologica*, *37*, 44–76.

Uwimbabazi, M., Rothman, J. M., Basuta, G. I., Machanda, Z. P., Conklin-Brittain, N. L., & Wrangham, R. W. (2019). Influence of fruit availability on macronutrient and energy intake by female chimpanzees. *African Journal of Ecology*, *57*(4), 454–465. https://doi.org/10.1111/aje.12636

Vahdati, A. R., Weissmann, J. D., Timmermann, A., Ponce de León, M. S., & Zollikofer, C. P. E. (2019). Drivers of Late Pleistocene human survival and dispersal: an agent-based modeling and machine learning approach. *Quaternary Science Reviews*, *221*, 105867. https://doi.org/10.1016/J.QUASCIREV.2019.105867

Van Casteren, A., Sellers, W. I., Thorpe, S. K. S., Coward, S., Crompton, R. H., Myatt, J. P., & Ennos, A. R. (2012). Nest-building orangutans demonstrate engineering know-how to produce safe, comfortable beds. *Proceedings of the National Academy of Sciences of the United States of America*, *109*(18), 6873–6877. https://doi.org/10.1073/pnas.1200902109

Van Leeuwen, K. L. (2019). *Landscapes of the apes: Modelling landscape use of chimpanzees and early hominins across an environmental gradient*. PhD Thesis. Bournemouth University.

Van Schaik, C. P., Ancrenaz, M., Borgen, G., Galdikas, B., Knott, C. D., Singleton, I., Suzuki, A., Utami, S. S., & Merrill, M. (2003). Orangutan cultures and the evolution of material culture. *Science*, *299*, 102–105. https://doi.org/10.1126/science.1078004

Van Schaik, C. P., Fox, E. A., & Sitompul, A. F. (1996). Manufacture and use of tools in wild

sumatran orangutans. Implications for human evolution. *Naturwissenschaften*, *83*, 186–188. https://doi.org/10.1007/s001140050271

Visalberghi, E., Addessi, E., Truppa, V., Spagnoletti, N., Ottoni, E., Izar, P., & Fragaszy, D. M. (2009). Selection of Effective Stone Tools by Wild Bearded Capuchin Monkeys. *Current Biology*, *19*(3), 213–217. https://doi.org/10.1016/j.cub.2008.11.064

Wadley, L., Esteban, I., de la Peña, P., Wojcieszak, M., Stratford, D., Lennox, S., D'Errico, F., Rosso, D. E., Orange, F., Backwell, L. R., & Sievers, C. (2020). Fire and grass-bedding construction 200 thousand years ago at Border Cave, South Africa. *Science*, *369*(6505), 863–866. https://doi.org/10.1126/science.abc7239

Washburn, S., & DeVore, I. (1961). Social behaviour of baboons and early Man. In S. Washburn (Ed.), *Social Life of Early Man* (pp. 91–105). Aldine.

Wessling, E. G., Deschner, T., Mundry, R., Pruetz, J. D., Wittig, R. M., & Kühl, H. S. (2018). Seasonal variation in physiology challenges the notion of Chimpanzees (*Pan troglodytes verus*) as a forest-adapted species. *Frontiers in Ecology and Evolution*, *6*, 60. https://doi.org/10.3389/fevo.2018.00060

Wessling, E. G., Kühl, H. S., Mundry, R., Deschner, T., & Pruetz, J. D. (2018). The costs of living at the edge: Seasonal stress in wild savanna-dwelling chimpanzees. *Journal of Human Evolution*, *121*, 1–11. https://doi.org/10.1016/j.jhevol.2018.03.001

"What Do We Get Out of It?" The Human Rights Impact of Bauxite Mining in Guinea. (2018). In Human Rights Watch (Ed.), *Human Rights Watch*. Human Rights Watch.

Wheatley, D., & Gillings, M. (2002). Archaeology, space and GIS. In *Spatial technology and archaeology: the archaeological applications of GIS* (1st ed., pp. 1–18). Taylor & Francis.

Whiten, A. (2019). *Cultural Evolution in Animals*. https://doi.org/10.1146/annurev-ecolsys-110218

Whiten, A. (2021). The burgeoning reach of animal culture. *Science*, *372*(6537), eabe6514.

https://doi.org/10.1126/science.abe6514

Whiten, A., Goodall, J., McGrew, W. C., Nishida, T., Reynolds, V., Sugiyama, Y., Tutin, C. E. G., Wrangham, R. W., & Boesch, C. (1999). Cultures in chimpanzees. *Nature*, *399*(6737), 682–685. https://doi.org/10.1038/21415

Whiten, A., Goodall, J., McGrew, W. C., Nishida, T., Reynolds, V., Sugiyama, Y., Tutin, C. E. G., Wrangham, R. W., & Boesch, C. (2001). Charting cultural variation in chimpanzees. *Behaviour*, *138*(11–12), 1481–1516.

Wild Chimpanzee Foundation. (2012). *Etat de la faune et des menaces dans les aires protegées terrestres et principales zones de forte biodiversité de Republique de Guinée*.

Wilensky, U. (1999). *NetLogo*. Center for Connected Learning and Computer-Based Modeling, Northwestern University.

Willis, M. D., Koenig, C. W., Black, S. L., & Castañeda, A. M. (2016). Archaeological 3D mapping: the structure from motion revolution. *Journal of Texas Archaeology and History*, *3*, 1–36.

Woittiez, L. S., van Wijk, M. T., Slingerland, M., van Noordwijk, M., & Giller, K. E. (2017). Yield gaps in oil palm: A quantitative review of contributing factors. In *European Journal of Agronomy* (Vol. 83, pp. 57–77). https://doi.org/10.1016/j.eja.2016.11.002

Wondra, E. M., Van Casteren, A., Pascual-Garrido, A., Stewart, F. A., & Piel, A. K. (2016). A New Report of Chimpanzee Ant-fishing from the Issa Valley, Tanzania. *African Primates*, *11*(1), 1–18.

Wrangham, R. W. (1977). Feeding Behaviour of Chimpanzees in Gombe National Park, Tanzania. In T. H. Clutton-Brock (Ed.), *Primate Ecology: Studies of Feeding and Ranging Behavior in Lemurs, Monkey and Apes* (pp. 503–538). Aca. https://doi.org/10.1016/B978-0-12-176850-8.50022-6

Wren, C. D., Botha, S., De Vynck, J. C., Janssen, M. A., Hill, K., Shook, E., Harris, J. A., Wood, B. M., Venter, J., Cowling, R., Franklin, J., Fisher, E. C., & Marean, C. W. (2020). The foraging potential of the Holocene Cape south coast of South Africa without the Palaeo-Agulhas Plain. *Quaternary Science Reviews*, *235*, 105789. https://doi.org/10.1016/j.quascirev.2019.06.012

Wurzer, G., Kowarik, K., & Reschreiter, H. (2015). *Agent-Based Modeling and Simulation in Archaeology*. Springer.

Wynn, T. (1981). The intelligence of Oldowan hominids. *Journal of Human Evolution*, *10*(7), 529–541. https://doi.org/10.1016/S0047-2484(81)80046-2

Wynn, T., Hernandez-Aguilar, R. A., Marchant, L. F., & McGrew, W. C. (2011). "An ape's view of the Oldowan" revisited. *Evolutionary Anthropology*, *20*(5), 181–197. https://doi.org/10.1002/evan.20323

Wynn, T., & McGrew, W. C. (1989). An Ape's View of the Oldowan. *Man*, *24*(3), 383. https://doi.org/10.2307/2802697

Yamakoshi, G. (1998). Dietary responses to fruit scarcity of wild chimpanzees at Bossou, Guinea: Possible implications for ecological importance of tool use. *American Journal of Physical Anthropology*, *106*(3), 283–295. https://doi.org/10.1002/(SICI)1096-8644(199807)106:3<283::AID-AJPA2>3.0.CO;2-O

Yamakoshi, G. (2011). Pestle-pounding behavior: the key to the coexistence of humans and chimpanzees. In T. Matsuzawa, T. Humle, & Y. Sugiyama (Eds.), *The Chimpanzees of Bossou and Nimba* (pp. 107–115). Springer Japan.

Yamakoshi, G., & Sugiyama, Y. (1995). Pestle-pounding behavior of wild chimpanzees at Bossou, Guinea: A newly observed tool-using behavior. *Primates*, *36*, 489–500. https://doi.org/10.1007/BF02382871

Zamma, K., & Makelele, M. (2012). Comparison of the Longevity of Chimpanzee Beds

between Two Areas in the Mahale Mountains National Park, Tanzania. *Pan Africa News*, *19*(2), 25–28. https://doi.org/10.5134/168176

Zeven, A. C. (1967). *The semi-wild oil palm and its industry in Africa*. State Agricultural University, the Netherlands.

Zuur, A. F., & Ieno, E. N. (2016). A protocol for conducting and presenting results of regression-type analyses. *Methods in Ecology and Evolution*, *7*(6), 636–645. https://doi.org/10.1111/2041-210X.12577

Zuur, A. F., Ieno, E. N., & Elphick, C. S. (2010). A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution*, *1*(1), 3–14. https://doi.org/10.1111/j.2041-210X.2009.00001.x

Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A., & Smith, G. M. (2009a). GLM and GAM for Absence–Presence and Proportional Data. In *Mixed Effects Models and Extensions in Ecology with R* (pp. 245–259). Springer. https://doi.org/10.1007/978-0-387-87458-6_10

Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A., & Smith, G. M. (2009b). GLMM and GAMM. In *Mixed Effects Models and Extensions in Ecology with R* (pp. 323–341). Springer. https://doi.org/10.1007/978-0-387-87458-6_13

Appendix A

Supplementary information for Chapter 2

A1 - Custom-made tripod mount

The DistoX2 tripod mount was conceptualized by KAW and Paul Riggs (Science Oxford), to enable a setup more in line with the total station system and standard archaeological data collection protocols. The piece is designed so that the DistoX2 can be mounted on a standard camera tripod over a fixed point and rotated along vertical and horizontal planes, covering all directions except for the area within the tripod legs. The rotation axes align with the origin of the laser (at the base of the DistoX2) and over the fixed point at the base of the tripod, so that the DistoX2 can be rotated while maintaining the fixed position of the laser source. The build is sturdy and lightweight, with a space at the base to fit a small circular spirt-level to aid with setup (Fig A.1). The 3D file is freely available for download and printing through Thingivese (https://www.thingiverse.com/thing:4367548) where print instructions and related information can be found.

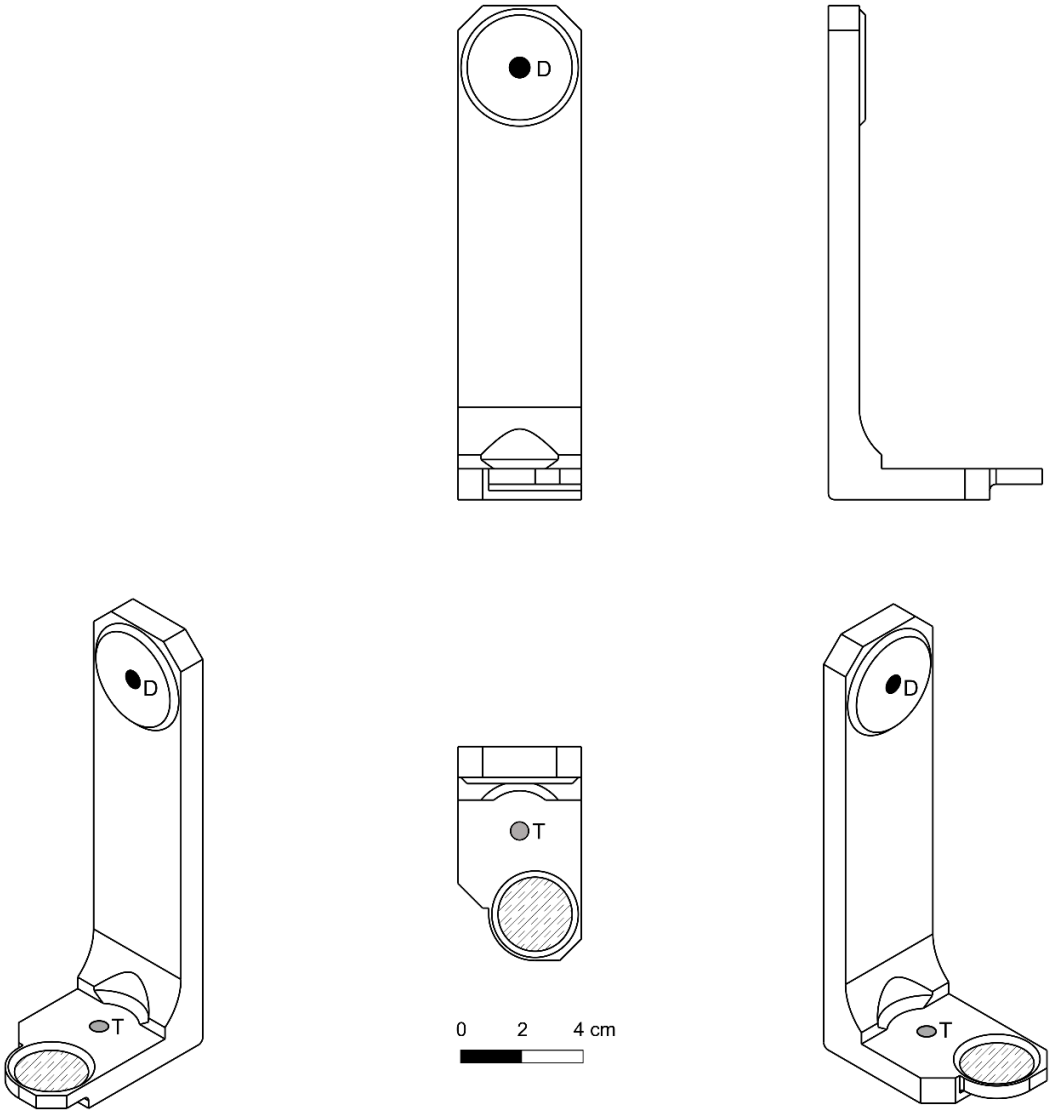


Figure A.1. Blueprint of DistoX2 custom-made tripod mount (Original composite by P. Riggs; with modifications by K. Almeida-Warren). Solid fill areas indicate screw attachments and connections to the DistoX2 (D), and tripod head (T). Hatch fill areas indicate surface for fitting a small circular spirit level.

The connections with the tripod and the DistoX2 are made using common photography tripod adaptor components available from eBay and other sources:

- 1/4" male to 1/4" female screw adaptor for camera tripod flash bracket
- 1/4" dual nuts tripod mount screw and camera flash hot shoe adapter

These pieces need to be non-magnetic (e.g. aluminium) so as not to interfere with the DistoX2's internal compass.

A2 – Arrow Gold GNSS Receiver

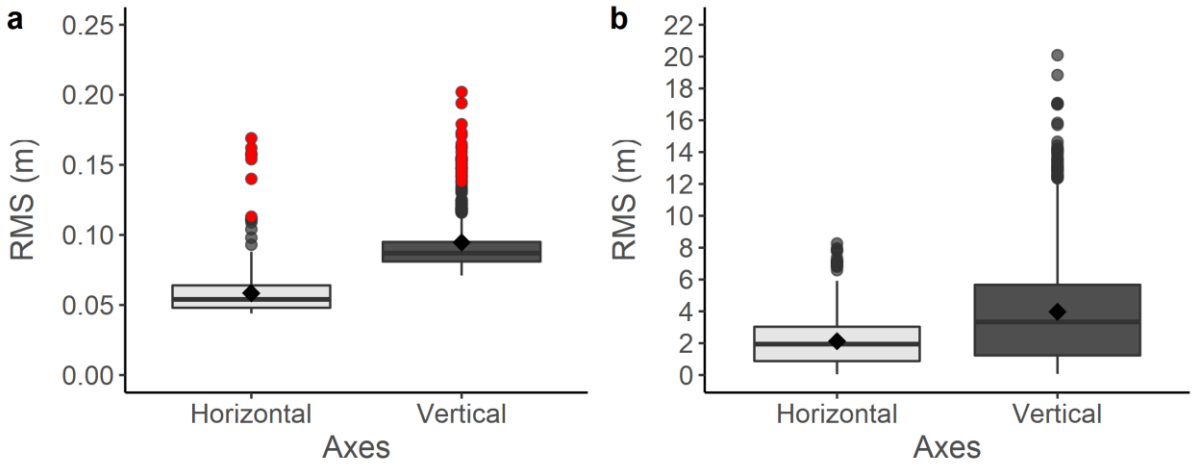


Figure A.2. Accuracy of the Arrow Gold GNSS Receiver as reported by the device during field surveys under two canopy conditions: a) open canopy; b) closed canopy. Values indicated as root mean square (RMS). Mean values represented by the diamond symbol, and major outliers highlighted in red.

Appendix B

Supplementary information for Chapter 3

B1 – Supplementary analyses: type of raw material selection

Table B.1. Pairwise results (P-values) comparing pairs of raw material types available for each site.

Site		Bark	Twig	Vine
Gombe	Twig	< 0.001		
	Vine	< 0.001	< 0.001	
	Grass	< 0.001	< 0.001	< 0.001
Issa	Twig	< 0.001		
	Vine	< 0.001	< 0.001	
	Grass	< 0.001	< 0.001	0.24
Mahale	Twig	< 0.001		
	Vine	< 0.001	< 0.001	
	Grass	< 0.001	< 0.001	0.015

Table B.2. Comparison of abundance of raw material types between sites relative to total suitable.

Type	Gombe	Issa	Mahale	χ^2	*P*
Bark	0.486	0.182	0.801	3150.747	< 0.001
Grass	0.116	0.023	0.017	580.773	< 0.001
Twig	0.871	0.936	0.983	550.708	< 0.001
Vine	0.013	0	0	110.908	0.003
Total (n)	457	264	639		

Table B.3. Pairwise results (P-values) comparing pair of sites for each raw material type. Comparison between Mahale and Issa for Vine listed as NA (not applicable) because no vines were recorded at either site.

Raw Material		Gombe	Issa
Bark	Issa	< 0.001	
	Mahale	< 0.001	< 0.001
Grass	Issa	< 0.001	
	Mahale	< 0.001	1
Twig	Issa	0.028	
	Mahale	< 0.001	0.001
Vine	Issa	0.297	
	Mahale	0.026	NA

Table B.4. Comparison of proportions of sourced plants relative to total suitable plants between sites. χ^2 and *P* values are a result of an equality of proportions test between sites.

	Gombe	Issa	Mahale	χ^2	*P*
Tool species	0.853	0.117	0.125	695.897	< 0.001
Suitable plants (n)	457	264	639		

Table B.5. Pairwise results (p-values) comparing proportions of tool species relative to all suitable plants between paired sites.

	Gombe	Issa
Issa	< 0.001	
Mahale	< 0.001	1

Table B.6. Pairwise Wilcoxon test (P-values) comparing average number of parts removed per source plant between paired sites.

	Gombe	Issa
Issa	< 0.005	
Mahale	< 0.05	< 0.001

B2 – Supplementary analyses: species selection

Table B.7. Proportion of source species abundance versus utilization at each site.

Site	Species	Available	Sourced	χ^2	*P*
Gombe	*Artabotrys congolanus*	0	0.007	0.21	0.647
	Annona senegalensis	0.006	0.007	0	1
	Dicyophlena condylocarpon	0.029	0.014	0.416	0.519
	Dicyophlena lucida	0.31	0.064	310.993	0
	Grewia sp.	0.012	0.057	60.604	0.01
	Grewia sylvestre	0	0.007	0.21	0.647
	Monanthotaxis poggei	0.614	0.752	70.775	0.005
	Saba comorensis	0	0.007	0.21	0.647
	Sabicea orientalis	0.018	0.007	0.207	0.649
	Uvaria angolensis	0.012	0.078	120.472	<0.001
	TOTAL (n)	342	141		
Issa	*Azanza garckeana*	0.158	0.018	50.347	0.021
	Artabotrys monteiroae	0.053	0.071	0	1
	Artabotrys collinus	0.316	0.416	0.326	0.568
	Annona senegalensis	0	0.009	0	1
	Cleistanthus polystachyus	0	0.168	20.492	0.114
	Dombeya burgessiae	0	0.009	0	1
	Grewia	0.053	0.018	0.013	0.91
	Saba comorensis	0.105	0.009	30.158	0.076
	Uvaria angolensis	0.211	0.062	20.957	0.086
	Uvaria sp. of FTEA	0.105	0.212	0.6	0.439
	Uvaria welwetschii	0	0.009	0	1
	TOTAL (n)	19	113		
Mahale	*A. congolanus*	0.033	0.045	0	1
	Grewia	0	0.068	30.596	0.058
	Monanthotaxis buchananii	0.077	0.091	0	1
	Mimusops kummel	0.099	0.023	10.521	0.217
	Paullinia pinnata	0.011	0.023	0	1
	Saba comorensis	0.066	0.023	0.419	0.518
	Uvaria angolensis	0.44	0.568	10.484	0.223
	Uvaria sp. of FTEA	0.22	0.159	0.356	0.551
	TOTAL (n)	91	44		

B2 – Supplementary GLMM results

Table B.8. Results from the full model investigating potential predictors influencing number of removals.

term	estimate	SE	Lower CI	Upper CI	χ^2	*df*	*P* [c]
Intercept	0.275	0.243	-0.201	0.752			NI[d]
SiteIssa[a]	0.397	0.285	-0.162	0.956			NI[d]
SiteMahale[a]	-1.279	0.463	-2.185	-0.372			NI[d]
Distance[b]	0.137	0.29	-0.432	0.706			NI[d]
Abundance[b]	-0.596	0.148	-0.887	-0.305			NI[d]
SiteIssa*Distance	-0.726	0.3	-1.313	-0.138			NI[d]
SiteMahale*Distance	0.18	0.607	-1.01	1.371			NI[d]
SiteIssa*Abundance	0.625	0.165	0.302	0.948			NI[d]
SiteMahale*Abundance	1.041	0.559	-0.056	2.137			NI[d]
Distance*Abundance	-0.205	0.317	-0.827	0.417			NI[d]
SiteIssa*Distance*Abundance	0.323	0.331	-0.325	0.972	3.145	2	0.208
SiteMahale*Distance*Abundance	1.279	0.768	-0.227	2.785			

[a] Site was dummy coded with Gombe as the reference category.

[b] Variables were Z-transformed to a mean of 0 and SD of 1.

[c] Results from the likelihood ratio test using the 'drop1' function.

[d] Not indicated because it has a limited interpretation.

Table B.9. Results from the reduced model (GLMM; lacking the non-significant three-way interaction) investigating potential predictors influencing number of removals.

term	estimate	SE	Lower CI	Upper CI	χ^2	*df*	*P*[c]
Intercept	0.228	0.251	-0.263	0.72			NI[d]
SiteIssa[a]	0.446	0.296	-0.133	1.026			NI[d]
SiteMahale[a]	-1.176	0.441	-2.04	-0.312			NI[d]
Distance[b]	0.096	0.29	-0.472	0.665			NI[d]
Abundance[b]	-0.496	0.109	-0.709	-0.282			NI[d]
SiteIssa*Distance	-0.686	0.3	-1.273	-0.098	6.744	2	0.034
SiteMahale*Distance	-0.011	0.529	-1.047	1.025			
SiteIssa*Abundance	0.525	0.132	0.266	0.785	16.674	2	<0.001
SiteMahale*Abundance	0.642	0.444	-0.229	1.513			
Distance*Abundance	0.113	0.088	-0.061	0.286	1.589	1	0.207

[a] Site was dummy coded with Gombe as the reference category.

[b] Variables were Z-transformed to a mean of 0 and SD of 1.

[c] Results from the likelihood ratio test using the 'drop1' function.

[d] Not indicated because it has a limited interpretation.

Appendix C

Supplementary information for Chapter 4

C1 – Description of response variables

Table C.1. Summary of the response variables used in this study and their descriptions.

Variable	Description	Units	Range
Raw materials	Total number of stones in the survey quadrat	Counts	0-99
Raw materials (size class 3-5)	Number of stones with sizes within the 95% confidence interval of tools used of nut-cracking	Counts	0-81
Tools	Total number of stones used for cracking nuts; Excludes unused fragments	Counts	0-28
Food trees	Total number of plants know to provide food sources to Bossou chimpanzees; Excludes plants with diameter at breast hight (DBH) under 2 cm	Counts	0-12
Fruit trees	Total number of plants know to be sources of fruit to Bossou chimpanzees; Excludes plants with diameter at breast hight (DBH) under 2 cm	Counts	0-9
THV	Total number of individual terrestrial herbaceous vegetation (THV) plants that are part of the Bossou chimpanzee diet	Counts	0-10
Nut availability	Approximate amount of nuts with edible kernels; Mean nut availability used in analysis	Categorical	0 (none); 1 (< 50); 2 (50 – 100); 3 (> 100)
Distance to nearest nest cluster	Distance, in metres, to nearest cluster of 21 nests; Cluster defined as nests within a 50-metre radius	Metres	50.01-781.06
Distance to nearest river	Distance, in metres, to nearest water course	Metres	6.92-399.84

C2 – Supplementary results for tool site selection

Table C.2. Likelihood ratio test results of the Full-Null model comparisons of the site selection models. Subset variables highlighted in bold.

Model	Resid. df	Resid. Dev	df	Deviance	p
~1 (Null model)	81	113.627			
~Raw materials + Wild food trees + THV + Nest +River	76	59.289	5	54.338	<0.001
~**Raw materials (size class 3-5)** + Wild food trees + THV + Nest +River	76	57.109	5	56.519	<0.001
~Raw materials + **Wild fruit trees** + THV + Nest +River	76	62.480	5	51.147	<0.001
~Raw materials (size class 3-5) + Wild fruit trees + THV + Nest +River	76	61.817	5	51.810	<0.001

Table C.3. Results of the AICc-Based Model Selection of the GLM for the predictors of tool site selection. Subset variables highlighted in bold.

Model	df	AICc
~Raw materials + Wild food trees + THV + Nest +River	6	72.409
~**Raw materials (size class 3-5)** + Wild food trees + THV + Nest +River	6	70.229
~Raw materials + **Wild fruit trees** + THV + Nest +River	6	75.599
~Raw materials (size class 3-5) + Wild fruit trees + THV + Nest +River	6	74.937

Table C.4. Results of the additional GLMs investigating potential predictors of tool site selection. Subset variables highlighted in bold.

Model	Term	Estimate	SE	χ^2	P[a]
~Raw materials + Wild food trees + THV + Nest +River	Intercept	-0.575	1.076		NI[b]
	Raw materials	0.195	0.057	19.748	<0.001
	Wild food trees	0.303	0.155	4.944	0.026
	THV	-0.101	0.159	0.419	0.518
	Distance to nearest nest cluster	-0.007	0.003	7.377	0.007
	Distance to nearest river	0.004	0.004	0.887	0.346
~Raw materials +**Wild fruit trees** + THV + Nest +River	Intercept	-0.305	1.052		NI[b]
	Raw materials	0.203	0.059	20.316	<0.001
	Wild fruit trees	0.241	0.193	1.753	0.185
	THV	-0.031	0.136	0.051	0.821
	Distance to nearest nest cluster	-0.008	0.003	8.469	0.004
		0.005	0.004	1.270	0.260
~**Raw materials (size class 3-5)** + **Wild fruit trees** + THV + Nest +River	Intercept	-0.700	1.079		
	Raw materials (size class 3-5)	0.351	0.102	20.978	0.000
	Wild fruit trees	0.199	0.202	1.049	0.306
	THV	-0.017	0.141	0.014	0.905
	Distance to nearest nest cluster	-0.007	0.003	7.715	0.005
	Distance to nearest river	0.006	0.004	1.967	0.161

[a] Results from the likelihood ratio test using the 'drop1' function.
[b] Not indicated because it has a limited interpretation.

C3 – Supplementary results for tool site re-use

Table C.5. Descriptive statistics and test results of the comparison between tool sites with low frequency (N = 10) and high frequency (N = 7) of nut-cracking events.

	Low frequency		High frequency		Test results			
Variable	Mean	SD	Mean	SD	Test[a]	t	df	p
Tools	7.100	3.143	11.429	3.780	tt	2.487	11.429	0.029
Distance to nearest nest cluster (m)	245.660	132.760	148.714	64.047	tt	-2.000	13.707	0.066
Raw materials (size class 3-5)	8.000[b]	5.250[c]	11.000[b]	3.500[c]	wt	50.000[d]	-1.430[e]	0.154
Raw materials	8.000[b]	14.500[c]	14.000[b]	4.000[c]	wt	49.000[d]	-1.320[e]	0.186
Mean nut availability	1.296	0.489	1.410	0.371	tt	0.547	14.835	0.593
Wild fruit trees	3.000	3.300	3.571	2.760	tt	0.387	14.401	0.704
Distance to nearest river (m)	139.613	77.486	124.710	84.836	tt	-0.369	12.265	0.718
Mean fruit bunches	1.252	0.630	1.188	0.630	tt	-0.204	13.069	0.842
Wild food trees	4.000	3.916	4.286	2.690	tt	0.178	15.000	0.861

[a] Test used: tt =t-test; wt = Wilcoxon rank sum test
[d] Reported as median
[e] Reported as inter-quartile range (IQR)
[b] Reported as w-statistic for Wilcoxon rank sum tests
[c] Reported as z-score for the w-statistic

C4 – Supplementary results for tool site inactivity

Table C.6. Likelihood ratio test results of the Full-Null model comparisons of the site inactivity models. Subset variables highlighted in bold.

Model	Resid. df	Resid. Dev	df	Deviance	p
~1 (Null model)	81	113.627			
~Mean nut availability + Raw materials + Wild food trees	36	46.532	3	8.017	0.046
~Mean nut availability + **Raw materials (size class 3-5)** + Wild food trees	36	46.518	3	8.030	0.045
~Mean nut availability + **Tools** + Wild food trees	36	41.350	3	13.198	0.004
~Mean nut availability + **Raw materials (size class 3-5)** + **Wild fruit trees**	36	46.621	3	7.928	0.048
~Mean nut availability + **Tools** + **Wild fruit trees**	36	41.968	3	12.581	0.006

Table C.7. Results of AICc-Based Model Selection of the GLM for the predictors of tool site inactivity. Subset variables highlighted in bold.

Model	df	AICc
~Mean nut availability + Raw materials + Wild food trees	4	55.675
~Mean nut availability + **Raw materials (size class 3-5)** + Wild food trees	4	55.661
~Mean nut availability + **Tools** + Wild food trees	4	50.493
~Mean nut availability + Raw materials (size class 3-5) + **Wild fruit trees**	4	55.764
~Mean nut availability + **Tools** + **Wild fruit trees**	4	51.110

Table C.8. Results of the additional GLM models investigating potential predictors of tool site inactivity. Subset variables highlighted in bold.

Model	Term	Estimate	SE	χ^2	P[a]
~Mean nut availability + Raw materials + Wild food trees	Intercept	1.275	0.927		
	Mean nut availability	-1.909	0.788	7.757	0.005
	Raw materials (size class 3-5)	0.001	0.017	0.001	0.973
	Wild food trees	0.083	0.111	0.567	0.452
~Mean nut availability + **Raw materials (size class 3-5)** + Wild food trees	Intercept	1.310	0.923		NI[b]
	Mean nut availability	-1.911	0.787	7.796	0.005
	Raw materials (size class 3-5)	-0.003	0.022	0.015	0.903
	Wild food trees	0.086	0.109	0.625	0.429
~Mean nut availability + Raw materials (size class 3-5) + **Wild fruit trees**	Intercept	1.838	0.971		NI[b]
	Mean nut availability	-1.895	0.773	7.757	0.005
	Raw materials (size class 3-5)	0.004	0.022	0.036	0.849
	Wild fruit trees	-0.104	0.145	0.522	0.470
~Mean nut availability + **Tools** + **Wild fruit trees**	Intercept	3.282	1.268		NI[b]
	Mean nut availability	-2.077	0.812	8.491	0.004
	Tools	-0.170	0.088	4.689	0.030
	Wild fruit trees	-0.053	0.144	0.135	0.714

[a] Results from the likelihood ratio test using the 'drop1' function.
[b] Not indicated because it has a limited interpretation.

Appendix D

Supplementary information for Chapter 5

D1 – Model Overview Design Details

Model Description

This document is a description of the model following the Overview Design Details (ODD) protocol for individual based models (Grimm et al., 2010).This version of the model is used in Chapter 5 of this thesis.

Overview

PURPOSE

The purpose of the model is to explore how ecological and foraging landscapes affect the distribution of tool-using activities by primates within their home range. The environment and behaviour relate to the use of stone tools by wild chimpanzees for nut-cracking, with a

focus on the influence of the distribution of food, water and shelter. The model has an empirical landscape, which is drawn from real world data collected from the chimpanzee field site of Bossou, Guinea. There is also a set of artificially generated landscapes, that allow for the exploration and cross-comparison of the effect of different ecological conditions. The ultimate goal of the model is to provide new perspectives on the relationship between ecology, landscape use, and the formation of stone tool assemblages in the early hominin record.

ENTITIES, STATE VARIABLES, AND SCALES

There are five types of entities in the model: habitat patches, and three types of agents (groups, chimpanzees, and nests). Each patch represents one hectare (100 x 100 metres) of a foraging landscape bounded by the agent's home range. The Bossou landscape is 728 hectares, with 311 hectares representing the home range in which the agents can move. The artificial landscape is 3024 hectares which is approximately equivalent to the average home range for chimpanzees (~36 km^2; Humle et al., 2016; Lindshield et al., 2021).

Each patch contains information relating to availability of raw materials for tools, oil palms for nuts, wild food trees, nests and water. This data is imported from georeferenced raster and vector maps generated in QGIS either from the real Bossou data, or an artificially generated landscape (See Input Data). To facilitate the calculations of caloric intake by chimpanzees, wild food trees are converted to grams of food relative to an adjustable value of maximum food availability per m^2. Food availability (in grams) follows a seasonal cycle (See Food availability and plant cycles). Similarly, oil palms are converted to a value of nut availability (in grams) for each patch.

Chimpanzee-agents represent individual primates, who log their daily caloric intake from foraging, the daily distance they have travelled, the number of nuts cracked over time, and the mean food availability of visited patches. Chimpanzees move in groups, as defined by group-agents, and the activity of chimpanzee-agents is determined at the group level. The activity options include travelling to food, foraging, cracking nuts, snacking, drinking, and travelling to nest. Group and chimpanzee variables are used to keep track of energy levels, hydration, food availability at visited patches, and coordinates of target patches during travel. Group sizes and member composition can vary over time in accordance with the hunger levels of individuals or time of day (See Grouping), however, the total chimpanzee population remains constant throughout the simulation.

Nest-agents represent individual nests that are constructed by each chimpanzee-agent at the end of each day. This type of agent is stationary and impermanent, whereby its chance of survival in the landscape decreases with age.

The model also includes nodes and links which join up all the patches within the home-range. These entities merely serve as the travel network by which group-agents can move, and do not contain any additional variables.

PROCESS OVERVIEW AND SCHEDULING

One day cycle consists of 72 time-steps (ticks), representing blocks of 10 minutes in a 12-hour day. At the start of each day, energy levels and travel distances of chimpanzee-agents (hereafter chimpanzees) are reset, and at the end of each day chimpanzees make a nest. Throughout the day, chimpanzees move in groups between patches to forage and crack nuts in order to acquire their daily caloric targets (Figure D.1). Only one activity can occur

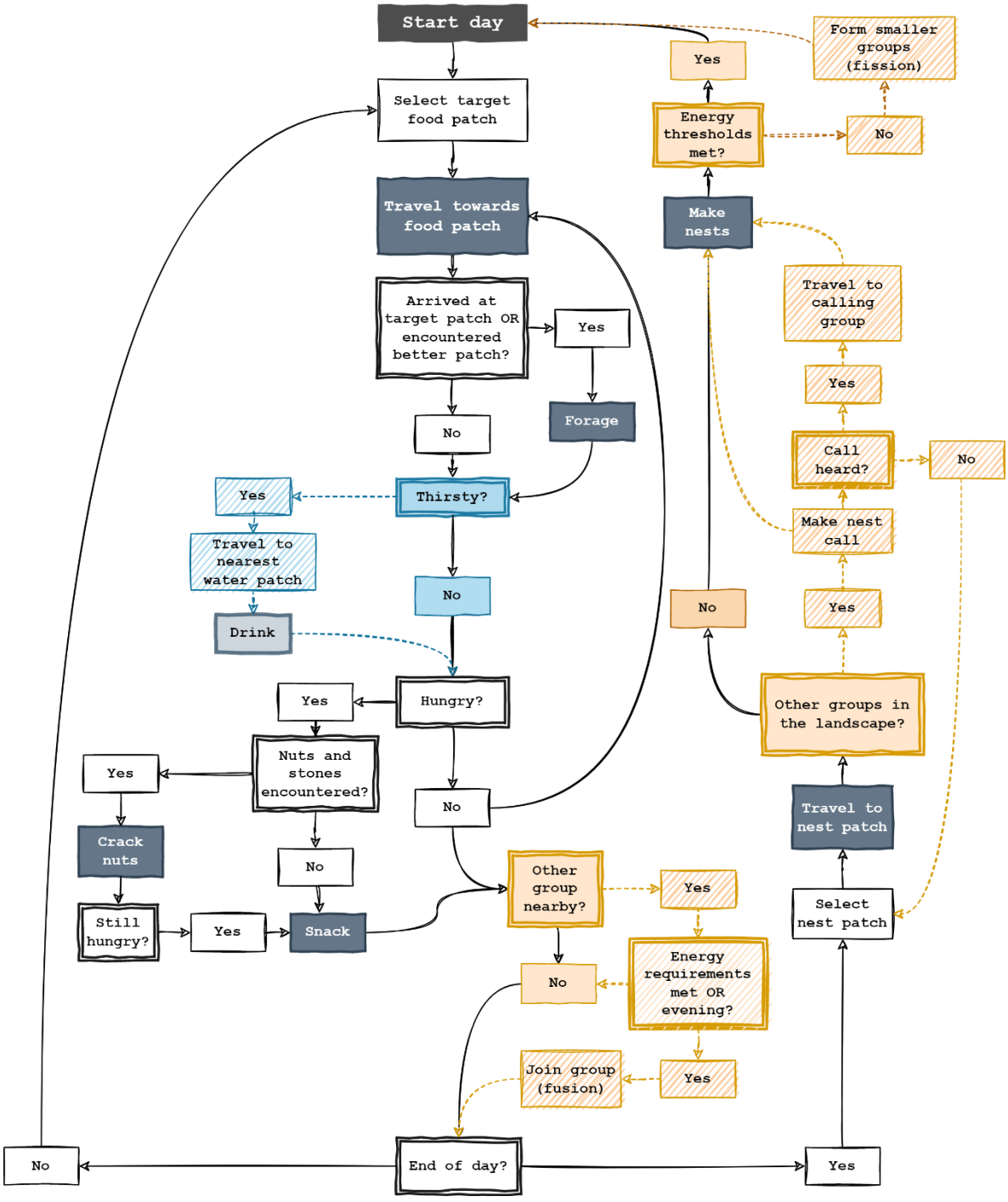


Figure D.1. Overview of chimpanzee-agent procedures. Dashed arrows and hashed boxes indicate steps that are only available under certain conditions. Light blue procedures are only available only when water-dependence is activated. Yellow procedures are active only when grouping-mode is set to "fission-fusion".

chimpanzees is subtracted from the food available at their current patch. A seasonal plant cycle also adjusts food availability (i.e. patch return rates) throughout a 360-day year, with growth and decay rates implemented at every step during growth and decay seasons, respectively.

Chimpanzee movement and foraging decisions are made at the group level by selecting from one of the suggestions put forward by group members. Individual suggestions are made using an epsilon-greedy strategy based on their pre-existing knowledge of food availability at patches. Final group selection is conditioned by the travel distance to suggested patches. However, if during travel towards a target patch, a group intersect a patch where food availability is greater than that of the target patch (if visited recently), or the mean of previously visited patches, they will choose the current patch as their new foraging destination. Before moving to a new patch, all members of the group check if they are hungry – i.e. if caloric intake at that point of the day is lower than required to achieve the minimum daily caloric threshold. If hungry, chimpanzees can crack nuts and/or snack (consume smaller amounts of wild foods), if these resources are encountered.

When engaged in "stationary" activities (i.e. foraging; cracking-nuts), groups will check the internal states of each member and the local environment (i.e. food availability) at the end of every tick and decide whether they will continue their current activity, or change to a new task.

relative to current food density. Nut-cracking occurrence is conditioned by chimpanzees Food intake from foraging and snacking is calculated following a modified Type II functional response equation to allow for a more realistic estimate of yield per tick. Nut-cracking

occurrence is conditioned by chimpanzees being hungry and the availability of resources (oil-palm trees with edible nuts; raw materials for tools) at patches that are intersected during the day. Chimpanzees will crack nuts until they are no longer hungry, or the nuts become depleted. Food and nut kernels consumed are converted to calorific intake (kcal) based on published estimates.

Every time a chimpanzee travels across a patch, they record the energy expended during travel. This includes both terrestrial travel and climbing. Calorific loss from terrestrial travel is a constant, calculated based on published estimates for speed and energetic costs of terrestrial travel in wild chimpanzees (see Pontzer and Wrangham, 2004). To account for some randomness in height climbed, energy expended during climbing is estimated based on a random value pooled from a maximum climb height and published estimates for energetic costs of climbing.

At the end of the day (tick = 70), chimpanzees search for a place to nest amongst patches within a 500m radius (the maximum distance a chimpanzee can travel in one tick). The nest site is selected relative to the nest-suitability of the patch and the number of existing nests at that patch. Once a nest site is chosen each chimpanzee moves to that location and produces a nest-agent. To reflect the ephemeral nature of chimpanzee nests, nest-agents are ephemeral too, with probability of decay increasing as nest age reaches 130 days (six months).

Design concepts

Basic principles

The primary goal of this model is to investigate how chimpanzees forage, crack nuts, sleep, and travel across the landscape within an optimal foraging framework and how different ecological habitats may influence the spatial distribution of nut-cracking activities (studied here, as a proxy for stone tool use). This version of the model is intended to represent generic wild chimpanzee physiology and behaviour, with the integration of details that are specific to the Bossou fieldsite and/or artificially generated data.

All agent decisions are guided by an Optimal Foraging Strategy with the additional ability of storing knowledge about the food availability and nest suitability of patches in their environment over time. While current field research is demonstrating that chimpanzee foraging decisions and planning are likely more complex (Janmaat et al., 2021; Trapanese et al., 2019), our understanding is still emerging. This model reproduces an intermediate scenario with the application of an epsilon-greedy strategy (Sutton & Barto, 2018), whereby agents are able to make decisions relative to an adjustable level accuracy. This enables the attribution of some degree of ecological knowledge without making explicit cognitive assumptions about the agents.

As per wild chimpanzee populations, the default form of social organization is fission-fusion (Humle et al., 2016), whereby a community will split up into smaller parties (fission) and join into larger groups (fusion) throughout the day. There are potentially a wide range of underlying factors driving fission-fusion dynamics (see Lehmann et al., 2007). However, because we are mainly interested in energy regulating activities (i.e., eating, drinking,

sleeping), in this version of the model fission-fusion is solely dictated by the energetic returns of individuals in the group under the assumption that when individuals are unable to meet their energetic requirements, it is more optimal for individuals to forage in smaller parties (Anderson et al., 2002; Furuichi, 2009; Itani & Suzuki, 1967; Wrangham, 1977). Nevertheless, users have the option to explore alternative grouping patterns by switching to solitary or single-group organisation.

In general, the chimpanzee diet is mainly composed of fruit, leaves, and other wild foods that do not require the use of tools (Hockings et al., 2009; Humle et al., 2016; Uwimbabazi et al., 2019). Therefore, in this version of the model it is assumed that agents will always prefer to consume wild foods before targeting nuts that need to be cracked with tools. Following an optimal foraging strategy, agents will seek to crack nuts when availability of wild foods does not meet their energetic requirements.

Chimpanzees are known to reuse the same nests and nesting locations and there is now a significant body of evidence that supports the idea that chimpanzees select nesting locations based on specific properties pertaining to ecology, topography and tree canopy (Badji et al., 2018; Carvalho et al., 2015; Hernandez-Aguilar, 2009; Hernandez-Aguilar et al., 2013; Koops et al., 2012; Ndiaye et al., 2018; Stewart et al., 2011). It is also known that nests can remain identifiable for an average of up to 6 months (see Table E.6; Ihobe, 2005; Kouakou, Boesch and Kuehl, 2009; Zamma and Makelele, 2012; Kamgang *et al.*, 2020). This information has been coded into the model, through a measure of nest decay, and an assumption that the presence and number of visible nests can act as visual cues to agents about the suitability of a patch for nesting. There is also an independent measure of patch suitability which is based on the empirical Bossou (or artificial) data on nest distribution.

Integrating the specific underlying factors of nesting suitability was beyond the scope of this model and research question, but it is something that could be explored in a future version of the model.

Wild food availability follows an annual cycle with two distinctive seasons, as described for Bossou. No distinction between wild food types is made in this version of the model, and it is assumed that all wild food follows a similar seasonal pattern. We are aware that this is not the case for all species found in Bossou (or other habitat for that matter), but it is unlikely to affect overall seasonality at the hectare or global scale given the empirical data. Nevertheless, patches are programmed to reach their maximum and minimum values at slightly different times, to account for some of this variation. In addition to these cycles, food consumed by agents is subtracted from patches in real time.

The role of permanent water sources can be explored by activating the water-dependence sub-model. This is presented as an option because most chimpanzee populations, especially those living in tropical forests, can achieve their hydration requirements simply through the water contained in the food they consume (Pontzer et al., 2021). This is also the case for Bossou. However, in some habitats where the climate is largely arid and hot, permanent water sources become a critical resource for chimpanzees to stay cool and hydrated (Lindshield et al., 2021). The water dependence sub-model allows users to explore this in alternative landscapes by restricting the amount of time that agents can spend away from water.

All these concepts and the empirical basis for these assumptions are explained further in the sub-models section of this document, as well as the accompanying publication.

Emergence

All spatial landscape-use data generated by agents during the simulation are emergent phenomena. This includes the frequency of nut-cracking events, number of visits, and number of nests in a patch. Collectively these measures are used to understand how tool use – as defined by nut-cracking in this model – emerges across the landscape in relation to other daily activities.

Adaptation

Groups and chimpanzees operate within simple optimal foraging rules, by which they make travel and foraging decisions relative to distance and predicted resource availability of patches. In other words, they will most often choose the closest patches with the highest food availability. However, if they encounter a patch with higher food availability than they predict at their destination, groups/chimpanzees can modify their choice of destination in accordance with the new information they have received. If moving in groups, group members can decide to leave or join a group according to the group's overall energy levels. When groups are nesting, they will make a call to other groups so they can join them and nest in the same patch.

Objectives

The objective of the chimpanzee agents is to maintain their daily energy (and hydration) levels by foraging, cracking nuts, snacking, and drinking.

Learning

Groups or chimpanzee-agents do not learn or adapt their decision-making strategies in this version of the model. However, chimpanzee-agents acquire cumulative knowledge about the food availability (at time of encounter) and location of patches they have visited in their home range. This information is used by groups to decide which patch to travel to.

Prediction

The decision algorithms groups use to select which foraging patch to travel to is based on knowledge that their members have acquired regarding mean food availability of different patches. This enables groups to predict which patches offer the most optimal foraging destination when accounting for estimated food availability and the travel distance.

While not explicitly modelled, groups are assumed to have global knowledge of the suitability of patches for nesting throughout their home range. This allows groups to predict which patches are most optimal for nesting when they are deciding where to sleep.

Sensing

Chimpanzees keep track of the calories they acquire, the calories lost during travel, as well as the distance travelled throughout the day. They also track the amount of time they have spent away from a permanent water source, and the food availability of patches they have visited at the time of encounter. During nut-cracking, individuals also track the number of nuts they have cracked during that session.

Individual calories acquired are used to determine whether a chimpanzee is hungry and whether they need to forage, crack nuts or snack in order to maintain their energy levels. Similarly, time away from water is used to determine whether an individual is dehydrated. Group decisions on what daytime activity to do next are largely determined by the hunger and hydration levels of its chimpanzee members. However, dehydration checks only run when the water sub-model is activated (See Hydration).

The number of hungry chimpanzees in a group is also used to assess whether a group should break up into smaller parties and determine the maximum party size – in this case the number of individuals in the original group who are not hungry. This measure is also employed by groups to determine whether they should join together when they cross paths.

When members of a group are cracking nuts, the number of nuts cracked by each individual is used to calculate how many nuts are still available for the entire group to crack during this activity.

Travelling to a nest site and nesting are determined by the time of day at a global level, under the assumption that all groups and their members receive visual cues (i.e., dimming of daylight) that night-time is approaching. The model also assumes that groups know, with some uncertainty, where the best nesting patches are located and how many nests are still present there.

In the group decision algorithm to determine which foraging patch they should travel to, group members use their stored knowledge of food availability in an epsilon-greedy algorithm to propose a patch to the group. A separate algorithm is then employed by the

group to select one of the proposed patches. Groups can also keep track of the amount of food remaining in their current patch and compare it to the current food availability of the eight neighbouring patches to determine whether they should move to a new patch.

In this version of the model, calories lost during travel and distance travelled per day are not used in any other procedures except outputs and *post hoc* model checks.

Interaction

Group and chimpanzee interactions are minimal and principally relate to communication and the sharing information. Chimpanzees can share information about their hunger and hydration levels within their group, as well as knowledge of mean food availability at the patches they have visited. Groups can share knowledge about member's hunger levels when they intersect, and can make a call to other groups in their home-range when they begin to nest.

Heterogeneity (agents)

There is no heterogeneity in state variables of processes between agents of the same type (i.e. groups, chimpanzees, and nests).

Collectives

Groups are composed of chimpanzees who begin their day at in the nesting location of the previous day. Chimpanzees are assigned a group on initialization, but groups can merge or break-up throughout the day if using the fission-fusion grouping mode. Daily caloric returns and mean food availability of visited patches are calculated for individual chimpanzees, but

this information is collated and used to make group-level decisions under the assumption that chimpanzee-agents are able to communicate and share knowledge within their group.

Stochasticity

At the beginning of the simulation groups are distributed randomly amongst patches within their home range that have a nest suitability value that is greater than 30. The order in which groups move and initiate a stationary activity, and the allocation of chimpanzees to groups, is randomized. When groups are stationary, the order in which chimpanzees forage, crack nuts, snack and make nests, is also randomized. This ensures that resources are not monopolized by any one individual (or group, on the rare occasion that multiple groups intersect on the same patch). Some degree of randomization is attributed to the group decisions of which patch to travel to. For foraging patches each chimpanzee suggests a patch to their group through a probability value in the epsilon-greedy formula, one of the proposed patches is then selected by the group using a weighted decision draw. For nesting patches this is determined by a weighted decision draw. This reproduces the underlying assumption that knowledge of the environment is imperfect and that not all decisions are optimal. In the case of water, however, chimpanzees have perfect knowledge of water locations as these are permanent and do not change throughout the model.

The day in the year cycle that a patch reaches it's peak wild food availability is drawn from a random normal distribution around a mean at which global food availability is expected to be reached (See Food availability and plant cycles). The amount of calories a chimpanzee acquires through a foraging event is also determined using a random normal distribution (See Foraging). This reproduces the empirical distribution of kcal/g of known chimpanzee foods, and serves to accommodate the diversity of food types they consume.

The occurrence of nut-cracking is determined by the probability of productive oil palms and raw materials being encountered. This probability is drawn using a random float value capped at the global maximum of oil palms and raw materials present in a patch. When nuts are encountered, the number of nuts available is determined using a random normal distribution relative to the empirical distribution of mean nuts available per productive oil palm (See Nut-cracking).

When a group decides to make a nest, they may have the option to produce a call to other groups in the landscape, if present. The probability that another group hears the call is determined relative to the distance to the calling group, using a random float draw. This mimics the natural decay of sound through space, while also accounting for a small chance that the call may not be heard at shorter distances due to potential obstacles produced by topography or vegetation.

Finally, to accommodate the varying rates of nest decay, the probability of the disappearance of a nest is determined using a random float draw relative to the nest's age, up to a maximum lifespan of 130 days.

Observation

This model produces a range of outputs from spatially explicit patch data to agent specific information. Because our main research question pertains to the spatial distribution of nut-cracking activity and the formation of nut-cracking sites, we are most interested in patch level spatial data. This includes the number of nut-cracking events that have occurred, the number of visits, and the number of nests that were made in each patch. These values may be tracked at every tick for cross-comparison or examined at the end of the simulation. The

model also records the global food availability over time to enable the tracking of the seasonal carrying capacity of the environment relative to the number of chimpanzees.

Chimpanzee data is collected individually and mainly includes calories consumed, calories spend during travel, and distance travelled per day. This serves mainly to examine how well the agents are able to maintain the expected caloric intake, energy expenditure, and travel of an average adult chimpanzee in the wild.

Finally, the model also records the number and size of groups present at every tick. This allows us to assess the amount of time chimpanzees engage in activities as a single or multiple groups and how this affects foraging efficiency.

Details

Implementation details

The model is implemented in NetLogo 6.2.1 and will be made freely available for download from comses.net – an online repository for agent-based models.

Initialization

During setup, variable settings are read from the user interface to determine landscape characteristics (i.e., base maps, and maximum food density of a single patch), as well as the number of chimpanzees and their behaviour characteristics (i.e., grouping patterns, degree of randomness of movement, water dependence, and the level of water dependence in time or distance).

Setup spatially assigns all habitat variables (i.e., number of food trees, oil palms, raw materials, and water availability) according to the corresponding base maps. Maximum food density is used to rescale the food tree data into maximum grams of food for each patch. Because the simulation starts mid-growth-season, these values are then adjusted according to the time left until the patch reaches its peak growth. In this version of the model global peak growth is normally distributed around day 90 of the year-cycle, which is the estimated peak time for the Bossou habitat. Nut tree data is also rescaled to grams of edible kernels according to empirical data of nut availability at Bossou.

Global values including energetic intake thresholds, energetic expenditure, speed of travel, speed of eating and nut-cracking are constants and are based on published empirical data. Individual accounting variables such as calories acquired, distance travelled, frequency of water encounters, time spent away from water and number of nuts cracked are set to zero. The individual logs of food availability at visited patches are initialized as an empty list.

Groups and their chimpanzee-agents are assigned randomly to patches that are above a designated nesting suitability threshold. Chimpanzees are connected to their groups using links. Group variables are initialized with their first activity set as travel to food and their initial destination set as their current patch. To facilitate the movement procedures of agents across the landscape, routes connecting all patches to their neighbours within the home-range are generated using nodes and links.

Input data

BOSSOU LANDSCAPE

In the empirical version of the model (landscape = Bossou) ecological variables such as abundance of *food trees*, *oil-palms* and *raw materials* are sourced from raster maps of 100m resolution, generated from inverse distance weighted (IDW) interpolations of data collected during quadrat surveys in Bossou in 2018. Here, food trees are defined as trees with a diameter at breast height (DBH) above 10 cm, that provide at least one type of resource that Bossou chimpanzees are known to eat. Once loaded to the model, food trees are converted to grams of food as better suited units of measurement for integrating energy into the model. Further details on the conversion are described in the *patch-energy* section.

A rasterized heatmap of nest distributions recorded during fieldwork at Bossou is employed in this model as a proxy for *nest suitability*. This parameter is used to model chimpanzee nesting decisions at the end of the day (see the *nesting and nest decay* section).

The *home range*, representing the space in which the chimpanzee-agents move, is taken from a raster rendering of the Bossou forest.

Known tool site locations and rivers are mapped from vector GIS layers of spatial data collected by KAW in 2018 and SC in 2008, respectively. The patch variable *water-availability* is calculated relative to the distance to a mapped river and is used in the travel-to-water procedure when *water-dependence* is activated (see the *water-availability* and *water-dependence* sections). All raster (.ascii) and vector (.shp) layers used in the model were

generated and processed in QGIS 3.10.9 and were imported to the model using the gis extension.

EXPERIMENTAL LANDSCAPE

In the experimental version of the model (landscape = Experimental), the abundance of *raw materials* and *oil palms* are also drawn from the Bossou empirical data. This ensures these two variables remain constant while the effect of main variables of interest (water, food, nests) are tested.

Water-availability is obtained from vector layers (water-abundance) that have been generated from a digital elevation model (DEM) of the Bossou region. There are three options of water-abundance to choose from: low; medium; or high. The input vector layers were created in QGIS from the Advanced Spaceborne Thermal Emission and Reflection Radiometer (ASTER) Global DEM (GDEM) 30-metre resolution data (NASA/METI/AIST/Japan Spacesystems and U.S./Japan ASTER Science Team, 2019). The ASTER GDEM raster file was cleaned using the *r.fill.dir* tool from GRASS (Version 7.8.6) and was then converted into vectorized watercourses with the *r.stream.extract* tool, also from GRASS. The low, medium, and high options correspond to vectors generated with a flow accumulation of 1000, 250, and 50 cells, respectively.

Data for *food-trees* are artificially generated through NetLogo using a diamond-square algorithm (Fournier et al., 1982). This is also the case for *nest-suitability* which is created using a hotspot-diffusion method. Further details of these procedures are provided in the Landscape Generator section.

Table D.1. Free parameters and values.

Parameter	Description	Default value	Value range
Landscape	Chooser to set which model version to run	Bossou	Bossou Experimental
Pop-size	The size of the population	7	1-30 individuals
Min-party-size	The minimum size of a party/group	2	1-10 individuals
Grouping-mode	Chooser to set population-level movement	Fission-fusion	Solitary Fission-fusion One-group
Exploration probability	The search limit for a target foraging patch	7 patches	0-1
Growth-season	The duration of the plant (food-availability) growth season	150 days	0-360 days
Max-food-density	Sets the upper limit of food density for the environment	12.5 g/m2	0-100 g/m2
Max-time-water	Maximum time chimpanzees can spend away from water	1 day	0-5 days
Water-dependence	Switch to determine if movement is conditioned by water availability and distribution	Off	On Off
Nest-suitability-coefficient	Relative importance given to the nest-suitability of a patch when choosing a nest patch	0.5	0-1
Nest-count-coefficient	Relative importance given to the number of visible nests in a patch when choosing a nest patch	0.5	0-1
Nest-interaction-coefficient	Relative importance given to the interaction between nest-suitability and the number of visible nests in a patch when choosing a nest patch	0.5	0-1
Spatial-multiplier	Determines the dimensions of the experimental landscape relative to Bossou	3 times	1-10 times
Smoothness	Degree of spatial heterogeneity of food availability	0.50	0-1.50
Nest-site-count	Number of patches to be designated as nest hotspots	18 patches	0-50 patches
Hotspot-radius	The maximum radius of the nest hotspot	9 patches	0-10 patches
Water-abundance	The amount of water available in the landscape	Medium	Low Medium High

Parameter values

The parameters employed in this model include both free parameters (with adjustable values; Table E.1) and known parameter values that have either been collected during the fieldwork component of this study, or have been sourced from published scientific literature (Tables E.2 – E.6). In the latter instance, we preferentially used data from publications derived from Bossou, but also used data from other field sites (namely Kibale, Uganda) when information for Bossou was absent. We acknowledge that differences in habitat and study sub-species may produce different estimates, but consider it unlikely that such differences will affect the model and its outputs in a significant way, particularly with regards to parameters connected to physiology (i.e. calorific requirements; daily energetic expenditure; travel speed; food intake rates).

Sub-models

WILD FOOD AVAILABILITY AND SEASONALITY

At initialization, imported values of food trees are converted to food availability (g) to enable estimation of calorific returns and a more intuitive interpretation of the data. Because the exact conversion rates between tree abundance and food availability are unknown, this calculation is based on a free parameter, *max-food-density*, selected prior to initialization which sets the upper limit of food density (g/m^2) for the environment:

$$\boldsymbol{D_p(g/m^2) = N_{t \cdot p} * \frac{D_{max}}{N_{t \cdot max}}}$$

, where:

D_p = food density of patch (g/m^2)

N_{tp} = number of food trees in patch

D_{max} = max food density of environment (see Table for details)

$N_{t \cdot max}$ = max food trees

This is then converted to total food available at patch, in grams, by multiplying by 10,000 m^2 (the total area of a patch).

Food availability and, by consequence, food density at both patch and global levels change over time in response to food consumed by chimpanzee-agents during the simulation (see the Foraging section), as well as seasonal plant cycles.

The plant cycles in this model are based on the seasonal food availability patterns of Bossou which are broadly defined by a growth-period of five months (~150 days; Nov-Mar), and a decay-period of seven months (April-Oct), corresponding to dry and wet seasons, respectively (Bryson-Morrison et al., 2016; Hockings et al., 2009). We calculate plant growth (P_g) for each patch following a logistic function as defined by a modified Verhulst equation (Kingsland, 1985):

$$\boldsymbol{P(t) = \frac{K P_0 e^{rt}}{K + P_0 \, (e^{rt} - 1)}}$$

, where:

$P(t)$ = proportion of plant food available on day t of the growth cycle

K = theoretical maximum proportion of plant food available

P_0 = proportion of plant food available on the first day of the growth season

r = growth-rate

To allow food availability to reach its empirical maximum during the simulation (proportion = 1), we set K = 1.1. We set P_0 = 0.25, according to published data on monthly food availability for Bossou which shows that minimum food availability is approximately 25% of food at peak availability (Bryson-Morrison et al., 2016). The resulting equation is therefore:

$$\boldsymbol{P_g(t) = \frac{1.1}{1 + 3.4\, e^{-rt}}}$$

The growth-rate is computed by solving the above equation for r:

$$\boldsymbol{r = \frac{\ln\left(3.4\, P(t)/(1.1 - P(t))\right)}{t}}$$

Plant decay (P_d) is calculated in a similar manner, but with t replaced by -t, such that:

$$\boldsymbol{P_d(t) = \frac{1.1}{1 + 0.1\, e^{rt}}}$$

, and decay-rate:

$$\boldsymbol{r = \frac{\ln\left((1.1 - P(t))/(0.1\, P(t))\right)}{t}}$$

Daily growth and decay is calculated as the change relative to the previous day and converted to grams by multiplying by the empirical maximum of food in patch (F_{max}):

$$\Delta = \big(\boldsymbol{P(t) - P(t-1)}\big) \times \boldsymbol{F_{max}}$$

Given that the model is set to initialize at the start of the year (January) we calculate initial food values using the plant growth equation (P_g), with t computed relative growth season duration (G) and time to peak food availability, which is determined for each patch using a normal distribution:

$$\boldsymbol{t = G - (90 + X)}$$

, where $X \sim N[0, 9]$, and 90 is the initial time to global peak food availability which corresponds to the end of March - when wild food availability is highest in Bossou (Bryson-Morrison et al., 2016; Hockings et al., 2009).

Oil palms (*Elaeis guineensis*) are productive year-round (Woittiez et al., 2017; Zeven, 1967) and, therefore, nut availability is not modelled following seasonal patterns. Instead, imported values of oil palm density are converted to nut availability (in grams) for each patch based on recorded values on the proportion of palms providing edible nuts and the estimates for the number of nuts available in Bossou (Table 5; this study; Humle and Matsuzawa, 2004), as well as the average weight of edible kernels (Table 5; Davies, 2012):

$$\boldsymbol{F_i\,(g) = N_{p \cdot max} * P(nuts) * 200 * \mu_{nuts} * W_{nuts}}$$

, where:

$N_{p \cdot max}$ = max oil palms

$P(nuts)$ = probability/proportion of palms with edible kernels

μ_{nuts} = mean number of nuts per palm

W_{nuts} = average weight of an edible kernel

WATER AVAILABILITY

On initialization, water availability of patches is determined relative to the distance to the nearest patch that intersects a watercourse loaded from a GIS vector file. Patches that intersect a water line are attributed a water-availability of 1. Water availability for the remaining patches (W_a) is calculated using the following equation:

$$W_a = \frac{1}{d_{min} + 0.25}$$

, where:

d_{min} = distance (in patches) to the nearest patch with a water-availability of 1.

Unlike food availability, water availability at patches remains fixed throughout the simulation.

FORAGING AND TRAVEL DECISIONS

Chimpanzee-agents initialize with an assumption that every patch in their home-range has the same amount of food available which is set to the mean value of food present in the home range. During the simulation, chimpanzee-agents are able to acquire and update knowledge of the mean food availability of each patch they have visited. This is made possible by logging the food availability of the current patch using the *observe* command of the *dc* extension. At the start of every travel-to-food activity, each chimpanzee-agent

inspects the food availability values they have stored of all the patches in their home-range and suggests a food patch using the *dc:epsilon-greedy-chooser*. The accuracy of the chimpanzee-agents choice (i.e., the probability that they will choose a patch with hight food availability) is determined by the value given by the *exploration-probability*, whereby the higher the value, the more random the selection.

The group then selects one of the suggested patches using a weighted factor (w) conditioned by the distance (d) to the suggested patch:

$$\boldsymbol{w = \frac{1}{1 + d}}$$

A weighted decision ensures that chimpanzees most often select the patches with the highest food values that are closest to them, while allowing for some selection of more distant and/or lower value patches to account for uncertainty and unknown parameters. For example, chimpanzees may not always choose the patch with the highest overall food, potentially because: a) they cannot always accurately predict which patches have the most food; and, b) they prefer certain food types and/or species that occur in relatively lower value patches, but for which we do not have precise data.

Once a chimpanzee has identified its target patch, it calculates the most direct linear route (using the *nw* extension) and moves along the route, one patch at a time. At each intersected patch, chimpanzees may crack nuts (see nut-cracking section), and snack if they are hungry (see foraging section). When they arrive at the target patch, they forage (see foraging section). If they are still hungry after foraging, they can crack nuts and snack if these resources are encountered in the target patch.

Additional checks are made by the chimpanzees at each *en route* patch to evaluate whether they have encountered a better foraging patch. If the food available at the current patch is greater than the perceived food available at the target patch, then groups will reset their target foraging location to their current patch.If the *water-dependence* parameter is switched on, chimpanzees evaluate their hydration levels at the start of each step (see hydration section). If they are dehydrated, their target patch is set the nearest patch where a permanent water source is located and move directly to that location, forgoing hunger checks and opportunities for nut cracking or snacking. Only after restoring their hydration levels, can they resume foraging activities.

HYDRATION

Water-dependence: ON

Currently, data on frequency and quantity of water consumed for wild chimpanzee populations is very limited and highly variable (See Table 2). For this reason, we use time (in ticks) since last water encounter as a proxy to monitor the hydration levels of chimpanzee-agents. Throughout the simulation chimpanzees check every patch visited for the presence of a permanent water source. If a permanent water source is encountered, *time-from-water* is set to zero; while if water has not been encountered within that time-step *time-from-water* increases by one unit.

If *time-from-water* reaches the maximum threshold set by the corresponding initializing parameter (max-time-water; Table 1), then chimpanzees travel to the nearest water source to restore their hydration levels (as described in *foraging and travel decisions*).

Table D.2. Summary of published information of frequency of water intake through drinking.

Site	Dominant habitat type	Water intake (drink/day)	Reference
Bossou, Guinea	Secondary Forest	0.2	This study
Kibale, Uganda	Primary Forest	0.8	Wrangham, 1977
Fongoli, Senegal	Savannah and woodland	1	Lindshield *et al.*, 2021

Water-dependence: OFF

Due to limited knowledge surrounding the effect of water availability on chimpanzee behaviour under different ecological contexts (e.g. forest vs. savannah habitats), we also provide the option to switch off water-dependence. Under this condition, chimpanzees simply log the number of times water is encountered during the day, allowing for the potential influence of water to be explored without affecting chimpanzee-agent behaviour.

Water encounters are checked at every patch visited using a probability draw based on the water-availability of the patch (W_p):

$$\boldsymbol{r < W_p}$$

, where $r \in [0\,, 1]$ and is drawn randomly. Water is encountered if the condition is met.

FORAGING

To calculate the amount of food consumed (F) at a patch we used a modified type II functional response equation:

$$\boldsymbol{F\,(g) = \frac{a * T * D_p}{50 + a * h * D_p}}$$

, where:

a = searching efficiency (m^2/min)

T = foraging time (min)

D_p = food density of patch (g/m^2)

h = handling time (min/g)

This asymptotic equation produces values that are influenced by the local availability/density of food, while taking into account two key conditions: a) there is maximum amount of food that can be consumed once an upper threshold of food density is reached; b) when food density is low, the food consumed is lower in response to the lower encounter-rates and the greater time spent searching for food.

Food density (D_p), is taken directly from the chimpanzee's current patch in the model. This value varies over time in response to the food consumed and the seasonal plant cycles. *Searching efficiency* (a) and *handling time* (h) are constants estimated from published data, while foraging time (T) is set to the metric equivalent (minutes) of the duration of one tick.

Searching efficiency can be best described as the area that can be observed during the search for food per unit of time. While no direct data exist in published literature, we assume that the maximum value cannot exceed the average speed of terrestrial travel by a wild chimpanzee and that a minimum of one metre squared is visible per meter of travel. We use the mean velocity of 0.83 m/s reported by Hunt (1989; as cited in Pontzer and Wrangham 2004) converted to m^2/min, whereby:

$$\boldsymbol{a\ (m^2/min) = 0.83\ * 60s \sim 50}$$

Handling time pertains to the time it takes to process and consume a unit of food, equivalent to the inverse of the intake rate (i.e. the amount of food consumed per unit of time). Intake rates are known to vary with type and size of food item (Chemurot et al., 2012; Uwimbabazi et al., 2019; Venable et al., 2020; Wrangham et al., 1993). For the purpose of this model, we calculated the mean intake rate of the most common food items eaten by wild chimpanzees (ripe and unripe fruits; young leaves; and pith) from data on Kanyawara females in Kibale NP (Table E.3; Uwimbabazi *et al.*, 2019). The handling time is therefore:

$$\boldsymbol{h\ (min/g) = \frac{1}{intake\ rate} = \frac{1}{2.58} \sim 0.4}$$

Table D.3. Intake rates (g/min) of common food items consumed by female chimpanzees in Kanyawara, Kibale NP (adapted from Uwimbabazi et al. 2019)

Food item	Intake rate (g/min)[1]
Ripe fruits	3.40
Unripe fruits	3.00
Young leaves	2.10
Pith	1.8
Mean	**2.58**

[1]Dry weight

Foraging time is the time allocated for searching for, processing and consuming food. In this model, this is set to 10 minutes (equivalent to the duration of one tick).

Substituting *a*, *h* and *T* by the estimates provided we reach the following equation for food consumed per tick (*Ft*):

$$\boldsymbol{F_t\,(g) = \frac{50 * 10 * D_p}{50 + 50 * 0.39 * D_p} = \frac{500 * D_p}{50 + 19.5 * D_p}}$$

Chimpanzees can forage at the same patch over several ticks while it remains more optimal than moving to another patch (i.e. food availability is greater than neighbouring patches; or forest mean). If chimpanzees get hungry while travelling between patches they may *snack*, which involves foraging for one tick only before moving to the next patch towards the destination.

The food consumed ($\boldsymbol{F}$) is subtracted from the patch and is acquired by the chimpanzee as energy (kcal) using the following formula:

$$\boldsymbol{E_f\,(kcal) = F \times (3 + X)},$$

where $X \sim N[0\,,\,0.6]$. Values are based on the mean and standard deviation of the energetic return (kcal/100g) estimated for wild foods consumed by chimpanzees in Bossou (Table H.4; Bryson-Morrison *et al.*, 2020). A normal distribution (X) is employed to mimic the variation in the energetic yield of different food types and species.

These formulas are the result of tests designed to ensure that the daily caloric intake of the chimpanzee-agents does not exceed reported values for wild populations (4,931 kcal, including nursing females; Uwimbabazi *et al.* 2019); and follows expected patterns (range: 1,800 – 3,000; Conklin-Brittain, Knott and Wrangham, 2006; Uwimbabazi *et al.*, 2019) under normal foraging conditions and population levels (i.e.. within the carrying capacity of the environment; Table H.5).

Table D.4. Caloric value (kcal/g) of different wild foods consumed by the chimpanzees of Bossou (adapted from Bryson-Morrison et al. 2020).

Species	Food item	kcal/g
Parkia bicolor	Ripe fruit	4.21
Megaphrynium macrostachyum	Ripe fruit	2.15
Ficus sp.	Ripe fruit	2.46
Pseudospondias microcarpa	Ripe fruit	2.93
Canarium schwenfurthii	Ripe fruit	3.03
Spondias mombin	Ripe fruit	2.78
Myrianthus libericus	Ripe fruit	3.10
Myrianthus arboreus	Ripe fruit	4.06
Macaranga barteri	Ripe fruit	3.84
Morus mesozygia	Ripe fruit	3.71
Monodora tenuifolia	Ripe fruit	3.94
Discoreophyllum cumminsii	Ripe fruit	3.60
Musanga cecropioides	Ripe fruit	2.58
Antiaris africana	Ripe fruit	3.16
Aningeria altissima	Ripe fruit	3.67
Landolphia sp	Ripe fruit	3.17
Aframomum latifolium	Pith	2.05
Costus afer	Pith	2.44
Gongronema latifolium	Pith	2.81
Hypselodelphis sp.	Pith	2.94
Maranthochloa macrophylla	Pith	2.67
Megaphrynium macrostachyum	Pith	2.82
Pennisetum purpureum	Pith	2.20
Thaumatococus daniellii	Pith	2.69
Combined species	Leaf	2.77
Mean ± sd	**All**	**3.03 ± 0.61**

Table D.5. Summary of parameter values used for simulating foraging intakes in the model.

Parameter	Description	Value	Reference
min-kcal	Minimum calorific intake required per day	1200 kcal*	Conklin-Brittain, Knott and Wrangham, 2006; Uwimbabazi *et al.*, 2019
target-kcal	Target calorific intake per day	2500 kcal*	Conklin-Brittain, Knott and Wrangham, 2006; Uwimbabazi *et al.*, 2019
kcal-return	Calorific intake per gram of food consumed	3 ± 0.6 kcal/g	Bryson-Morrison *et al.*, 2020
velocity	Speed of terrestrial travel	0.83 m/s	Hunt 1989, as cited in Pontzer and Wrangham 2004
intake-rate	Amount of food (in dry grams) consumed per minute of feeding	2.58 g/min	Uwimbabazi *et al.*, 2019

NUT-CRACKING

The occurrence of a nut-cracking event is checked when a chimpanzee is hungry and is determined by a three-step probability draw based on the relative abundance of oil palms with edible kernels and raw materials for tools: 1) the chimpanzee-agent draws a number between zero and the maximum value of oil palm abundance of patches, to determine if an oil palm is encountered; 2) the chimpanzee-agent draws a number between zero and one, to evaluate if the palm has edible kernels; 3) the chimpanzee-agent draws a number between zero and the maximum value of raw material abundance of patches, to check if stone tools are available nearby. A nut-cracking event occurs only if the following three conditions are met: the number drawn in 1) is lower than the oil palm abundance of the current patch; the number drawn in 2) is lower than the probability of nuts being present at the palm; and the resulting value in 3) is lower than the raw material abundance at the current patch. This

procedure is designed to reproduce a nut-cracking strategy that is based on the encounter-rate and intersection of required resources within an opportunity hypothesis framework. All conditions met, the number of edible nuts available is calculated using the following equation:

$$\boldsymbol{N_{nuts} = 50 * 1.5 + X},$$

where $X \sim N[0\,, 0.7]$. Values are estimated from the mean and standard deviation of nut availability recorded for oil palms in Bossou (Table 6.6; this study; Humle and Matsuzawa, 2004).

Table D.6. Summary of parameter values associated to nut-cracking and kernel consumption.

Parameters	Mean	Reference
Probability of nuts	0.7	This study; Humle and Matsuzawa, 2004
Nut availability	1.5 ± 0.7 [range ~ 1 – 3] ≈ 75 ± 35 nuts/palm [range ~ 1 – >100]	This study; Humle and Matsuzawa, 2004
Kernel weight	3.0 g	Davies, 2012
Energetic value	615 kcal/100g ≈ 18.45 kcal/kernel	Bryson-Morrison *et al.*, 2020
Nuts consumed	2.02 ± 0.53 nuts/min [range = 1.30 – 2.50]	Humle, 2003

Hungry chimpanzees will crack nuts until they are no longer hungry, or nuts are depleted. The resulting calories obtained from nut kernel consumption are added separately to the daily energetic intake record:

$$\boldsymbol{E_{nc}\,(kcal) = N_k * 18.45},$$

where N_k is the number of kernels consumed, and 18.45 is the kcal return of an average kernel weighing 3g (Table 6.6; Davies, 2012; Bryson-Morrison *et al.*, 2020).

Grouping

This model presents three options of grouping behaviour: solitary, fission-fusion, and one-group.

Fission-fusion is the default setting of the model as it is the social system that is described for chimpanzees, including all sub-species (Humle et al., 2016). In this model fission-fusion is conditioned by food availability which is measured by the number of chimpanzees in a nesting group that are satiated (i.e., reached the minimum calorific threshold) at the end of the day. If more than half the chimpanzees did not reach the targets, then the group will fission into smaller groups with a maximum party size set at the number of satiated chimpanzees, or the parameter value for min-party-size, whichever is largest.

Throughout the day, if groups are in the same neighbourhood (within two patches of each-other), they will fusion if one of the following conditions is met: 1) less than 50% of chimpanzees in those groups are hungry; 2) there are under 2 hours left until the end of the day. The second condition enables groups to get together into a larger party in anticipation of their nesting time.

Solitary and *one-group* operate in similar ways in that party sizes remain static throughout the simulation. The only difference is that when *solitary*, chimpanzees move entirely independent from each other across the landscape; while as *one-group* they always move

as a single group and travel decisions are made collectively according to the status of the entire population.

NESTING AND NEST DECAY

At the end of every day-cycle (71 time-steps), the chimpanzee-groups select the best nesting patch within the distance that can be covered during one time-step (*travel-per-tick*) to construct their sleep nest. This selection is based on a nest score (χ_n) calculated from the suitability of the patch for nesting (S_n), the number of nests present in the patch (N_n), and the relative importance given to each of the values and their interaction:

$$\boldsymbol{\chi_n = (C_s \times S_n) + (C_N \times N_n) + (C_i \times S_n \times N_n)}$$

, where:

C_s = nest-suitability-coefficient

C_n = nest-count-coefficient

C_i = nest-interaction-coefficient

Chimpanzees then move to the chosen patch and make a nest. To reproduce effects of nest decay, we employ a condition where the probability of nest disappearance increases as nest age (A_n) approaches 130 days (the average nest longevity; see Table 6):

$$\boldsymbol{r < \frac{A_n + 1}{130}}$$

, where $r \in [0, 1]$ and is randomly drawn. If the condition is met, then the nest is removed from the environment.

These procedures are the same for all grouping conditions: solitary; fission-fusion; one-group. The following section applies to *fission-fusion* only.

After the first group has nested, they make a nesting call to remaining groups in the environment. Each of the remaining groups will check if they hear the call according to a probability draw based on their distance to the nesting group ($D_{n \cdot g}$) and a maximum hearing range of 10 patches (≈ 1 km; Table E.7):

$$\boldsymbol{r < 1 - \left(\frac{D_{n \cdot g}}{10}\right)}$$

, where $r \in [0, 1]$. If the condition is met, the group will move to the nesting group's location and form a nesting party with that group. Each group that did not hear the call will initiate a nesting procedure and make a nesting call to remaining un-nested groups until all groups have nested.

Table D.7. Summary of parameter values associated to nesting.

Parameters	Mean	Reference
Nest survival	~ 130 days [range: ~ 46 – 167][1]	Ihobe, 2005; Kouakou, Boesch and Kuehl, 2009; Zamma and Makelele, 2012; Kamgang *et al.*, 2020
Hearing range	~ 1 km	Piel, 2014; Kalan *et al.*, 2016

[1] range of reported means for nests in non-savannah habitats (see main text for further details)

LANDSCAPE GENERATOR

When the landscape variable is set to "Experimental", the NetLogo world dimensions can be adjusted to multiples of the Bossou landscape using the *spatial-multiplier*. For example, if the spatial-multiplier is set to 2, the width and height of the NetLogo world increases to double that of the original Bossou landscape, which corresponds to a four-fold increase in the home range area. The fixed variables – *raw-materials* and *oil-palms* – are kept constant by scaling the corresponding input rasters to fit the world dimensions of the new landscape.

Under this setting, the model also generates artificial landscapes for *food-trees* and *nest-suitability*. These procedures are described below.

Food-trees

The experiment data for *food-trees* is generated using a diamond-square algorithm (Fournier et al., 1982), which produces a realistic looking continuous landscape of values. The spatial heterogeneity of the landscape (i.e., the degree at which low and high values are spatially segregated) is determined by the *smoothness* value, where higher values correspond to greater environmental heterogeneity.

The algorithm starts with a two-dimensional array with a width and height of $2^n + 1$ and consists of two main steps – diamond and square – which alternate until the entire array has been populated with values. The diamond step works along diagonal lines from the corners towards the centre of the array, while the square step operates along horizontal and vertical lines from the centre towards the corners of the array (Fig D.2).

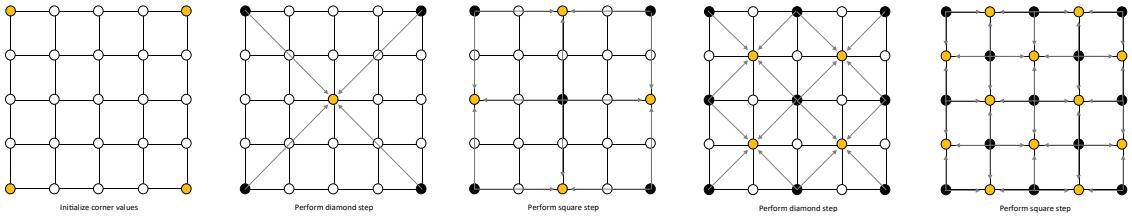


Figure D.2. Visualization of the diamond-square algorithm on a 5 × 5 array. Credit: Christopher Ewin, CC BY-SA 4.0 (https://creativecommons.org/licenses/by-sa/4.0/), via Wikimedia Commons.

To allow the algorithm to run on an landscape of any dimensions, the model performs an initial alignment step which calculates the nearest power value in 2^n to the halved length of the longest axis of the model world. The initial step length is then set to 2^n patches and the first values for the centre and corner patches are randomly drawn from a range of 0-1. At the end of every diamond-square iteration, the step length is halved and the upper threshold (r_{max}) for the random draw is updated as follows:

$$\boldsymbol{r_{max}(t) = (2 \times 2^{-st}) - 2^{-st}}$$

, where $\boldsymbol{t}$ is the number of completed iterations, and $\boldsymbol{s}$ is the *smoothness* value. The algorithm stops running when the step length is less than 1.

Once all patches have been populated, the *food-tree* values are normalized to a scale of 0-100 and are then rescaled so that the total number of trees present in the home-range is constant for all simulations using the same world dimensions. The scale factor ($\boldsymbol{c}$) is calculated from the number of trees present in the Bossou empirical landscape (n = 576) and the world dimensions relative to the Bossou landscape:

$$\boldsymbol{c} = \frac{\mathbf{576} \times (\boldsymbol{M^2})}{\sum \boldsymbol{N_{tp}}}$$

, where:

N_{tp} = number of food trees in a patch;

M = the *spatial-multiplier* that determines the dimensions of the landscape relative to Bossou

Nest-suitability

Nest-suitability is determined by the number of patches designated as nest hotspots (*nest-site-count*) and the radius chosen for those hotspots (*hotspot-radius*). The nest hotspots are allocated randomly across the landscape and any patches within the *hotspot-radius* (R) are attributed the maximum nest-suitability (100) using a probability draw that is determined by the distance to the hotspot (d_h):

$$\boldsymbol{r} > \left(\frac{\boldsymbol{d_h}}{\boldsymbol{R}}\right)^{\mathbf{3}}$$

, where $r \in [0, 1]$. If the condition is met, then the patch is given a nest-suitability of 100. A percentage of this value is then diffused to neighbouring patches using the *diffuse* command. This percentage (D_r) is calculated from the hotspot-radius (R):

$$\boldsymbol{D_r} = \frac{\boldsymbol{R}}{\boldsymbol{R} + \mathbf{1}}$$

D2 - GIS processing

All data was processed and analysed in QGIS 3.10.9 using inbuilt features as well as additional tools available from the SAGA 2.3.2 and GRASS 7.8.3 modules. The coordinate reference system (CRS) used was WGS 84 / UTM zone 29N (EPSG:32629).

D2.1. – Spatial interpolation and rasterization of empirical data

The Bossou chimpanzee home-range was defined by creating a new vector layer and tracing, using the polygon tools, the outline of the Bossou forest that surrounded the GPS tracks recorded during chimpanzee follows. This vector was then converted into a raster layer with a 100 x 100 m resolution using the 'Rasterize (Vector to Raster)' tool (Table H.1).

Table D.8. Input parameters used in the 'Rasterize (Vector to Raster)' window to convert the outline of the Bossou forest into a gridded raster of the chimpanzee home-range.

Parameters	Selected option
Input layer	[Shapefile: Bossou forest]
A fixed value to burn	1
Output raster size units	Pixels
Width/Horizontal resolution	100
Height/Vertical resolution	100
Assign a specified nodata value	0

Quadrat data for wild food trees, oil palms, and raw materials was converted into gridded continuous landscapes (rasters) composed of 100 x 100 m cells using the 'inverse distance weighted interpolation' tool (SAGA 2.3.2), which allows for non-sampled areas to be populated according to the value of and distance to sampled areas. A complete description of the input parameters is listed in Table H.2.

Table D.9. Input parameters used in the 'inverse distance weighted interpolation' window to convert the quadrat data into a gridded raster.

Parameters	Selected option
Input (data)	[Shapefile: Quadrat Data]
Attribute	wild food trees; oil palms; and raw materials
Distance Weighting	[0] inverse distance to a power
Inverse Distance Power	2
Search range	[0] search radius (local)
Search Radius	500 metres
Number of points	[0] maximum number of nearest points
Minimum	1
Maximum	10
Search Mode	[0] all directions
Cellsize	100
Target Grid System	[0] user defined
Fit	[1] cells
Target System	[Bossou forest grid]

Nest data, which was collected using forest-wide surveys, was interpolated into a gridded raster using the QGIS 'Heatmap (Kernel Density Estimation)' tool (Table H.3).

Table D.10. Input parameters used in the 'Heatmap (Kernel Density Estimation)' window to convert the quadrat data into a gridded raster.

Parameters	Selected option
Point layer	[Shapefile: Nests]
Radius	250
Rows	26
Columns	28
Pixel size (X & Y)	100
Kernel shape	Triangular
Decay ratio	0.5
Output value scaling	1

To avoid any spatial misalignments between grids, all generated rasters were then aligned using the 'Align Rasters…' tool, with the home-range raster selected as the reference layer. The cell size was set to 100 x 100. Compatibility with NetLogo was achieved by converting the aligned rasters into ACSII files using the QGIS tool 'Translate'. The nodata value was set to -1, and to ensure the cellsize was maintained during conversion, the command *-co FORCE_CELLSIZE = TRUE* was entered under additional command-line parameters.

D2.2. – Extracting water courses from DEMs

The water vector layers used in the ABM experiment were created in QGIS from the ASTER Global DEM (GDEM) 30-metre resolution data (NASA/METI/AIST/Japan Spacesystems and U.S./Japan ASTER Science Team, 2019). To reduce processing time, the original ASTER GDEM raster file that spatially overlapped the Bosssou forest was cropped to a rectangular area approximately nine times larger than the Bossou home range. The raster was then cleaned using the r.fill.dir tool from GRASS (Version 7.8.6) and converted into vectorized watercourses with the r.stream.extract tool (with v.out.ogr = line), also from GRASS. The low,

medium, and high options correspond to vectors generated with a minimum flow accumulation value of 1000, 250, and 50 cells, respectively.

D3 – Supplementary information for the experimental setup

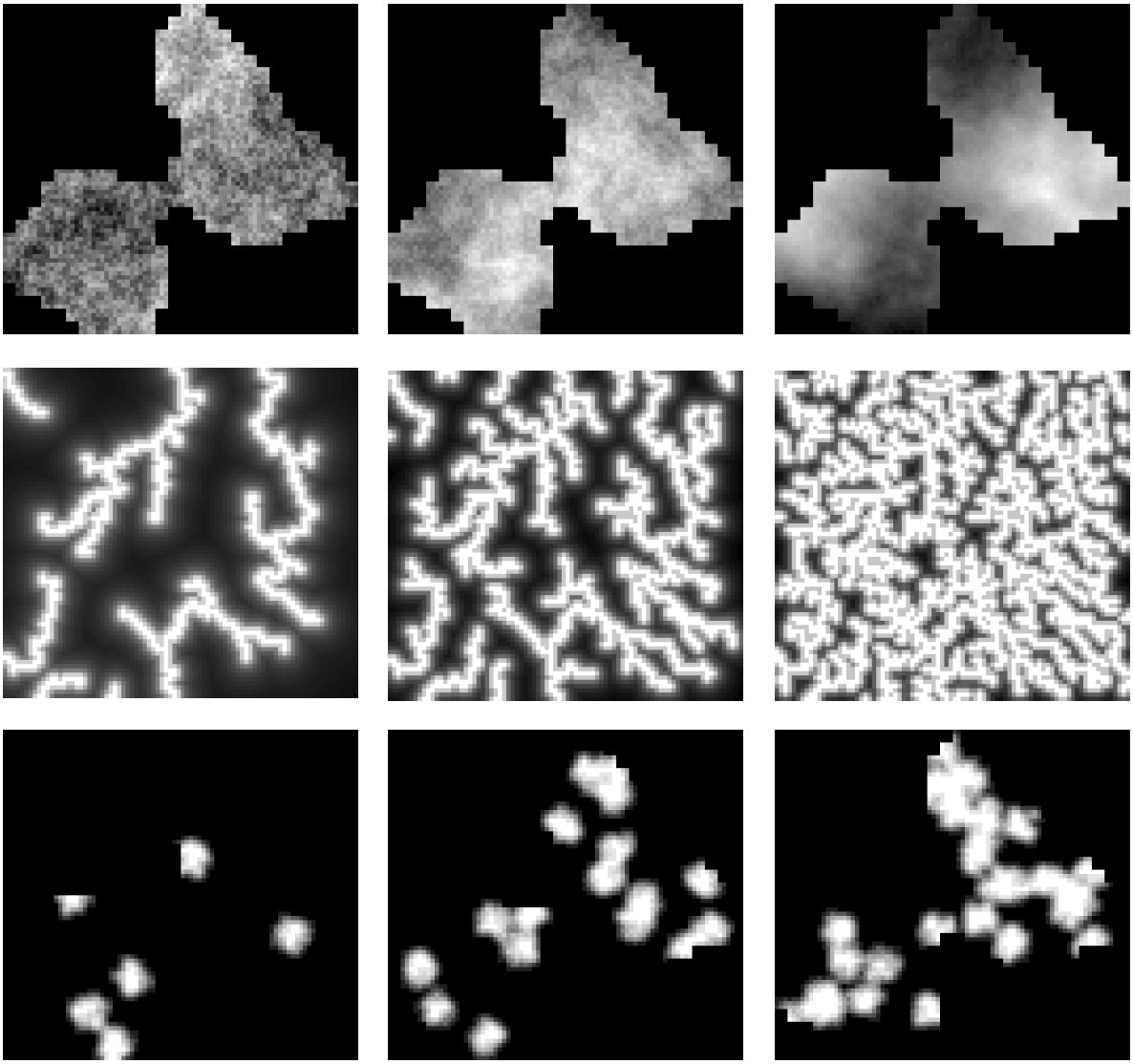


Figure D.3. Examples of artificially generated landscapes used in the experimental setup. Top row: *smoothness* of wild food distribution (Left = 0.01; Middle = 0.51; Right = 1.01); Midde row: *water-abundance* (Left = low; Middle = medium; Right = high); Bottom row: *nest-site-count* (Left = 6; Middle = 18; Right = 30).

D4 – Simulation outputs

D4.1. Parameter estimation: supplementary results

Table D.11. Reference table results for *exploration-probability*.

method	prediction	min	max	performance	rank
quantile random forest	0.242	0.016	0.667	0.960	1
random forest	0.191	-0.115	0.506	0.950	2
rejection abc	0.302	0.015	0.933	0.947	3
gam	-3.855	-11.811	4.224	0.944	4
linear regression	7.327	6.054	8.730	0.941	5
Semiauto abc	0.807	0.090	0.984	0.929	6
neural network abc	0.132	-0.056	0.369	0.909	7

Table D.12. Reference table results for *max-food-density*.

method	prediction	min	max	performance	rank
quantile random forest	12.900	2.600	24.900	0.986	1
rejection abc	20.550	9.145	25.628	0.970	2
semiauto abc	19.200	2.425	25.445	0.961	3
random forest	12.581	6.681	17.405	0.955	4
gam	56.062	-155.679	265.493	0.949	5
linear regression	322.995	297.893	347.288	0.946	6
neural network abc	11.217	2.931	17.532	0.923	7

Table D.13. Reference table results for *min-party-size*.

method	prediction	min	max	performance	rank
rejection abc	2.000	1.000	3.000	1.000	1
semiauto abc	2.000	1.000	3.000	1.000	1
quantile random forest	2.000	1.000	3.000	1.000	1
linear regression	0.860	-3.354	4.913	0.989	2
gam	-1.719	-16.787	13.530	0.980	3
random forest	1.753	0.493	2.948	0.976	4
neural network abc	1.529	-0.276	4.247	0.869	5

Table D.14. Reference table results for *nest-count-coefficient*.

method	prediction	min	max	performance	rank
random forest	0.523	-0.013	1.061	0.972	1
gam	-1.406	-4.463	1.727	0.945	2
linear regression	-0.376	-1.904	1.247	0.941	3
rejection abc	0.463	0.019	0.958	0.933	4
quantile random forest	0.498	0.025	0.968	0.923	5
semiauto abc	0.496	0.046	0.948	0.915	6
neural network abc	0.512	0.017	0.981	0.867	7

Table D.15. Reference table results for *nest-interaction-coefficient*.

method	prediction	min	max	performance	rank
random forest	0.471	-0.062	1.014	0.960	1
gam	0.543	0.068	1.011	0.947	2
linear regression	0.363	-1.103	1.833	0.943	3
rejection abc	0.498	0.067	0.963	0.941	4
quantile random forest	0.498	0.019	0.980	0.925	5
semiauto abc	0.586	0.073	0.958	0.915	6
neural network abc	0.268	-0.250	0.753	0.875	7

Table D.16. Reference table results for *nest-suitability-coefficient*.

method	prediction	min	max	performance	rank
random forest	0.432	-0.095	0.976	0.965	1
gam	0.495	0.019	0.975	0.942	2
linear regression	0.370	-0.990	2.102	0.942	3
rejection abc	0.516	0.008	0.986	0.930	4
quantile random forest	0.395	0.009	0.954	0.923	5
semiauto abc	0.464	0.009	0.929	0.918	6
neural network abc	0.204	-0.148	0.606	0.869	7

D4.2. Sensitivity analysis: supplementary results

Table D.17. Results from the multiple regression model investigating potential predictors of variation in daily caloric intake.

Characteristic	Beta[1]	SE[2]	95% CI[2]	p
min-party-size	-6.1	5.66	-17, 5.0	0.3
max-food-density	741***	5.65	730, 753	<0.001
exploration-probability	73***	5.66	62, 84	<0.001
nest-suitability-coefficient	1.7	5.67	-9.4, 13	0.8
nest-count-coefficient	6.4	5.66	-4.7, 18	0.3
nest-interaction-coefficient	5.6	5.66	-5.5, 17	0.3
min-party-size * max-food-density	3.1	5.65	-8.0, 14	0.6
min-party-size * exploration-probability	11	5.63	-0.52, 22	0.062
min-party-size * nest-suitability-coefficient	-6.6	5.66	-18, 4.5	0.2
min-party-size * nest-count-coefficient	6.5	5.70	-4.7, 18	0.3
min-party-size * nest-interaction-coefficient	4.8	5.72	-6.4, 16	0.4
max-food-density * exploration-probability	21***	5.66	9.8, 32	<0.001
max-food-density * nest-suitability-coefficient	-1.8	5.65	-13, 9.3	0.7
max-food-density * nest-count-coefficient	-3.3	5.74	-15, 7.9	0.6
max-food-density * nest-interaction-coefficient	9.1	5.60	-1.9, 20	0.10
exploration-probability * nest-suitability-coefficient	0.94	5.58	-10, 12	0.9
exploration-probability * nest-count-coefficient	-7.0	5.66	-18, 4.1	0.2
exploration-probability * nest-interaction-coefficient	-2.1	5.65	-13, 9.0	0.7
nest-suitability-coefficient * nest-count-coefficient	8.2	5.75	-3.1, 19	0.2
nest-suitability-coefficient * nest-interaction-coefficient	5.0	5.71	-6.2, 16	0.4
nest-count-coefficient * nest-interaction-coefficient	-4.0	5.70	-15, 7.2	0.5

[1]*p<0.05; **p<0.01; ***p<0.001
[2]SE = Standard Error, CI = Confidence Interval
R^2 = 0.922; AIC = 20,432; σ = 218

Table D.18. Results from the multiple regression model investigating potential predictors of caloric efficiency.

Characteristic	Beta[1]	SE[2]	95% CI[2]	p-value
max-food-density	8.0***	0.074	7.8, 8.1	<0.001
exploration-probability	-1.1***	0.074	-1.3, -1.0	<0.001
nest-suitability-coefficient	0.01	0.074	-0.14, 0.15	>0.9
nest-count-coefficient	0.02	0.074	-0.12, 0.17	0.7
nest-interaction-coefficient	-0.04	0.074	-0.18, 0.11	0.6
min-party-size * max-food-density	0.03	0.074	-0.12, 0.17	0.7
min-party-size * exploration-probability	0.02	0.073	-0.12, 0.17	0.7
min-party-size * nest-suitability-coefficient	-0.04	0.074	-0.18, 0.11	0.6
min-party-size * nest-count-coefficient	0.15*	0.074	0.00, 0.29	0.050
min-party-size * nest-interaction-coefficient	0.12	0.075	-0.03, 0.27	0.10
max-food-density * exploration-probability	-0.30***	0.074	-0.44, -0.15	<0.001
max-food-density * nest-suitability-coefficient	0.00	0.074	-0.15, 0.14	>0.9
max-food-density * nest-count-coefficient	0.13	0.075	-0.01, 0.28	0.076
max-food-density * nest-interaction-coefficient	0.01	0.073	-0.14, 0.15	>0.9
exploration-probability * nest-suitability-coefficient	-0.07	0.073	-0.22, 0.07	0.3
exploration-probability * nest-count-coefficient	0.11	0.074	-0.04, 0.25	0.14
exploration-probability * nest-interaction-coefficient	0.06	0.074	-0.09, 0.20	0.4
nest-suitability-coefficient * nest-count-coefficient	-0.02	0.075	-0.17, 0.12	0.7
nest-suitability-coefficient * nest-interaction-coefficient	0.03	0.074	-0.12, 0.17	0.7
nest-count-coefficient * nest-interaction-coefficient	0.11	0.074	-0.03, 0.26	0.13

[1]*p<0.05; **p<0.01; ***p<0.001
[2]SE = Standard Error, CI = Confidence Interval
R^2 = 0.891; AIC = 7,413; σ = 2.84

Table D.19. Results from the multiple regression model investigating potential predictors of variation in distance travelled per day.

Characteristic	Beta[1]	SE[2]	95% CI[2]	p
min-party-size	-0.01***	0.002	-0.02, -0.01	<0.001
max-food-density	-0.10***	0.002	-0.10, -0.09	<0.001
exploration-probability	0.08***	0.002	0.08, 0.09	<0.001
nest-suitability-coefficient	0.00	0.002	-0.01, 0.00	0.7
nest-count-coefficient	0.00	0.002	-0.01, 0.00	0.5
nest-interaction-coefficient	0.00	0.002	0.00, 0.01	0.5
min-party-size * max-food-density	0.01***	0.002	0.00, 0.01	<0.001
min-party-size * exploration-probability	0.00	0.002	0.00, 0.01	0.076
min-party-size * nest-suitability-coefficient	0.00	0.002	0.00, 0.00	>0.9
min-party-size * nest-count-coefficient	0.00	0.002	-0.01, 0.00	0.083
min-party-size * nest-interaction-coefficient	0.00	0.002	-0.01, 0.00	0.2
max-food-density * exploration-probability	-0.01***	0.002	-0.02, -0.01	<0.001
max-food-density * nest-suitability-coefficient	0.00	0.002	0.00, 0.01	0.6
max-food-density * nest-count-coefficient	0.00	0.002	-0.01, 0.00	0.3
max-food-density * nest-interaction-coefficient	0.00	0.002	0.00, 0.00	>0.9
exploration-probability * nest-suitability-coefficient	0.01*	0.002	0.00, 0.01	0.035
exploration-probability * nest-count-coefficient	0.00	0.002	-0.01, 0.00	0.077
exploration-probability * nest-interaction-coefficient	0.00	0.002	-0.01, 0.00	0.8
nest-suitability-coefficient * nest-count-coefficient	0.00	0.003	0.00, 0.01	0.2
nest-suitability-coefficient * nest-interaction-coefficient	0.00	0.002	-0.01, 0.00	0.9
nest-count-coefficient * nest-interaction-coefficient	0.00	0.002	-0.01, 0.00	0.063

[1]*p<0.05; **p<0.01; ***p<0.001
[2]SE = Standard Error, CI = Confidence Interval
R^2 = 0.661; AIC = -2,789; σ = 0.095

Table D.20. Results from the multiple regression model investigating potential predictors of variation in rates of fusion.

Characteristic	Beta[1]	SE[2]	95% CI[2]	p
min-party-size	0.06***	0.002	0.05, 0.06	<0.001
max-food-density	0.21***	0.002	0.21, 0.22	<0.001
exploration-probability	-0.04***	0.002	-0.05, -0.04	<0.001
nest-suitability-coefficient	0.00	0.002	0.00, 0.01	0.4
nest-count-coefficient	0.00	0.002	0.00, 0.01	0.5
nest-interaction-coefficient	0.00	0.002	0.00, 0.01	0.060
min-party-size * max-food-density	-0.05***	0.002	-0.05, -0.04	<0.001
min-party-size * exploration-probability	-0.01***	0.002	-0.01, 0.00	<0.001
min-party-size * nest-suitability-coefficient	0.00	0.002	-0.01, 0.00	0.3
min-party-size * nest-count-coefficient	0.00	0.002	0.00, 0.00	>0.9
min-party-size * nest-interaction-coefficient	0.00	0.002	-0.01, 0.00	0.6
max-food-density * exploration-probability	0.02***	0.002	0.01, 0.02	<0.001
max-food-density * nest-suitability-coefficient	0.00	0.002	-0.01, 0.00	0.4
max-food-density * nest-count-coefficient	0.00	0.002	0.00, 0.01	0.4
max-food-density * nest-interaction-coefficient	0.00	0.002	0.00, 0.01	0.3
exploration-probability * nest-suitability-coefficient	0.00	0.002	0.00, 0.01	0.7
exploration-probability * nest-count-coefficient	0.00	0.002	-0.01, 0.00	0.6
exploration-probability * nest-interaction-coefficient	0.00	0.002	0.00, 0.01	0.7
nest-suitability-coefficient * nest-count-coefficient	0.00	0.002	0.00, 0.01	0.4
nest-suitability-coefficient * nest-interaction-coefficient	0.00	0.002	-0.01, 0.00	0.4
nest-count-coefficient * nest-interaction-coefficient	0.00	0.002	-0.01, 0.00	0.8

[1] *p<0.05; **p<0.01; ***p<0.001
[2] SE = Standard Error, CI = Confidence Interval
R^2 = 0.865; AIC = -2,936; σ = 0.090

D3.3. Experimental outputs: supplementary results

Table D.21. Results from the multiple regression analysis of the experimental data investigating potential predictors of daily caloric intake.

Characteristic	Beta[1]	SE[2]	95% CI[2]	p
water_abundance				
low	—	—	—	
medium	26*	10.6	5.6, 47	0.013
high	23*	10.6	2.3, 44	0.029
smoothness	26*	11.0	4.5, 48	0.018
nest_site_count	0.21	0.389	-0.55, 1.0	0.6
water_abundance * smoothness				
medium * smoothness	-6.5	10.7	-28, 14	0.5
high * smoothness	-10	10.7	-31, 11	0.3
water_abundance * nest_site_count				
medium * nest_site_count	-0.01	0.446	-0.88, 0.87	>0.9
high * nest_site_count	0.14	0.446	-0.73, 1.0	0.7
smoothness * nest_site_count	-0.02	0.446	-0.90, 0.85	>0.9

[1]*p<0.05; **p<0.01; ***p<0.001
[2]SE = Standard Error, CI = Confidence Interval
R^2 = 0.021; AIC = 32,130; σ = 92.7

Table D.22. Results from the multiple regression analysis of the experimental data investigating potential predictors of distance travelled per day.

Characteristic	Beta[1]	SE[2]	95% CI[2]	p
water_abundance				
low	—	—	—	
medium	-0.29***	0.017	-0.32, -0.26	<0.001
high	-0.43***	0.017	-0.46, -0.39	<0.001
smoothness	0.05**	0.018	0.01, 0.08	0.007
nest_site_count	0.00	0.001	0.00, 0.00	0.6
water_abundance * smoothness				
medium * smoothness	0.06**	0.017	0.02, 0.09	0.001
high * smoothness	0.04*	0.017	0.01, 0.08	0.013
water_abundance * nest_site_count				
medium * nest_site_count	0.00	0.001	0.00, 0.00	0.2
high * nest_site_count	0.00	0.001	0.00, 0.00	0.3
smoothness * nest_site_count	0.00	0.001	0.00, 0.00	0.7

[1]*p<0.05; **p<0.01; ***p<0.001
[2]SE = Standard Error, CI = Confidence Interval
R^2 = 0.579; AIC = -2,572; σ = 0.150

Table D.23. Results from the multiple regression analysis of the experimental data investigating potential predictors of rates of fusion.

Characteristic	Beta[1]	SE[2]	95% CI[2]	p
water_abundance				
low	—	—	—	
medium	0.01	0.017	-0.03, 0.04	0.6
high	-0.01	0.017	-0.05, 0.02	0.4
smoothness	0.06**	0.018	0.02, 0.09	0.001
nest_site_count	0.00	0.001	0.00, 0.00	0.9
water_abundance * smoothness				
medium * smoothness	0.01	0.018	-0.03, 0.04	0.6
high * smoothness	-0.01	0.018	-0.04, 0.03	0.7
water_abundance * nest_site_count				
medium * nest_site_count	0.00	0.001	0.00, 0.00	0.2
high * nest_site_count	0.00	0.001	0.00, 0.00	0.6
smoothness * nest_site_count	0.00	0.001	0.00, 0.00	>0.9

[1]*p<0.05; **p<0.01; ***p<0.001
[2]SE = Standard Error, CI = Confidence Interval
R^2 = 0.026; AIC = -2,493; σ = 0.152

Table D.24. Results from the multiple regression analysis of the experimental data investigating potential predictors of overall nut-cracking frequency.

Characteristic	Beta[1]	SE[2]	95% CI[2]	p
water_abundance				
low	—	—	—	
medium	10	73.8	-134, 155	0.9
high	71	73.8	-74, 216	0.3
smoothness	114	76.5	-36, 264	0.14
nest_site_count	3.7	2.70	-1.6, 9.0	0.2
water_abundance * smoothness				
medium * smoothness	84	74.2	-61, 230	0.3
high * smoothness	35	74.2	-110, 181	0.6
water_abundance * nest_site_count				
medium * nest_site_count	0.75	3.09	-5.3, 6.8	0.8
high * nest_site_count	0.01	3.09	-6.1, 6.1	>0.9
smoothness * nest_site_count	-2.4	3.09	-8.4, 3.7	0.4

[1]*p<0.05; **p<0.01; ***p<0.001
[2]SE = Standard Error, CI = Confidence Interval
R^2 = 0.011; AIC = 42,588; σ = 643

Table D.25. Results from the multiple regression analysis of the experimental data investigating potential predictors of spatial patterning of nut-cracking sites (Moran's I Index).

Characteristic	Beta[1]	SE[2]	95% CI[2]	p
water_abundance				
low	—	—	—	
medium	0.00	0.014	-0.03, 0.03	>0.9
high	0.01	0.014	-0.02, 0.04	0.5
smoothness	0.02	0.015	-0.01, 0.04	0.3
nest_site_count	0.00	0.001	0.00, 0.00	0.2
water_abundance * smoothness				
medium * smoothness	0.01	0.014	-0.02, 0.04	0.5
high * smoothness	-0.01	0.014	-0.04, 0.02	0.4
water_abundance * nest_site_count				
medium * nest_site_count	0.00	0.001	0.00, 0.00	0.6
high * nest_site_count	0.00	0.001	0.00, 0.00	0.8
smoothness * nest_site_count	0.00	0.001	0.00, 0.00	0.4

[1]*p<0.05; **p<0.01; ***p<0.001
[2]SE = Standard Error, CI = Confidence Interval
R^2 = 0.003; AIC = -3,632; σ = 0.123

Appendix E

Supplementary information for Chapter 6

e E.1. – List of animal species encountered indirectly during surveys in the Korohouan area of the Diécké Forest Reserv

ntific name	Local name (Manon)	English name	Conservation Status[2]	Year recorded
copithecidae[1]	?	Unknown monkey	EN/VU*	2006, 2018
halophus dorsalis	Blè	Bay duiker	NT*	2018
halophus sylvicultor	Sòu	Yellow-backed duiker	NT*	2018
pestes sanguineus	Kèle	Slender mongoose	LC	2018
ochoerus nertzhageni	?	Forest hog	LC*	2018
thera pardus	Goh	Leopard	VU*	2009
taginus tricuspis	Zöoh	White-bellied pangolin	EN*	2018
amochoerus porcus	Loubho	Red river hog	LC*	2018
cerus caffer nanus	Douö	Forest buffalo	U*	2006, 2018
anus sp.	Zoula	Monitor lizard	LC*	2018

ost likely to be one of the following: *Cercopithecus diana* (EN), *Piliocolobus badius* (EN), *Colobus polykomos* (EN), *cocebus atys* (VU)

= Endangered; NT = Near threatened; LC = Least concern; U = Unknown; * = decreasing. Source: IUCN Red List; m et al. 2017 (for *S. c. nanus*).

Le E.2. List of plant species recorded during surveys in the Korohouan area of the Diécké Forest Reserve.

Scientific name	Local name (Manon)	English name	Conservation Status[2]	Year recorded
Acridocarpus spectabilis	?		LC	2006
Aframomum longiscapum	Yièlasin		LC	2008, 2009, 2018
Carapa procera	Gbon	Kobi	LC	2018
Chidlowia sanguinea	Peingzoti		LC	2018
Chrysophyllum africanum[1]	Bomo	African star apple	LC	2018
Cola cordifolia	Boba		LC	2006
Coula edulis	See	African walnut	LC	2006, 2008, 2018
Drypetes aframensis	Wénitii		LC	2018
Funtumia elastica	Sékélé (B)	Silkrubber	LC	2018
Landolphia owarensis	Sénédé	White rubber vine		2006, 2009
Lophira alata[2]		Azobe	VU	2018
Maesobotrya barteri	Kin		LC	2018
Manilkara obovata	Ze-i		LC	2018
Marantochloa leucantha	Bera			2018
Panda oleosa	Siakpala	Panda	LC	2006, 2008, 2018
Parinari excelsa	Koin		LC	2006
Pentadesma butyracea	Long	Buttertree	LC*	2009
Raphia hookeri	Duo	Raphia palm	LC	2006, 2009, 2018

[1] Also known as: *Gambeya africana*
[2] Extracted timber found outside the protected area
[3] LC = Least concern; * = decreasing. Source: IUCN Red List

Le E.2 (cont.) List of plant species recorded during surveys in the Korohouan area of the Diécké Forest Reserve.

Scientific name	Local name (Manon)	English name	Conservation Status[3]	Year recorded
Saccharum officinarum	Kwiyoo	Sugarcane		2018
Salacia owabiensis	Sokologbé			2009
Samanea dinklagei[4]	Sein-bera			2018
Strychnos spinosa	Kouinkana	Monkey orange		2006
Treculia africana	Yiiri	African breadfruit	LC*	2009
Trilepisium madagascariense[5]	Pâa			2018
Uapaca guineensis	Sona	Sugar plum	LC	2018

[2] LC = Least concern; * = decreasing. Source: IUCN Red List
[4] Also known as: *Albizia dinklagei*
[5] Also known as: *Bosqueia angolensis*

Appendix F

Supplementary information for Chapter 7

F1 – Koobi Fora Field Reports

Project Title: "Scatters-between-patches" revisited: A primate archaeology approach to the ecology of site selection, re-use and raw material transportation

SUMMARY OF RESEARCH PROJECT

The project aims to model and reconstruct patterns of hominin landscape-use by combining both early hominin archaeology with comparative data from chimpanzee archaeology, and investigating the ecological variables that drive the selection and re-use of particular localities for stone tool use and tool making activities in the hominin record. The current report refers to the field season of the "Hominin Phase". Data collection took place in the Koobi Fora Region (Kenya) and aimed to investigate diachronic and synchronic differences in the spatial distribution and composition of surficial archaeological material and

associated fossil assemblages during the Plio-Pleistocene, specifically between 4 distinct chrono-stratigraphic horizons - Tulu Bor (3.43 – 2.68 Ma), Burgi (2.68 – 1.88 Ma), KBS (1.88 – 1.6 Ma), and Okote (1.6 – 1.39 Ma) Members.

F1.1 – 2017 Field Season

Research Period: 10/06/2017 – 5/08/2017

Collaborators: Dr. David Braun (George Washington University); Dr. Emmanuel Ndiema (National Museums of Kenya); Angelina Curley (Columbia University)

REPORT

This season, data was collected from the outcrop surfaces of Area 131 (Okote Member) and Area 40 (Tulu Bor Member). This was achieved by running 1 km transects from a known archaeological site, sampling 5 x 5 m quadrats at every 50-100 metres, approximately. At area 131, the transect ran NE from the archaeological site FxJj20 M to FxJj43, sampling a total of 12 quadrats. At area 40, the transect ran W-E intersecting the archaeological site FwJj52, sampling a total of 4 quadrats.

From Area 131, a total of 14 lithics, 4 fossil bones, and 1 piece of fossil wood were collected. From Area 40, a total of 125 lithics and 4 fossil wood flakes were collected. Coordinates were recorded using a laser distance measurer with a retrofitted compass and clinometer – Disto X2 – for relative coordinates from a central Datum, paired with an RTK system, providing sub-cm coordinates for the Datums. This methodology was different than originally

proposed, and constitutes a more portable alternative to the Total Station, particularly in harsh and less accessible environments.

Although further data collection is required in a second season, preliminary results suggest that there are differences in relative assemblage compositions between the two stratigraphic horizons, both in terms of raw material composition and size classes. Differences were also found in the flake/core ratio (a measure commonly used in the assessment of transport intensity) of quadrat assemblages relative to distance to the know archaeological sites FxJj20, FxJj43, and FwJj52. In the Okote survey, flake/core ratio decreased with distance to FxJj20 and FxJj43, whereas in the Tulu Bor indicates the inverse trend, albeit to a lesser degree. Although there are fewer quadrats recorded for the Tulu Bor, this preliminary data reveals tentative evidence for differences in landscape use and mobility patterns between hominins living in the two geological periods investigated so far. Data collected in a second season, combined with faunal and palaeoecological data retrieved from the Turkana Database and current literature, will help determine the nature of these differences and the ecological variables that could be driving them.

Data was collected in tandem with the Koobi Fora Field School (George Washington University) and approved by the National Museums of Kenya. Further research in the "Hominin Phase" is scheduled for June 2018, expanding to new collection areas within Upper Burgi and KBS deposits, with a possibility of exploring further areas within the Okote and Tulu Bor Members.

Research for the "Chimpanzee Phase" of this research project is scheduled for December 2017 – May 2018, and plans are underway. This phase of the project will take place at the

chimpanzee field site of Bossou (Guinea), where I will be collecting data on chimpanzee nut-cracking assemblages and conducting geological and ecological surveys at a lasdscape-wide scale. This data will serve to model scenarios of hominin landscape-use, which will be tested against the patterns revealed in hominin data collected in the Koobi Fora region.

Preliminary results will be presented at the IPS Congress in Nairobi in 2018.

F1.2 – 2018 Field Season

Research period: 23/06/2017 – 08/07/2017

Collaborators: David R. Brown; Christina Costa (Student research assistant)

Research areas: Area 105 (near FxJj1 and FxJj2); Area 40 (near FwJj52)

REPORT

The 2018 data collection made up the second phase of data collection for my PhD project investigating the ecological variables that drive the selection and re-use of particular localities for stone tool use and tool making activities in the hominin record at a landscape-wide scale, with a particular focus on the 'scatters-between-patches' as envisioned by Isaac (1981). It is a cross-comparative study, where I am investigating the archaeology of chimpanzee technology (in Guinea) as a vehicle for modelling early hominin patterns of landscape use and subsistence strategies associated to the archaeological assemblages of the Koobi Fora region.

In East Turkana, the research goals were to collect data on the spatial distribution of surficial archaeological materials and associated finds (fossils and wood) in different stratigraphic contexts to investigate changes in archaeological assemblages through time.

This season, data was collected from the outcrop surfaces of Area 105 (Okote Mbr) and Area 40 (Tulu Bor). This was achieved by running 1 km transects, following the outcrops, from a known archaeological site, sampling 5 x 5 m quadrats at every 50-100 metres, approximately. At area 105, the transect ran NW-SE from FxJj1 towards FxJj3, sampling a total of 10 quadrats. At area 40, the transect ran W-E intersecting the site FwJj52, sampling a total of 6 quadrats.

From Area 105, a total of 22 lithics, six bones, two teeth, and one piece of fossil wood were collected. Three lithics (201.2015; 201.2016; 201.2017) were recovered from the eroding surfaces of the FxJj1 excavation site. A further two lithics (201.2004; 201.2005) and one fossil bone fragment (201.2006) were collected from the eroding surfaces of the FxJj3 excavation.

From Area 40, a total of 191 lithics, one tooth and four pieces of fossil wood were collected. Coordinates were recorded using an EOS Arrow Gold GNSS Receiver (providing ~5cm accuracy). Coordinates and details for these artefacts are provided in the associated NMK collection sheet.

F2 – "Stones on the move" project report

National Geographic Grant #GEFNE102-14

Stones on the move: the real life of a chimpanzee tool

We drilled cavities in 12 stones of a variety of different local raw materials, seven of which had already been used by chimpanzees for nut-cracking in previous experiments. The GPS devices were placed in the cavities and fixed with epoxy resin. The devices were set to record location at set times during the day (6:00; 10:00; 14:00; 18:00). We were unable to increase the frequency of recordings or set recordings based on movement-detection as this would have reduced battery life, and, therefore, compromised the duration of the project.

The project involved two stages: 1) pilot study in an experimental setting (1month); and 2) deployment to two true nut-cracking locations (6 months). The goal of the first phase was to test whether the satellite signal was received by the micro-GPS devices in the forest setting, and whether the chimpanzees would pick up and use the modified stones for nut-cracking. This took place at the outdoor experimental laboratory where the chimpanzees have been artificially provided with palm nuts and palm fruit for over 30 years. This laboratory is an open space in the forest which the chimpanzees visit at their own will and can be observed without disturbance. We removed all existing stones from the location and replaced them with the 12 GPS-stones. These stones were placed together in rows, while we distributed small piles of nuts in different locations of the clearing – this would ensure that the stones would need to be moved for nut cracking to take place. We also set up three camera traps that would enable us to monitor tool transport when direct recording/observation was not possible. The modified stones were left at the experimental location for the period of approximately one month (11NOV18 – 14DEC18), during which

we witnessed (directly and indirectly) several episodes of individuals transporting the modified stones and using them as nut-cracking tools. One GPS device was smashed during nut-cracking and was removed from the experiment.

The success of phase one, enabled us to progress to stage two on 14DEC18. The 11 GPS-stones were deployed to two real nut-cracking locations where nut-cracking has been frequently observed and where nuts would be available for the remainder of the study. One of the sites was fitted with a camera trap to monitor activity. This stage is ongoing and is due for completion on 11JUN18, when we will be able to collect the final data for this six-month period.

F3 – Lithic analysis results

With assistance from the University of Oxford, Earth Sciences Department, a total of 20 lithic samples were processed and analysed using the X-Ray Diffraction (XRD) Method.

The results identified four main types of raw materials: Aluminium-rich (n = 3; Figure F.1); Amphibole-rich (n = 11; Figure F.2); Kaolinite-Iron-Oxide-rich (n = 4; Figure F.3); and Quartz-rich (n = 2; Figure F.4). Cross-comparison with field records revealed that these correspond to the Laterite, Granite, Conglomerate, and Quartzite categories recorded in the field. The comparisons also revealed that visual identification in the field was not always accurate. However, examination of the field notes indicates that the errors were largely because: a) the source material was heavily weathered (n = 2); or b) the identification was made during the first week of fieldwork when I was still becoming familiar with the different types of materials (n = 2). In all cases, the material was incorrectly recorded as Laterite. One other sample revealed an unexpected result. This sample was recorded as granite, but analysis indicates it is Quartz-rich. However, visual comparison of the two Quart-rich samples suggests that they are considerably different. Further analysis is needed to resolve this discrepancy.

Following XRD analysis, the intention was to select another 10-20 samples for thin-sectioning and optical mineralogy. This would include a selection of new samples as well as a sub-sample of material analysed using XRD. However, due to the imposition of COVID-19 restrictions and closure of the Earth Sciences Labs in March 2020, this planned work was halted. Attempts were made to resume work in November 2020, but new restrictions in early 2021 led to the decision in consultation with my supervisor to reprioritize research efforts

to other components of the PhD project. Further discussion in May 2021 led to the reformulation of some components of the PhD Thesis in response to the impact of COVID-19 and the decision to conclude this part of the project without any further analysis. The present results will, however, be made available as an Appendix of the Thesis with the possibility to conduct further research at a future date.

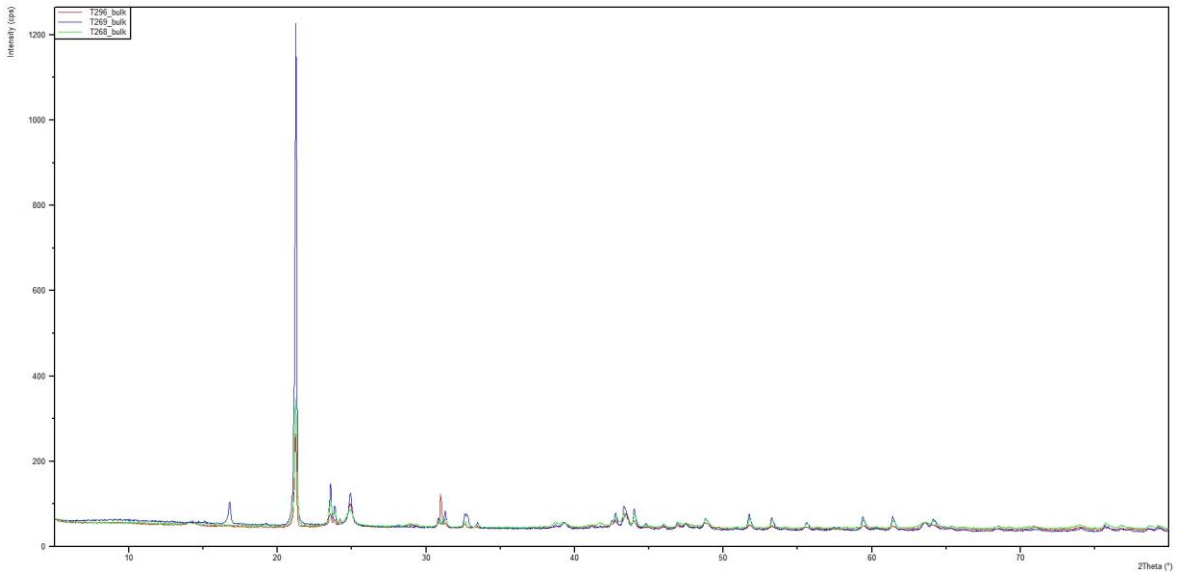


Figure F.1. XRD results of the Aluminium-rich samples.

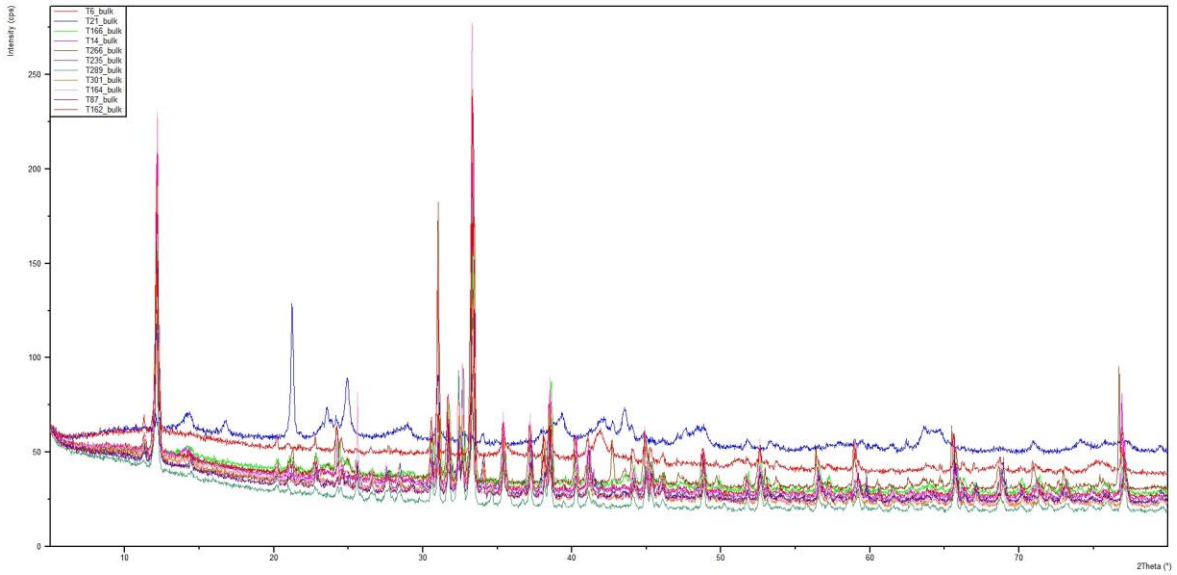


Figure F.2. XRD results of the Amphibole-rich samples.

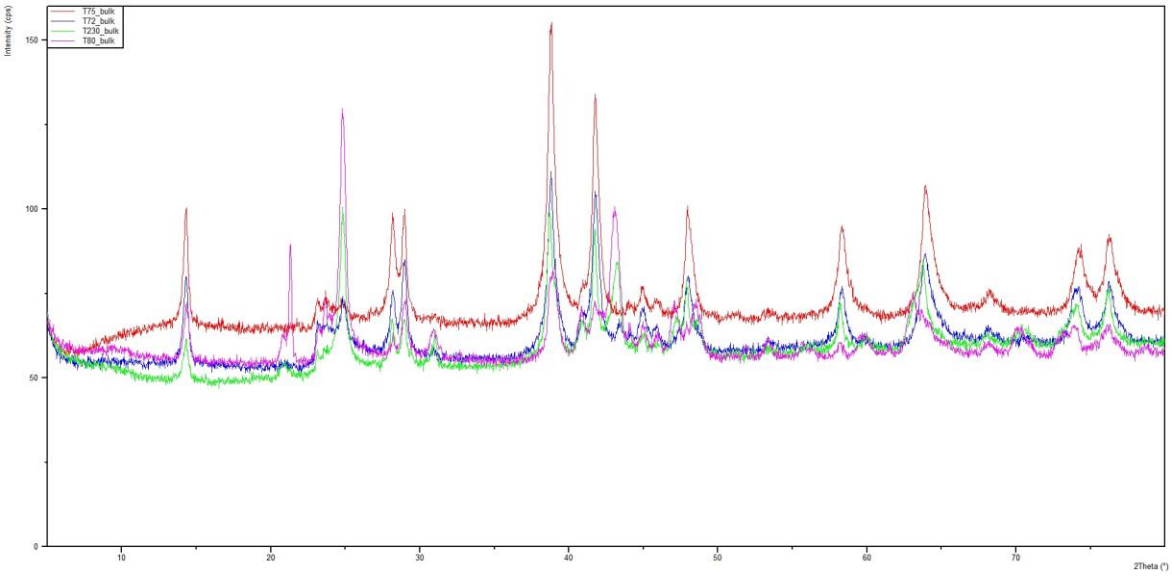


Figure F.1. XRD results of the Kaolinite-Iron-Oxide-rich samples.

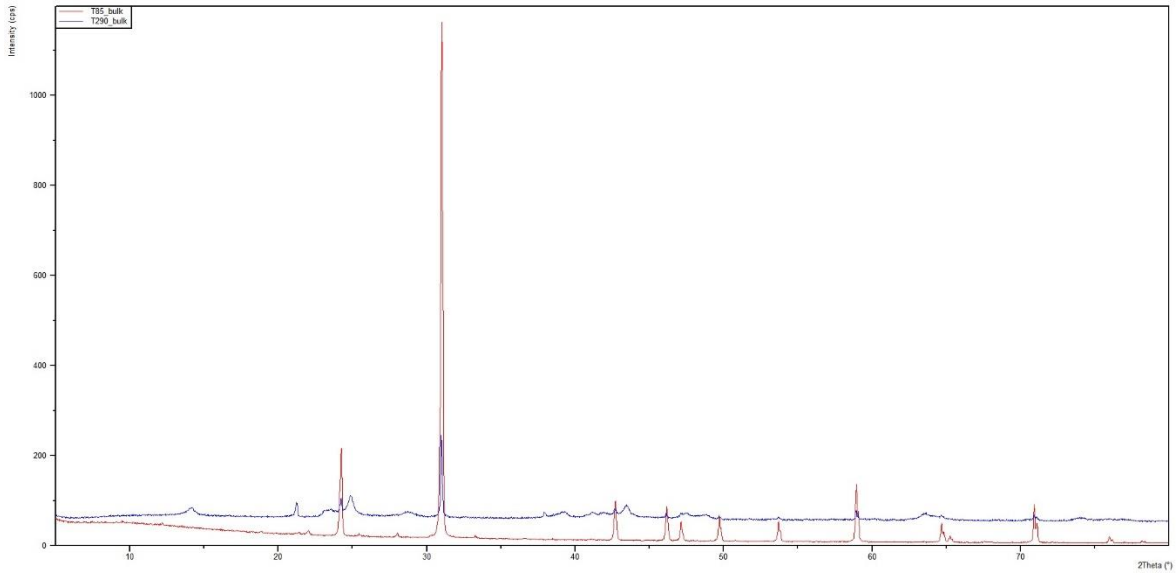


Figure F.2. XRD results of the Quartz-rich samples.

Appendix G

Publications

Received: 18 August 2016 | Revised: 31 March 2017 | Accepted: 31 May 2017

DOI: 10.1002/ajpa.23269

RESEARCH ARTICLE

WILEY American Journal of PHYSICAL ANTHROPOLOGY

Raw material procurement for termite fishing tools by wild chimpanzees in the Issa valley, Western Tanzania

Katarina Almeida-Warren[1,2] | Volker Sommer[1] | Alex K. Piel[3,4] | Alejandra Pascual-Garrido[5]

[1]Department of Anthropology, University College London, London, WC1 E6BT, United Kingdom

[2]Institute of Cognitive and Evolutionary Anthropology, University of Oxford, Oxford, OX2 6PN, United Kingdom

[3]School of Natural Sciences and Psychology, Liverpool John Moores University, Liverpool, L3 3AF, United Kingdom

[4]Ugalla Primate Project, PO Box 108, Uvinza, Tanzania

[5]RLAHA, School of Archaeology, Leverhulme Trust Early Career Fellow, University of Oxford, Oxford, OX1 3QY, United Kingdom

Correspondence
Katarina Almeida-Warren, Institute of Cognitive and Evolutionary Anthropology, 64, Banbury Rd., Oxford OX2 6PN, United Kingdom.
Email: katarina.almeida-warren@anthro.ox.ac.uk

Funding information
UCL; The Leverhulme Trust; The Boise Trust Fund, University of Oxford; UCSD.

Abstract

Objectives: Chimpanzee termite fishing has been studied for decades, yet the selective processes preceding the manufacture of fishing tools remain largely unexplored. We investigate raw material selection and potential evidence of forward planning in the chimpanzees of Issa valley, western Tanzania.

Materials and Methods: Using traditional archaeological methods, we surveyed the location of plants from where chimpanzees sourced raw material to manufacture termite fishing tools, relative to targeted mounds. We measured raw material abundance to test for availability and selection. Statistics included Chi-Squared, two-tailed Wilcoxon, and Kruskall–Wallace tests.

Results: Issa chimpanzees manufactured extraction tools only from bark, despite availability of other suitable materials (e.g., twigs), and selected particular plant species as raw material sources, which they often also exploit for food. Most plants were sourced 1–16 m away from the mound, with a maximum of 33 m. The line of sight from the targeted mound was obscured for a quarter of these plants.

Discussion: The exclusive use of bark tools despite availability of other suitable materials indicates a possible cultural preference. The fact that Issa chimpanzees select specific plant species and travel some distance to source them suggests some degree of selectivity and, potentially, forward planning. Our results have implications for the reconstruction of early hominin behaviors, particularly with regard to the use of perishable tools, which remain archaeologically invisible.

KEYWORDS
plant tools, primate archaeology, raw material selection, termites

INTRODUCTION

While there has been extensive research on hominin lithic technology, which has recently been dated to at least 3.3 mya (Harmand et al., 2015), few studies address plant-based implements, largely because direct evidence is lacking in the archaeological record (Carvalho, Biro, McGrew, & Matsuzawa, 2009). Still, there can be little doubt that technological industries of early hominins included plant tools (Hardy, 2016; Panger, Brooks, Richmond, & Wood, 2002; Schick and Toth, 2000). This gap in our knowledge reaffirms the value of studying chimpanzees (*Pan troglodytes*) as referential models for the emergence and transmission of human technology (Carvalho et al., 2009; Sanz, Deblauwe, Tagg, & Morgan, 2014; Toth and Schick, 2009). *Pan* and *Homo* shared a last common ancestor around 7-8 mya (Langergraber et al., 2012), and extant chimpanzees are known for their versatile use not only of lithic, but also plant-based tools for foraging and other activities (e.g. social interactions, personal hygene) (McGrew, 1992, 2004; Whiten et al., 1999). Furthermore, one of the earliest known hominins, *Ardipithecus ramidus*, lived in environments comparable to those inhabited by some extant chimpanzee populations (cf., Moore, 1992, 1996; WoldeGabriel et al., 1994).

Thus, early hominins are expected to have consumed similar diets of fruits, nuts and invertebrates, and likely exploited them with similar technologies (Copeland, 2007; McGrew, 2014; Panger et al., 2002).

 © 2017 Wiley Periodicals, Inc.

The earliest tentative evidence for early humans harvesting social insects is a bone implement dating between 1.8-1.0 mya, thought to have been used to dig up termite mounds (Backwell and D'Errico, 2001). However, wooden artifacts do not occur in the record until 0.8–0.4 mya (Goren-Inbar, Werker, & Feibel, 2002; Wilkins, Schoville, Brown, & Chazan, 2012).

Studying plant-based tool use by non-human primates can therefore serve as a proxy to reconstruct such archaeologically invisible aspects of hominin behavior (McGrew, Tutin, & Baldwin, 1979; McGrew, 2004). However, explicit etho-archaeological research on perishable materials used as tools or for shelter is still rare (Pascual-Garrido, Buba, Nodza, & Sommer 2012; Stewart, Piel, & McGrew, 2011).

Plant-based implements used by wild chimpanzees to "fish" for termites were first described half a century ago (Goodall, 1964). Termite fishing is now recognized as one of the most widespread forms of chimpanzee technology (Sanz and Morgan, 2011; Whiten, Schick, & Toth, 2009; Whiten et al., 2001). Termites also feature in the contemporary human diet, suggesting that early hominins also ate them (Lesnik, 2014; O'Malley and Power, 2014; Panger et al., 2002). Techniques to extract termites vary regionally. For example, chimpanzees at Gombe (Tanzania) insert a plant probe into exit-holes on the surface of a termite mound to obtain the insects inside (Goodall, 1964). This simple technology is also recorded for chimpanzees in the Mahale Mountains (Tanzania), Mt. Assirik (Senegal), Okorobiko (Equatorial Guinea) and Belinga (Gabon), amongst others (McGrew and Collins, 1985; McGrew and Rogers, 1983; McGrew et al., 1979; Nishida and Hiraiwa, 1982). Simple plant probes are also used in the Issa valley (Stewart and Piel, 2014). In contrast, central African chimpanzees use different implements consecutively for the task (Bermejo and Illera, 1999; Deblauwe, Guislain, Dupain, & van Elsacker, 2006; Sanz and Morgan, 2009, 2011). Raw materials for tools differ as well. For example, at Gombe, virtually all tools are made from bark and grass. These plant parts are not used at Mt. Assirik. The absence of grass implements may reflect the rareness of suitable sources at the start of the wet season when termite fishing is most frequent, given that much grass is burned during the long dry season (McGrew et al., 1979). However, the lack of bark tools is difficult to explain as the raw materials are available. This suggests that differences between populations may extend beyond ecological factors.

To better understand the selective processes preceding the manufacture of fishing tools, including whether certain raw materials are preferred, we studied chimpanzees at one of the driest habitats - Issa valley, western Tanzania - where these apes habitually exploit termite mounds (Stewart and Piel, 2014). Using archaeological methods (Haslam et al., 2009), we investigated the following:

a Raw materials: From which types are termite fishing tools manufactured? How does this compare to general abundance?

b Taxonomy: Which species constitute sources of raw material and with which frequency? How does this compare to species density?

c Dimensions: What is the detachment height and thickness of sourced parts? How do these factors affect selection between and within the same species?

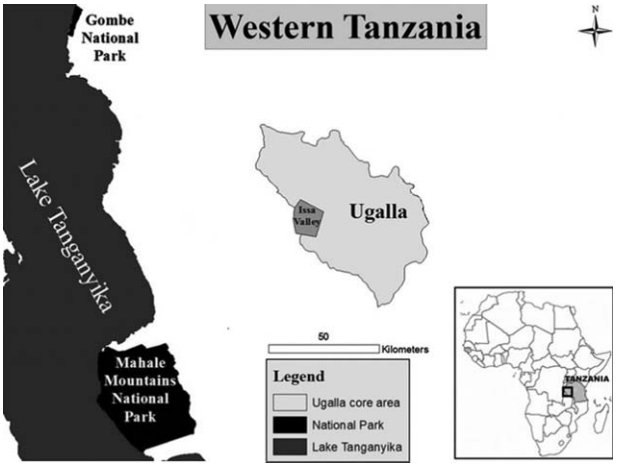


FIGURE 1 Chimpanzee study site of Issa in West Tanzania relative to long-term study communities at Gombe and Mahale (Map: Stewart and Piel, 2014)

d Distance to targeted mound: From how far away are tools sourced? How are plant sources spatially distributed around the mound?

e Dietary connection: Are species used for tools also sources of food?

f Medicinal properties: Can tool source species be linked to health-giving qualities?

The complete *chaîne opératoire* (operational sequence) of tool use includes technical processes and social acts of the step-by-step production, use, and eventual disposal of artifacts (Carvalho, Cunha, Sousa, & Matsuzawa, 2008). Typically employed for lithic tools, the concept can be applied to the steps of perishable technology, such as termite fishing, which include selection of plant raw material, its modification (e.g., removing leaves; cropping the tip) to produce a functional tool, the use of the implement to harvest termite prey, and discarding it afterwards.

Our research aims to reconstruct the commonly neglected initial stages of the *chaîne opératoire* (raw material selectivity and transport) that are nevertheless critical to understand subsequent steps of actual use.

2 | MATERIALS AND METHODS

2.1 | Study subjects and sites

Research was conducted on a population of *P. t. schweinfurthii* that lives in the Issa valley, Ugalla (S 5.50, E 30.56; 900–1800 m altitude), western Tanzania (Figure 1; Hernandez-Aguilar, 2009; Piel et al., 2015; Stewart and Piel, 2014). Issa is one of the driest, most open and seasonal chimpanzee habitats, with broad valleys broken up by steep mountains and plateaus. The vegetation is mainly miombo woodland, dominated by *Brachystegia* and *Julbernardi*, intersected by patches of swamp, grassland, as well as evergreen gallery and thicket riverine forest. A wet season (Nov–Apr) is followed by a distinct dry spell (May–Oct).

Following short-term studies since 2001, the Ugalla Primate Project established a permanent research base in 2008. Based on genetic

analyses, the chimpanzee study community encompasses approximately 67 individuals, with a minimum home range of 85 km^2 (Rudicell et al., 2011). As of April 2016, the apes are now partially habituated, with 14 identifiable individuals. During the wettest months of the year (Nov-Feb), the Issa chimpanzees habitually harvest *Macrotermes* termites (Stewart and Piel, 2014). The chimpanzees also use perishable tools to obtain arboreal *Camponotus* ants (Wondra, van Casteren, Pascual-Garrido, Stewart, & Piel, 2016) and to dig for tubers (Hernandez-Aguilar, Moore, & Pickering, 2007).

2.2 | Data collection

APG and KAW conducted three seasons of fieldwork for a total of 16 weeks, aided by Tanzanian field assistants (APG: 09Jan15 - 09Feb15; KAW: 17May15 - 27May15; KAW: 02Nov15 - 15Dec15). During the first season, 20 termite mounds were selected for study, 15 of which had been targeted by chimpanzees (Figure 2a). Records included a unique identifier (ITMXXX), GPS location, nest dimensions (cross-section width and height) as well as habitat (open/closed forest, woodland, miombo woodland, savannah; cf., McBeath and McGrew, 1982; Pascual-Garrido et al., 2012). We established a Site Datum (cf., Carvalho et al., 2008) at a nearby tree to allow measurements within a standardized coordinate system, for example, for the distance of a tool source to study mounds. Eight targeted mounds and their surroundings were selected for detailed study.

On the basis of previous research of chimpanzee termite fishing (e.g., McBeath and McGrew, 1982; McGrew et al., 1979; Nishida and Uehara, 1980), we considered the following potential categories of tool raw material: bark (the outermost layers of tissue overlaying the wood of trees, shrubs and climbers or vines that can easily peel lengthways in strips); twigs (thin branches of woody plants); leaf stalks (mid ribs of large leaves of woody plants that can easily be removed from the blades); grass stems (the hollow vertical structural axes of grass plants that provide support for flowers at the top and leaves attached at the nodes).

The availability of raw material was ascertained for living plants growing within 5 m from a targeted mound's center (cf., Koops, McGrew, & Matsuzawa, 2013; McBeath and McGrew, 1982). Using

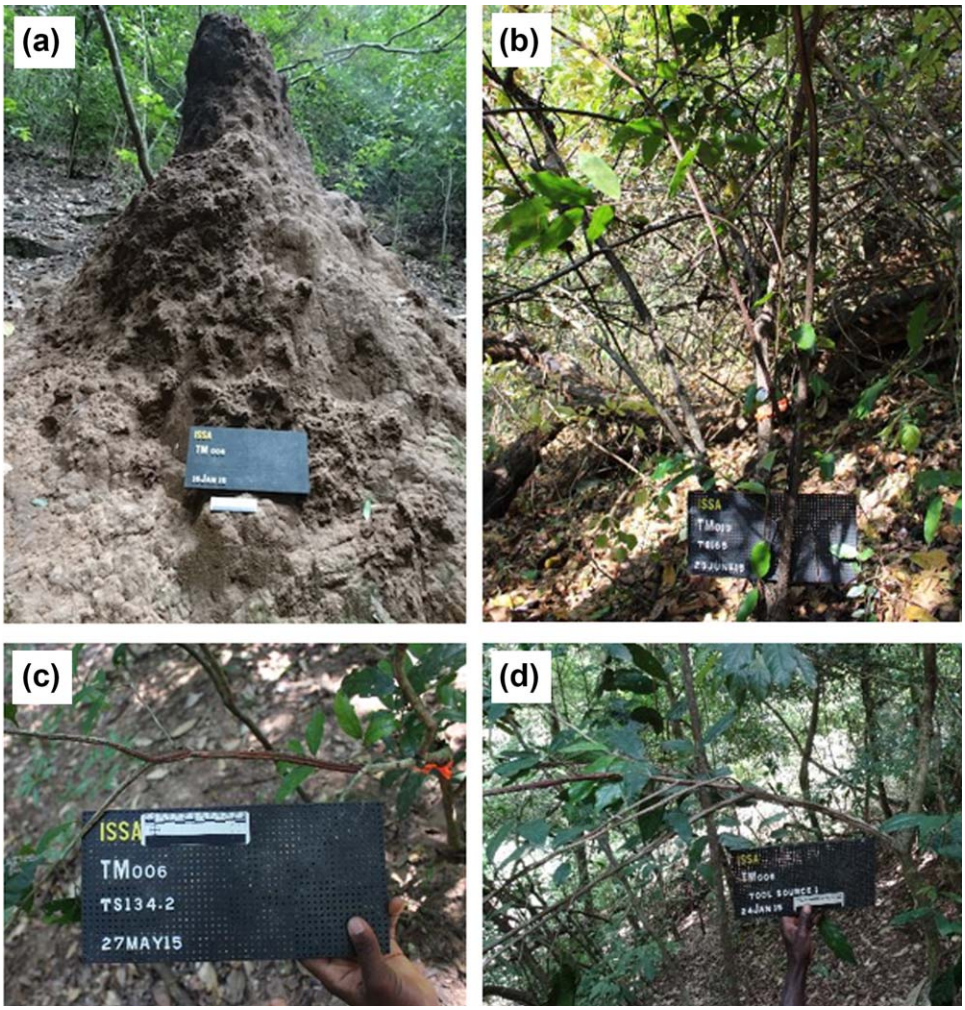


FIGURE 2 Termite mound targeted by chimpanzees and plants sourced to obtain raw material for termite-fishing tools. (a) Mound ITM004; (b) Climber (*Uvaria* sp. *A of FTEA*) at ITM013; (c) Climber (*Uvaria* sp. *A of FTEA*) at ITM006; (d) Tree (*Cleistanthus polystachyus*) at ITM006. (Photos: APG - a, d; KAW - b, c)

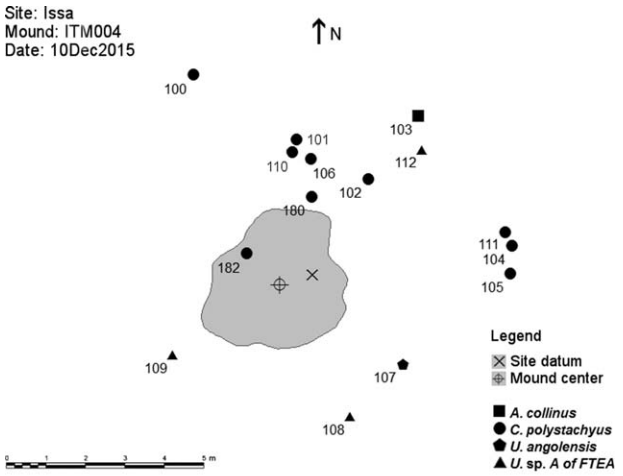


FIGURE 3 Map of individual sourced plants (indicated by numbers) used by chimpanzees to fish at a termite mound (ITM004)

cardinal orientations (N-S, E-W), the mound vicinity was divided into four quadrants numbered clockwise from north. The northwest quadrant, IV, was arbitrarily selected for scrutiny. If obstacles such as steep terrain prevented this, an adjacent quadrant was chosen. Recorded parameters included: number and species of plants suitable to provide raw material; growth type (tree, shrub, climber, grass); raw material type (twig, bark, leaf stalk, grass stem); and whether each plant was a known chimpanzee food source. Suitable raw materials were defined as long, thin and flexible pieces, capable of providing termite fishing probes, which a researcher could easily detach with hands or fingernails.

The surroundings of eight targeted mounds were surveyed for tool source plants (Figure 2b–d), using signs of broken or removed parts as indicators, by walking back and forth from the mound in a clockwise fashion (cf., Pascual-Garrido et al., 2012). Traits of source plants were recorded as follows: position relative to targeted mound (Figure 3); whether visible from mound or if vegetation or terrain contours obscured the line of sight; species; number of plants of same species within a 3-m radius; height; number of sourced and unsourced parts within the source plant; height at point of detachment; diameter of sourced parts at proximal, medial and distal points of detachment; medial diameter of unsourced parts. Used tools abandoned by chimpanzees were also recorded and classified according to raw material.

Herbarium samples of study species were collected and identified at the Botany Department, University of Dar es Salaam, Tanzania.

2.3 | Tool source identification

The question of how to distinguish an assemblage of tools from a naturally occurring aggregation of plant fragments has been previously addressed by McGrew et al. (1979). Similar to stone tools, plant-based tools also acquire recognizable signs of use-wear. In the case of termite fishing implements, these included evidence of modification (e.g., peeled bark, stripped leaves) or wear from insertion into the mound (e.g., fraying at the tips) and termite bite marks. Plant parts with these characteristics are often associated with other signs of previous termite fishing activity, such as chimpanzee footprints, hairs, feces as well as discarded termite heads and freshly stripped leaves resulting from tool manufacture (cf., Bermejo and Illera, 1999; Deblauwe et al., 2006; McGrew and Collins, 1985; McBeath and McGrew, 1982; McGrew and Rogers, 1983; Nishida and Uehara, 1980; Sanz, Call, & Morgan, 2009; Sanz and Morgan, 2011; Sanz, Morgan, & Gulick, 2004; Stewart and Piel, 2014).

Tool sources are more difficult to discern (McBeath and McGrew, 1982; McGrew et al., 1979; Pascual-Garrido et al., 2012) but can normally be distinguished from specimens that suffered breakage caused by other processes: (a) chimpanzees will often pluck multiple parts from a single source plant; (b) branch sections from where tool material has been removed are often also stripped of leaves and minor offshoots; (c) only a select number of species will show signs of breakage; (d) plants with breakage are concentrated around the mound periphery.

2.4 | Statistics

Given non-normal distribution of our data ($p < 0.05$), we employed non-parametric statistics. Chi-squared tests compared proportions between groups (raw material classes; species), while two-tailed Wilcoxon (aka Mann–Whitney U test) were employed to compare means. When comparing two independent proportions between multiple groups, we calculated individual p values of paired groups via a Post-hoc Chi-squared analysis with Bonferroni correction. Kruskal–Wallis tests were used as a non-parametric equivalent to ANOVA to compare multiple groups (e.g., mounds, species). Pairwise Wilcoxon tests with Bonferroni correction were employed to ascertain the individual p values of paired groups analyzed in the Kruskal–Wallis test. Linear regression analyses were used to arrive at linear correlation between numerical datasets. All analyses were performed in R (R Development Core Team, 2014). Level of significance was set at $p < 0.05$.

3 | RESULTS

We identified 113 individual source plants, some of them having been exploited from multiple parts. This resulted in a combined total of 349 sourced parts belonging to 13 species from six families from which Issa chimpanzees manufactured termite fishing tools. We also recovered 140 fishing implements (Table 1).

3.1 | Selection of raw materials

Approximately two thirds of plants within the surveyed 5 m radius quadrant in the vicinity of termite mounds could have provided one or multiple suitable raw materials (bark, twig, leaf stalk, grass stem) that are known constituents of termite fishing tools (cf., Table 1).

Overall, there were significant differences between the proportions of available raw material classes by individual plant unit (Chi-squared: $\chi^2 = 344.751$; $df = 3$; $p < 0.001$). The most abundant material sources were plants that afforded good twigs (94%), followed by bark (18%; i.e., bark that can easily be peeled off in long and flexible strips for termite fishing probes), whereas plants that could provide

TABLE 1 Main parameters of vegetation cover within a quarter section of a 5-m radius circle of study mounds targeted by chimpanzees for termite fishing (abundance of plants suitable to provide raw material for termite fishing probes; identified individual tool source plants and sourced parts within the source plant; recovered tools that were abandoned by chimpanzees at the targeted mound)

	Plants (*n*)							Near targeted termite mound		
Termite mound	Total within quadrant	Suitable to extract raw material[a]	Potential sources of bark	Potential sources of twig	Potential sources of leaf stalk	Potential sources of grass	Specimens belonging to known tool source species	Individual tool source plants (n)	Sourced plant parts (n)	Recovered tools (n)
ITM004	39	39	6	38	4	0	1	15	45	21
ITM006	42	42	3	41	16	0	2	26	80	46
ITM007	74	4	0	4	0	0	0	1	14	21
ITM008	74	28	15	28	0	0	0	7	14	9
ITM009	45	28	7	17	1	6	6	22	50	3
ITM013	25	24	4	20	0	0	4	25	97	19
ITM015	25	25	5	25	11	0	1	12	36	6
ITM016	74	74	8	74	0	0	17	5	13	15
Sum	398	264	48	247	32	6	31	113	349	140
Mean	49.8	33.0	6.0	30.9	4.0	0.8	3.88	14.1	43.6	17.5
% relative to total plants	100.0	66.3								
% relative to plants suitable as raw material sources			18.2	93.6	12.1	2.3	11.7			

[a]Note that the same plant may provide more than one type of raw material.

appropriate leaf stalks (12%) and grass stems (2%) were even rarer. However, only bark was actually sourced for tools (Table 2), both in terms of parts sourced (Chi-squared with null-probability = 1/4: $\chi^2 = 1043.004$; $df = 1$; $p < 0.001$), as well as recovered tools (Chi-squared with null-probability = 1/4: $\chi^2 = 416.010$; $df = 1$; $p < 0.001$; cf., also Stewart and Piel, 2014). Nevertheless, post-hoc experiments with twigs and grass demonstrated that these materials were also suitable as efficient termite fishing tools (Figure 4).

3.2 | Selection of plant species

While 66% of plants in the vicinity of targeted termite mounds were deemed suitable as tool sources, only 12% of these constituted species from which chimpanzees actually sourced material (Chi-squared with null-probability = 0.99: $\chi^2 = 2450.6$; $df = 1$; $p < 0.001$). The difference was equally significant when analyzing the proportions for each individual mound (Chi-squared for all individual tests with null-probability = 0.99; $p < 0.001$). Post-hoc Chi-squared tests aimed to determine which pairs of mounds were different in terms of species availability returned no significant results. This indicates that chimpanzees selected certain species from which to source tool materials.

TABLE 2 Main classes of raw material sourced by chimpanzees to manufacture termite fishing probes relative to the average abundance of potential raw material sources near studied termite mounds

	Raw material source				
	Bark	Twig	Leaf stalk	Grass	Total
Tools sourced (*n*)	140	0	0	0	140
Parts sourced (*n*)	349	0	0	0	349
Abundance of suitable raw material (mean of study mounds)	6.00	30.88	4.00	0.75	49.75

3.3 | Taxonomy of plant sources

Plant tool sources belonged to 13 species from six families (Table 3). More than four fifths (82%) of identified raw materials came from *A. collinus*, *Uvaria* sp. *A of FTEA*, and *C. polystachyus*. Compared to abundance, these plants were over-selected at a significant level (Chi-squared for all individual tests: $p < 0.002$; Figure 5).

However, mounds varied significantly with regard to the species sourced (Chi-squared: $\chi^2 = 260.350$; $df = 70$; $p < 0.001$). For example, *C. polystachyus* was only sourced at ITM004 and ITM006, *Grewia sp.* only at ITM006 and ITM016 and *D. burgessiae* only at ITM007 (cf., Table 3). Similarly, certain species were only over-selected at certain mounds. Thus, *A. collinus* was significantly over-selected at all mounds (Chi-squared for all individual tests: $p < 0.02$) except ITM004 (Chi-squared: $\chi^2 = 0.1599$; $df = 1$; $p = 0.689$) and ITM007, where no plants of this species were found within the surveyed area. *U.* sp. *A of FTEA* was only over-selected at ITM013 (Chi-squared: $\chi^2 = 6.182$; $df = 1$; $p = 0.013$) and ITM006 (Chi-squared: $\chi^2 = 4.069$; $df = 1$; $p = 0.043$). *C.*



FIGURE 4 Termites cling to a twig tool after an experimental fishing attempt by APG at mound ITM006. The tool was manufactured from the surrounding vegetation. (Photo: APG)

polystachyus was over-selected at both mounds where plants of this species were sourced, that is, ITM004 (Chi-squared: $\chi^2 = 14.265$; $df = 1$; $p < 0.001$) and ITM006 (Chi-squared: $\chi^2 = 9.865$; $df = 1$; $p = 0.002$). The same applies to *D. burgessiae*, which was only recorded at ITM007 (Chi-squared: $\chi^2 = 8.874$; $df = 1$; $p = 0.003$).

3.4 | Dimensions at point of detachment

Plant parts from which raw materials were sourced had a diameter at point of detachment of up to 27 mm, with 85% of values between 3 and 11 mm (Figure 6). A comparison with nonsourced plant parts indicated a significant difference between the two groups (two-tailed Wilcoxon: $w = 50310.5$; $p < 0.001$). However, in absolute terms, the difference was only 1.0 mm (Table 4).

Plant parts were sourced from a mean height of 1.2 m (Table 4), with half from below 1 m (49%), a quarter from above 1.5 m (25%) and a maximum height of 3.8 m. Cross-species comparison revealed a significant difference between species means (Kruskal–Wallis: $\chi^2 = 62.833$; $df = 9$; $p < 0.001$). Thus, *U. welwetschii* and *C. polystachyus* were sourced from significantly higher than *U.* sp. *A of FTEA*, *A. collinus* and *A. monteiroae*. These findings could be an artefact of different plant heights (Table 4). To test this, we plotted height at point of detachment against total height of plant (Figure 7), which indicated a significant positive trend, albeit with poor goodness of fit ($p < 0.001$; $R^2 = 0.044$).

3.5 | Distance of plant tool sources to targeted mound

To reveal potential spatial patterns of raw material procurement, we plotted the total number of sourced parts alongside the total number of sourced plants for every 1 m block (Figure 8). 83% of plants were sourced 1–16 m away from the mound, with a maximum distance of 33.4 m. Only one pair of mounds differed significantly with respect to these distances, with plants sourced from ~7 m further away at ITM006 than at ITM004 (Kruskal–Wallis: $\chi^2 = 19.680$; $df = 7$; $p = 0.006$; Figure 9).

We also investigated if sourcing distances differed between plant species, taking into account the number of times each species was individually sourced, and restricting the sample to species sourced more than once (Figure 10). Thus, *A. garckeana* was sourced from nearest the mounds (mean 3.2 m), while *A. senegalensis* was sourced from the greatest distance (mean 13.4 m). An overall cross-species comparison yielded statistically significant results (Kruskal–Wallis: $\chi^2 = 42.207$; $df = 14$; $p < 0.001$).

3.6 | Visibility of plant tool sources to targeted mound

If a source plant was not visible from the targeted mound (i.e., the line of sight was obstructed by dense vegetation or terrain contours), it seems likely that raw material was collected *en route*, rather than upon arrival at the mound. This applies to 21% of source plants (Table 5). These constituted about half (55%) of the 42 plants that were sourced from a distance of more than 10 m. Plants visible from the mound were more than twice as often sourced (3.5 times) than non-visible plants (1.6 times); and those that were within 10 m of the mound were also sourced much more often (3.7 times) than encountered further away (2.0 times).

3.7 | Food species as sources for tool material

Twelve out of 13 species sourced were also known chimpanzee food sources (Table 6). This is significantly different from a 0/1 ratio (Chi-squared with np = 0.01: $\chi^2 = 1004.5$; $df = 1$; $p < 0.001$).

3.8 | Medicinal properties of plant sources

Of 13 identified tool source species, 10 (75%) are known to provide ingredients for traditional medicine in Tanzania and elsewhere, in the treatment of human ailments (Table 7).

4 | DISCUSSION

Our research focuses on an under-researched component of the operational sequence of chimpanzee termite fishing: raw material selectivity and transport. Although not relying on direct behavioral observation, our results nevertheless reveal that rich information can be gleaned solely from indirect archaeological approaches.

TABLE 3 Percentage of plants sourced per species relative to the species' general abundance for each mound

			ITM004		ITM006		ITM007		ITM008		ITM009		ITM013		ITM015		ITM016	
Family	Species	Type[a]	TS (%)	AB (%)	TS (%)	AB (%)	TS (%)	AB (%)	TS (%)	AB (%)	TS (%)	AB (%)	TS (%)	AB (%)	TS (%)	AB (%)	TS (%)	AB (%)
Annonaceae	*Annona senegalensis*	T											4					
	Artabotrys collinus	C	7		27				57	2	73	4	36	4	67	6	40	1
	Artabotrys monteiroae	C			8						9		4		25	4		
	Uvaria angolensis	C	7		4				14	3	5	4	12					
	Uvaria sp. *A of FTEA*	C	20	3	23	1			14				40		8	7		
	Uvaria welwetschii	C											4					
	Monanthotaxis buchananii[a]	S																
Apocynaceae	*Saba comorensis*	C							14	3								
Euphorbiaceae	*Cleistanthus polystachyus*	T	67		35													
Malvaceae	*Azanza garckeana*	T															40	4
	Dombeya burgessiae	T					100											
Tiliaceae	*Grewia sp.*	C			4												20	1
Rubiaceae	*Rothmannia urcelliformis*[b]	T																
	Non-sourced			97		99		100		92		92		96		83		94
	Total plants (n)		15	39	26	42	1	74	7	74	22	45	25	25	12	25	5	74

[a]T = tree, C = climber, S = shrub.
[b]Excluded from quantitative analysis as identified at two mounds that were not part of raw material availability studies.
TS = total sourced plants; AB = abundance.

4.1 | Raw material classes

Consistent with initial findings (Stewart and Piel, 2014), bark was the only raw material sourced by Issa chimpanzees to manufacture their termite fishing tools (cf., Table 2). Our results reveal that exclusive use of bark is not simply a corollary of availability. On the contrary, twig-providing plants are far more abundant, yet this material does not appear in tool assemblages. One might query the relatively rough quantification of available twig versus bark as derived from counts of potential source plants, without quantifying the actual amounts of raw material on plants of different sizes and growth types. However, the simple fact remains that Issa chimpanzees *only* source bark, and thus, clearly neglect twigs.

Bark is used by chimpanzees in East and West Africa, but not Central Africa, to harvest termites (Stewart and Piel, 2014). Bark is also a popular termite-extraction tool elsewhere in western Tanzania, albeit

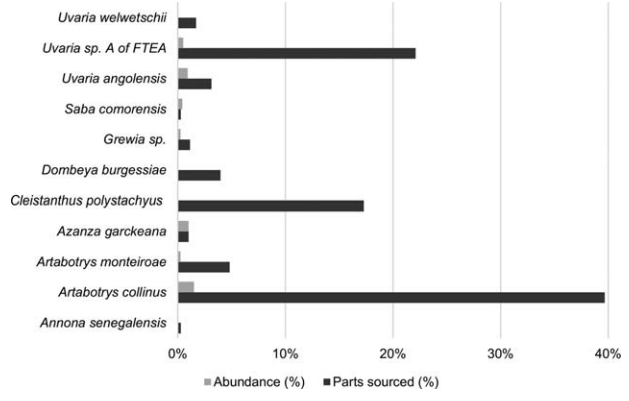


FIGURE 5 Number of plant parts sourced by species used as tool sources relative to their general abundance. *M. buchananii* and *R. urcelliformis* are not included as they were identified at mounds that were not part of the raw material availability studies

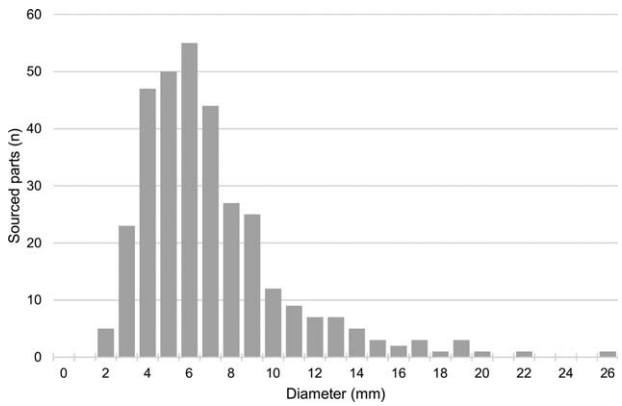


FIGURE 6 Frequency distribution of diameters of sourced plant parts at point of detachment over 1-mm classes (0 = 0.0–0.9 mm; 1 = 1.0–1.9 mm; 2 = 2.0 mm; etc.)

TABLE 4 Plant species exploited by chimpanzees as sources for termite fishing tools and their main physical properties (diameter of sourced and unsourced parts of tool source species at point of detachment; height of sourced branch; total height of sourced plant)

		Diameter of sourced plant parts at point of detachment				Diameter of unsourced plant parts				Height of sourced plant parts at point of detachment[a]				Height of sourced plant			
Species	Type[b]	Mean (mm)	Min (mm)	Max (mm)	(n)	Mean (mm)	Min (mm)	Max (mm)	(n)	Mean (mm)	Min (m)	Max (m)	(n)	Mean (mm)	Min (m)	Max (m)	(n)
Annona senegalensis	T	5.1			1	8.5	3.3	2.7	6	1.1			1	2.2			1
Artabotrys collinus	C	7.0	2.6	19.9	137	8.9	1.6	69.9	88	1.0	0.0	3.5	145	2.6	0.8	2.3	47
Artabotrys monteiroae	C	6.6	4.2	12.7	18	7.3	2.0	30.9	32	0.9	0.4	1.8	19	2.5	1.7	2.1	8
Azanza garckeana	T	7.7	5.0	13.3	11	4.5	2.1	12.4	16	0.6	0.0	1.8	11	1.7	0.6	3.0	7
Cleistanthus polystachyus	T	6.9	2.8	20.5	78	8.0	1.8	29.3	56	1.0	0.0	2.6	78	2.1	0.9	4.0	24
Dombeya burgessiae	T	5.6	3.6	8.6	6					2.0	1.5	2.3	6	8.0			1
Grewia sp.	C	9.6			1									4.0			1
Saba comorensis	C	8.5	2.5	16.5	60	7.2	1.9	44.8	58	1.6	0.4	3.8	62	3.5	1.7	3.5	19
Uvaria angolensis	C	9.8	5.5	13.1	3	17.8	11.3	30.6	3	1.2	0.8	1.5	5	4.5	4.0	4.5	2
Uvaria sp. *A of FTEA*	C	10.0	4.1	19.0	11					1.4	0.3	2.3	14	2.0			1
Uvaria welwetschii	C	19.5	10.7	26.5	5	15.1	10.1	22.9	3	0.8	0.4	1.2	7	4.0	3.0	5.0	2
All species		8.7				9.7				1.2				3.4			

[a]For species with more than one sourced part.
[b]T = tree, C = climber.

not the only material used (McGrew and Collins, 1985; Uehara, 1982). Gombe chimpanzees employ mostly grass for termite fishing (McGrew et al., 1979), although this might have changed during the last decades (but certainly since at least 2014, Pascual-Garrido, in prep.). While the absence of grass tools at Issa may be related to low abundance, the dearth of commonly available twigs is harder to understand. Ecological reasons are therefore not sufficient to explain the exclusive bark use. Given historical gene flow between the termite-fishing communities of Gombe, Issa and Mahale (Piel et al., 2013; Stewart and Piel, 2014), genetics are also an unlikely cause. Furthermore, other Issa tools, such as sticks to dig for tubers and tools to obtain arboreal *Camponotus* ants, are not exclusively made from bark (Hernandez-Aguilar et al., 2007; Wondra et al., 2016). This demonstrates that Issa chimpanzees are versatile in the type of raw material they use. It thus seems possible that the exclusive use of bark to fish for termites indicates a cultural preference at Issa, that is, an arbitrary behavior not brought about by genetic or ecological factors (Boesch, 2003; Janson and Smith, 2003; McGrew, 2004).

4.2 | Source species

Source plants for termite fishing tools have been identified at various sites (see Deblauwe et al., 2006, for review), but studies based on abundance are so far restricted to McBeath and McGrew (1982). Our research broadens this small database.

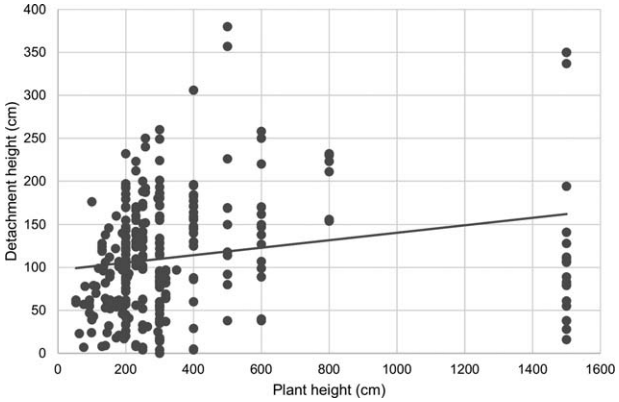


FIGURE 7 Height at point of detachment relative to total height of source plant

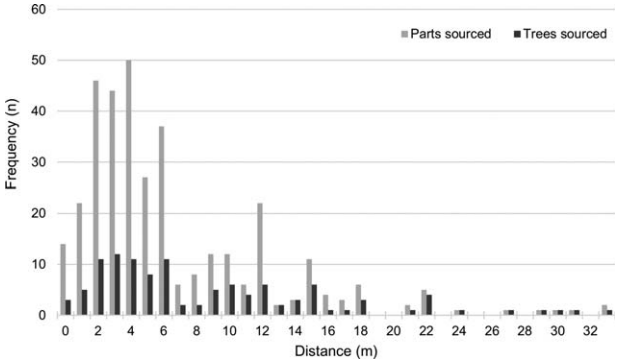


FIGURE 8 Frequency distribution of distance of sourced plant parts and sourced trees over 1-m classes (0 = 0.0–0.9 m; 1 = 1.0–1.9 m; 2 = 2.0; etc.)

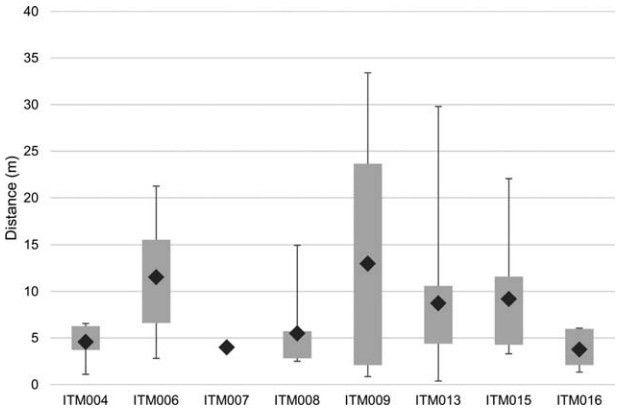


FIGURE 9 Distance of sourced plants to termite mounds targeted by chimpanzees. Diamonds = mean values

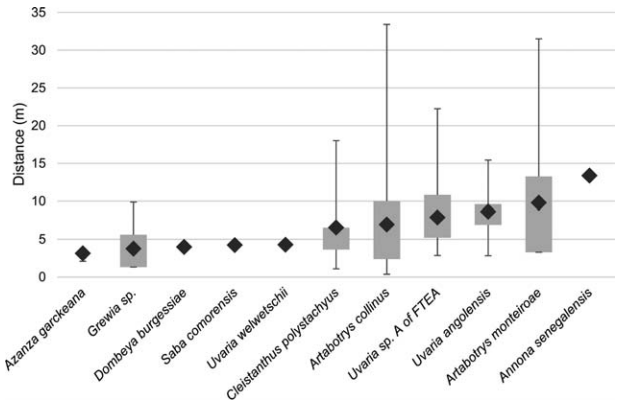


FIGURE 10 Distance of sourced plants to targeted mounds by plant species. Diamonds = mean values. *M. buchananii* and *R. urcelliformis* are not included as they were identified at mounds that were not part of the raw material availability studies

Accordingly, chimpanzees of the Issa valley sourced 13 plant species from six families for tool raw material (cf., Table 3). Three of these species also provide for termite fishing tools elsewhere, that is, *A. monteiroae*, *U. angolensis* and *Grewia sp.* at Mahale (Uehara, 1982), as well as *Grewia sp.* at Mt. Assirik (McBeath and McGrew, 1982) and Fongoli (McGrew et al., 2005).

Issa chimpanzees did not use many plants with supposedly suitable raw material growing in the vicinity of targeted mounds, while species such as *A. collinus*, *C. polystachyus* and *Uvaria* sp. *A of FTEA* were overselected, as was *D. burgessiae* at individual mounds. The exploitation of other taxa (*A. garckeana*, *A. monteiroae*, *U. angolensis*, *Grewia sp.*) did not differ from what was expected by their general abundance. However, even these were probably not sourced opportunistically because one or more individual specimens were sourced multiple times (cf., Table 1). Except for *A. garckeana*, these species are also used at Gombe and Mahale (McBeath and McGrew, 1982; Uehara, 1982). Taken together, these findings imply some degree of selectivity.

TABLE 6 Tool source species that chimpanzees also exploit as food sources

Species	Plant parts eaten by chimpanzees[a]	Eaten at Issa?[b]	Eaten elsewhere?[b]
Annona senegalensis	F, L, B	Yes (1)	Yes (3, 4)
Artabotrys collinus	F	Yes (2)	
Artabotrys monteiroae	F	Yes (2)	Yes (3)
Uvaria angolensis	F, L	Yes (1)	Yes (3, 4)
Uvaria sp. *A of FTEA*	F	Yes (6)	Yes (4)
Uvaria welwetschii	F		Yes (4)
Monanthotaxis buchananii	U	U	U
Saba comorensis	F, L	Yes (1)	Yes (4)
Cleistanthus polystachyus	F, W		Yes (5)
Azanza garckeana	F, Bl	Yes (2)	Yes (3)
Dombeya burgessiae	N		Yes (6)
Grewia sp.	F, L, Bl	Yes (1)	Yes (3)
Rothmannia urcelliformis	F		Yes (7)

[a]F = fruit, L = leaves, B = bark, W = wood, Bl = blossom, U = unknown.
[b]Sources: 1 = Piel et al. unpublished; 2 = local field assistant; 3 = Nishida and Uehara, 1983; 4 = Moscovice et al., 2007; 5 = Reynolds, 2005; 6 = Russak, 2013; 7 = Wrangham, n.d.

4.3 | Food species as tool sources

Chimpanzees are reluctant to interact with novel or unfamiliar items (Biro et al., 2003). The fact that 92% of tool source species at Issa were also exploited for food (cf., Table 6) suggests that, apart from physical characteristics such as being flexible (cf., Teleki, 1974; McGrew, 1992), familiarity might also play a role in their selection. Frequent contact with species that provide nourishment (fruit, leaves, etc.) may conceivable trigger preferential sourcing of materials from these same species, not least because food acquisition is coupled with haptic experiences. Alternatively, one might hypothesize that chimpanzees should avoid

TABLE 5 Visibility of individual sourced plants from targeted mounds and sourced parts used to manufacture tools

	Distance of source plants from targeted mound			Visible from targeted mound?		
	All plants	<10m	≥10m	Yes (all plants)	No (all plants)	No (plants sourced from ≥10m)
Plants (*n*)	113	71	42	89 (78.8 %)	24 (21.2%)	23 (54.8%)
Parts sourced (*n*)	349	266	83	311	38	37
Parts sourced per plant (*n*)	3.1	3.7	2.0	3.5	1.6	1.6

TABLE 7 Medicinal properties of chimpanzee plant tool sources

Species	Medicinal properties (B = bark, L = leaves, R = roots, S = sap)	Reference
Annona senegalensis	Dermatosis (R, L), digestive and stomach disorders (R, B, L, F), intestinal worms (B), chest colds (R), toothache (B), respiratory infections (L), antidote for snake and scorpion venom (B, R), convulsions (L), fever (L), malaria (B), infertility (R), venereal diseases (R), seal and treat cuts and wounds (B, L, S)	Ruffo, Birnie, & Tenganäs, 2002; Arbonnier, 2004; Huffman, 2015; Mustapha, 2013
Artabotrys collinus	Stomach disorders (R), antidote for snakebite (R)	Ruffo et al., 2002
Artabotrys monteiroae	Back aches (R), digestive and stomach disorders (R), malaria (R, B)	Tan and Wiart, 2014
Azanza garckeana	Digestive and stomach disorders (S, R), menstrual pains (R), fertility (R), urinary retention (R), venereal diseases (R), chest pain (R), ear pain (R, L), coughs (R), ulcers (R)	SEPASAL[a]
Dombeyia burgessiae	Aphrodisiac (B), stomach pain (B), leprosy sores (L)	Bosch, 2011
Grewia sp.	Anemia (R), chest pains and colds (R), digestive and stomach disorders (R, L), constipation in domestic animals (L), female infertility (R), treatment of wounds (B, R), menstrual problems (R), pregnancy pains (R), snake bites (R)	Huffman, 2015; Ruffo et al., 2002
Rothmannia urcelliformis	Antidote to poisoning (R)	Neuwinger, 1996
Saba comorensis	Digestive and stomach disorders (R), vermifuge (R), jaundice (R), hepatitis (R), gonorrhoea (R), snake bites (R), aphrodisiac (R), splenosis (R), galactagogue for humans and cattle (S), abcesses (S), night blindness (S), hypertension (L), rheumatism and female infertility (B, R), applied on sores (S)	Ruffo et al., 2002; Arbonnier, 2004; SEPASAL
Uvaria angolensis	Antimicrobial and cytotoxic properties (B, R)	Hufford and Oguntimein, 1982
Uvaria welwetschii	Stomach disorders (R)	Moriyasu et al., 2011

[a]SEAPASAL = online database of plants of arid and semi-arid lands developed by The Royal Botanical Gardens, Kew (1999).

damaging food plants and therefore not source tools from them. However, most material is obtained from low heights where plants will generally not bear fruit (cf., Table 4). Furthermore, removing bark from a fruiting branch will have little or no detrimental effect for fruit production.

4.4 | Medicinal properties of source plants

Many species sourced for tool material by chimpanzees possess medicinal properties, and are used by human populations in ethnomedicinal treatments (cf., Table 7). Conceivably, chimpanzees may prefer certain tool sources because the interaction with them may have health-giving side-effects (Huffman, 2015; Pascual-Garrido et al., 2012). For example, when Nigerian chimpanzees gather honey, they do this most frequently with tools from species that possess strong antibacterial properties (e.g. *Sorindeia warneckei*, *Chassalia kolly*). Furthermore, dental benefits that locals derive from chewing sticks of *S. warneckei* may also apply to Nigerian chimpanzees when they suck and bite on such sticks to ingest honey (Pascual-Garrido et al., 2012). While we cannot infer whether chimpanzees are actively selecting tool materials based on their medicinal properties, such benefits may nevertheless influence a preferred sourcing of certain species over others.

4.5 | Physical properties of source plants

Not all parts of an individual tree nor all individuals of a certain species may be good sources of tool raw material. For example, some individual plants, or parts of them, may be too short, too thin or too thick for extracting long and flexible pieces of bark. One possible way of assessing whether chimpanzees are selecting for particular properties is to look at the diameter and height of the sourced plant part at the point where raw material is detached (cf., Pascual-Garrido et al., 2012).

In our study, despite the fact that sourced and unsourced plant part diameters were significantly different, the absolute difference was just 1.0 mm (cf., Table 4). Similarly, at the level of absolute values, differences between sourced and unsourced parts at the species level and differences between species were minimal. It is therefore likely that all sourced species generally encompass the necessary dimensions for providing suitable termite fishing tools. A future task would therefore be to measure the properties of non-sourced species.

A quarter of plant parts were sourced from above 1.5 m, indicating that chimpanzees are climbing with some frequency to reach desired tool sources. The highest detachment point was at 3.8 m. However, we cannot exclude that some sources were too high to be detected by researchers from ground level. Only by using climbing equipment (cf.,

Stewart et al., 2011) would we be able to minimize this potential bias in our data collection.

Some plant species were sourced from higher points than others (cf., Table 4) and source height was positively correlated with absolute plant height (cf., Figure 7). Thus, the number of potential source parts available at a certain height may play a role. This is likely the case for *C. polystachyus*, a tree that only branches higher up. Similarly, while *U. welwetschii* is best classified as a climber (Moscovice et al., 2007), its bark may only provide suitable fishing material above a certain height. This would need further exploration, as all *U. welwetschii* material came from a single specimen. Apart from active selection for particular properties, a simple depletion effect could be at work whereby Issa chimpanzees start to exploit the plants at ground level and move higher up into the trees when lower plant parts become unavailable.

4.6 | Sourcing distances

The greatest distances between tool sources and the exploited termite mounds on which they were used reported from other sites are between 75 and 800 m (Goodall, 1986; McGrew et al., 1979; Sanz et al., 2004). However, these are exceptional distances recorded *ad libitum*. According to the only comparative study so far (McGrew et al., 1979), around 90% of tool sources at Mt. Assirik (Senegal) and Gombe (Tanzania) were within two meters from the mound, while at Okorobiko (Equatorial Guinea), most grew more than two meters away. Preferences for raw materials may influence this difference, because chimpanzees at Gombe and Assirik employ a wide variety of materials, while only twigs are used at Okorobiko.

Similar to Okorobiko, chimpanzees at Issa might need to acquire suitable material from relatively greater distances, given that only few species harboring adequate raw material for the exclusively used bark tools grew near mounds. Overall, Issa chimpanzees sourced plants growing up to 33 m from the mound, with half more than 10-m away and out of sight from the tool use area (cf., Table 5, Figure 9). That chimpanzees at Issa acquire tool material from further away compared to other populations is conceivably linked to the drier and more open habitat of the Issa valley, with its correspondingly low plant density and scarcity of preferred raw material, while apes in forests with greater vegetation density and raw material abundance can source it from nearer to the mound (Pascual-Garrido, Sommer, & Almeida-Warren, 2016).

Our study is the first to assess species-specific distances between sourced plants and termite mounds. Accordingly, at Issa, some plants were sourced from more than twice the distance than others (cf., Figure 10). A greater sourcing distance might indicate a stronger preference for a certain species. However, we surveyed abundance only up to 5 m from the targeted mound, and can therefore not exclude that preferred species are more abundant outside this radius.

That said, chimpanzees are not exclusively sourcing plants in the immediate vicinity of the mound, and neither only from further away. A greater sourcing distance suggests that chimpanzees source plants *en route* before they actually see the subsequently targeted mound. Alternatively, an individual may opportunistically source raw material nearest to the mound, and once this is depleted, travel back and forth for a greater distance to obtain more. Direct behavioral observations are currently absent to confirm these assumptions. In any case, at the cognitive level, raw material sourced *en route* might indicate a degree of forward planning instead of pure opportunism.

Debates as to whether chimpanzees and other non-human primates are capable of foresight have persisted for decades (de Waal and Ferrari, 2010). Recently, however, studies of populations both in captivity (Osvath and Osvath, 2008) and in the wild (Byrne, Sanz, & Morgan, 2013; Janmaat, Polansky, Ban, & Boesch, 2014) have demonstrated that chimpanzees plan for the future. It would seem more likely, therefore, that they also plan ahead of their termite fishing sessions.

5 | CONCLUSION

Studies of stone tool assemblages have provided insight into the ranging patterns of early hominins - whether they selected for specific raw materials, from how far away they sourced them, and what this may suggest about their cognitive abilities (Goldman-Neuman and Hovers, 2009; Harmand, 2009; Schick and Toth, 2006). However, the vast majority of such evidence is restricted to lithic artifacts. Research into chimpanzees is therefore a particularly valuable model for the reconstruction of early hominin behavior (Carvalho et al., 2009; Haslam, 2012; Haslam et al., 2009; Mikkelsen et al., 2005; Panger et al., 2002), as extant chimpanzees also use perishable tools that are typically lost in the archaeological record through processes of natural decomposition (McGrew, 2004; McGrew et al., 1979; Panger et al., 2002). Our study provides yet another piece in this puzzle.

ACKNOWLEDGMENTS

The authors are grateful to the Tanzanian Wildlife Research Institute (TAWIRI) and the Commission for Science and Technology (COSTECH) for permission to conduct research at Issa Valley. They greatly appreciate assistance in the field by Shedrack Lucas, Patrick Hassan, Godfrey Stephano, Mashaka Kalutwa, Busoti Juma, Mlema Juma, Msigwa Rashid, Sebastian Ramirez-Amaya, and Eden Wondra. They are also thankful to Frank Mbago, Botany Department, University of Dar es Salaam, who kindly identified plants. KAW benefitted from a Daryll Forde studentship, Department of Anthropology of UCL. APG is supported by a Leverhulme Trust Early Career Fellowship and received further funding for fieldwork from The Boise Trust Fund, University of Oxford. Long-term support for research at Issa comes from the UCSD/SALK Institute Center for Academic Research and Training in Anthropogeny (CARTA).

REFRENCES

Arbonnier, M. (2004). *Trees, shrubs and lianas of West African dry zones*. Paris: CIRAD.

Backwell, L. R., & D'errico, F. (2001). Evidence of termite foraging by Swartkrans early hominids. *Proceedings of the National Academy of Sciences of the United States of America*, *98*, 1358–1363.

Bermejo, M., & Illera, G. (1999). Tool-set for termite-fishing and honey extraction by wild chimpanzees in the Lossi Forest, Congo. *Primates*, *40*, 619–627.

Biro, D., Inoue-Nakamura, N., Tonooka, R., Yamakoshi, G., Sousa, C., & Matsuzawa, T. (2003). Cultural innovation and transmission of tool use in wild chimpanzees: Evidence from field experiments. *Animal Cognition*, *6*, 213–223.

Boesch, C. (2003). Is culture a golden barrier between human and chimpanzee? *Evolutionary Anthropology*, *12*, 82–91.

Bosch, C. H. (2011). Dombeya burgessiae Gerrard ex Harv. Record from PROTA4U. In M. Brink & E. G. Achigan-Dako, (Eds.), PROTA (Plant Resources of Tropical Africa / Ressources végétales de l'Afrique tropicale). Wageningen, Netherlands.

Byrne, R. W., Sanz, C. M., & Morgan, D. B. (2013). Chimpanzees plan their tool use. In: C. M. Sanz, J. Call, & C. Boesch (Eds.), *Tool use in animals: Cognition and ecology* (pp 48–64.). Cambridge: Cambridge University Press.

Carvalho, S., Biro, D., McGrew, W. C., & Matsuzawa, T. (2009). Tool-composite reuse in wild chimpanzees (*Pan troglodytes*): Archaeologically invisible steps in the technological evolution of early hominins?. *Animal Cognition*, *12*, S103–S114.

Carvalho, S., Cunha, E., Sousa, C., & Matsuzawa, T. (2008). Chaînes opératoires and resource-exploitation strategies in chimpanzee (*Pan troglodytes*) nut cracking. *Journal of Human Evolution*, *55*, 148–163.

Copeland, S. R. (2007). Vegetation and plant food reconstruction of lowermost Bed II, Olduvai Gorge, using modern analogs. *Journal of Human Evolution*, *53*, 146–175.

Deblauwe, I., Guislain, P., Dupain, J., & van Elsacker, L. (2006). Use of a tool-set by *Pan troglodytes troglodytes* to obtain termites (Macrotermes) in the periphery of the Dja Biosphere Reserve, southeast Cameroon. *American Journal of Primatology*, *68*, 1191–1196.

de Waal, F. B., & Ferrari, P. F. (2010). Towards a bottom-up perspective on animal and human cognition. *Trends in Cognition Science*, *14*, 201–207.

Goldman-Neuman, T., & Hovers, E. (2009). Methodological considerations in the study of Oldowan raw material selectivity: Insights from A. L. 894 (Hadar, Ethiopia). In E. Hovers & D. R. Braun (Eds.), *Interdisciplinary approaches to the Oldowan*. Dordrecht: Springer.

Goodall, J. (1964). Tool-using and aimed throwing in a community of free-living chimpanzees. *Nature*, *201*, 1264–1266.

Goodall, J. (1986). *The chimpanzees of Gombe: Patterns of behaviour*. Cambridge: Harvard University Press.

Goren-Inbar, N., Werker, E., & Feibel, C. S. (2002). *The Acheulian site of Gesher Benot Ya'aqov, Israel. The wood assemblage* (Vol. *1*). Oxford: Oxbow Books.

Hardy, K. (2016). Plants as raw materials. In K. Hardy & L. Kubiak-Martens, (Eds.), *Wild harvest. Plants in the hominin and pre-agrarian human worlds* (pp. 71–90). Oxford: Oxbow Books.

Harmand, S. (2009). Variability in raw material selectivity at the Late Pliocene sites of Lokalalei, West Turkana, Kenya. In E. Hovers & D. R. Braun (Eds.), *Interdisciplinary approaches to the oldowan* (pp. 85–97). Dordrecht: Springer.

Harmand, S., Lewis, J. E., Feibel, C. S., Lepre, C. J., Prat, S., Lenoble, A., … Roche, H. (2015). 3.3-million-year-old stone tools from Lomekwi 3, West Turkana, Kenya. *Nature*, *521*, 310–315.

Haslam, M. (2012). Towards a prehistory of primates. *Antiquity*, *86*, 299–315.

Haslam, M., Hernandez-Aguilar, A., Ling, V., Carvalho, S., de la Torre, I., DeStefano, A., … Warren, R. (2009). Primate archaeology. *Nature*, *460*, 339–344.

Hernandez-Aguilar, R. A. (2009). Chimpanzee nest distribution and site reuse in a dry habitat: Implications for early hominin ranging. *Journal of Human Evolution*, *57*, 350–364.

Hernandez-Aguilar, R. A., Moore, J., & Pickering, T. R. (2007). Savanna chimpanzees use tools to harvest the underground storage organs of plants. *Proceedings of the National Academy of Sciences of the United States of America*, *104*, 19210–19213.

Huffman, M. A. (2015). Chimpanzee self-medication: A historical perspective of the key findings. In M. Nakamura, K. Hosaka, N. Itoh, & K. Zamma (Eds.), *Mahale chimpanzees: 50 years of research* (pp. 340–353). Cambridge: Cambridge University Press.

Hufford, C. D., & Oguntimein, B. O. (1982). New dihydrochalcones and flavanones from Uvaria angolensis. *Journal of Natural Products*, *45*, 337–342.

Janmaat, K. R., Polansky, L., Ban, S. D., & Boesch, C. (2014). Wild chimpanzees plan their breakfast time, type, and location. *Proceedings of the National Academy of Sciences of the United States of America*, *111*, 16343–16348.

Janson, C. H., & Smith, E. A. (2003). The evolution of culture: New perspectives and evidence. *Evolutionary Anthropology*, *12*, 57–60.

Koops, K., McGrew, W. C., & Matsuzawa, T. (2013). Ecology of culture: Do environmental factors influence foraging tool use in wild chimpanzees, *Pan troglodytes verus*?. *Animal Behaviour*, *85*, 175–185.

Langergraber, K. E., Prüfer, K., Rowney, C., Boesch, C., Crockford, C., Fawcett, K., Inoue, E., … Muller, M. N. (2012). Generation times in wild chimpanzees and gorillas suggest earlier divergence times in great ape and human evolution. *Proc Natl Acad Sci 109*, 15716–15721.

Lesnik, J. J. (2014). Termites in the hominin diet: A meta-analysis of termite genera, species and castes as a dietary supplement for South African robust australopithecines. *Journal of Human Evolution*, *71*, 94–104.

McBeath, N. M., & McGrew, W. C. (1982). Tools used by wild chimpanzees to obtain termites at Mt Assirik, Senegal: The influence of habitat. *Journal of Human Evolution*, *11*, 65–72.

McGrew, W. C. (1992). *Chimpanzee material culture: Implications for human evolution*. Cambridge: Cambridge University Press.

McGrew, W. C. (2004). *The cultured chimpanzee: Reflections on cultural primatology*. Cambridge: Cambridge University Press.

McGrew, W. C. (2014). The "other faunivory" revisited: Insectivory in human and non-human primates and the evolution of human diet. *Journal of Human Evolution*, *71*, 4–11.

McGrew, W. C., & Collins, D. A. (1985). Tool use by wild chimpanzees (*Pan troglodytes*) to obtain termites (*Macrotermes herus*) in the Mahale Mountains, Tanzania. *American Journal of Primatology*, *9*, 47–62.

McGrew, W. C., & Rogers, M. E. (1983). Chimpanzees, tools, and termites—New record from Gabon. *American Journal of Primatology*, *5*, 171–174.

McGrew, W. C., Tutin, C. E. G., & Baldwin, P. J. (1979). Chimpanzees, tools, and termites: Cross-cultural comparisons of Senegal, Tanzania, and Rio Muni. *Man, New Series*, *14*, 185–214.

McGrew, W. C., Pruetz, J. D., Fulton, S. J. (2005). Chimpanzees use tools to harvest social insects at Fongoli, Senegal. *Folia Primatol 76*, 222–226.

Mikkelsen, T. S., Hillier, L. W., Eichler, E. E., Zody, M. C., Jaffe, D. B., Yang, S., … Waterston, R. H. (2005). Initial sequence of the chimpanzee genome and comparison with the human genome. *Nature*, *437*, 69–87.

Moore, J. (1992). "Savanna" chimpanzees. In T. Nishida, W. C. McGrew, P. Marler, M. Pickford, & F. B. M. DeWaal (Eds.), *Topics in primatology: Human origins* (Vol. *1*, pp. 99–118.). Tokyo: University of Tokyo Press.

Moore, J. (1996). Savanna chimpanzees, referential models and the last common ancestor. In W. C. McGrew, L. F. Marchant, & T. Nishida (Eds.), *Great ape societies* (pp. 275–292). Cambridge: Cambridge University Press.

Moriyasu, M., Nakatani, N., Ichimaru, M., Nishiyama, Y., Kato, A., Mathenge, S. G., … Halo Mutiso, P. B. (2011). Chemical studies on the roots of *Uvaria welwitschii*. *Journal of Natural Medicines*, *65*, 313–321.

Moscovice, L. R., Addessi, E., Petrselkova, K. J., Keuler, N. S., Snowdown, C. T., & Huffman, M. A. (2007). Fruit availability, chimpanzee diet, and grouping patterns on Rubondo Island, Tanzania. *American Journal of Primatology*, *69*, 487–502.

Mustapha, A. A. (2013). Annona senegalensis Persoon: A multipurpose shrub, its phytotherapic, phytopharmacological and phytomedicinal uses. *International Journal of Scientific Technology*, *2*, 862–865.

Neuwinger, H. D. (1996). *African ethnobotany: Poisons and drugs: chemistry, pharmacology, toxicology*. London: Chapman & Hall.

Nishida, T., & Hiraiwa, M. (1982). Natural history of a tool-using behavior by wild chimpanzees in feeding upon wood-boring ants. *Journal of Human Evolution*, *11*, 73–99.

Nishida, T., & Uehara, S. (1980). Chimpanzees, tools, and termites: Another example from Tanzania. *Current Anthropology*, *21*, 671–672.

Nishida, T., & Uehara, S. (1983). Natural diet of chimpanzees (*Pan troglodytes schweinfurthii*): Long-term record from the Mahale Mountains, Tanzania. *African Study Monographs*, *3*, 109–130.

O'Malley, R. C., & Power, M. L. (2014). The energetic and nutritional yields from insectivory for Kasekela chimpanzees. *Journal of Human Evolution*, *71*, 46–58.

Osvath, M., & Osvath, H. (2008). Chimpanzee (*Pan troglodytes*) and orangutan (*Pongo abelii*) forethought: Self-control and pre-experience in the face of future tool use. *Animal Cognition*, *11*, 661–674.

Panger, M. A., Brooks, A. S., Richmond, B. G., & Wood, B. (2002). Older than the Oldowan? Rethinking the emergence of hominin tool use. *Evolutionary Anthropology*, *11*, 235–245.

Pascual-Garrido, A., Buba, U., Nodza, G., & Sommer, V. (2012). Obtaining raw material: Plants as tool sources for Nigerian chimpanzees. *Folia Primatology*, *83*, 24–44.

Pascual-Garrido, A., Sommer, V., & Almeida-Warren, K. (2016). Raw material procurement for termite fishing tools in wild chimpanzees. *PeerJ Preprints*, *4*, e1844v1.

Piel, A. K., Cohen, N., Kamenya, S., Ndimuligo, S. A., Pintea, L., & Stewart, F. A. (2015). Population status of chimpanzees in the Masito-Ugalla Ecosystem, Tanzania. *American Journal of Primatology*, *10*, 1027–1035.

Piel, A. K., Stewart, F. A., Pintea, L., Li, Y., Ramirez, M. A., Loy, D. E., . . . Hahn, B. H. (2013). The Malagarasi River does not form an absolute barrier to chimpanzee movement in western Tanzania. *PLoS One*, *8*, e58965.

R Development Core Team. (2014). *R: A language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing.

Reynolds, V. (2005). *The chimpanzees of the Budongo forest: Ecology, behaviour, and conservation*. Oxford: Oxford University Press.

Royal Botanic Gardens, Kew (1999). Survey of Economic Plants for Arid and Semi-Arid Lands (SEPASAL) database. Available at: http://apps.kew.org/sepasalweb/sepaweb. Last accessed, 15-04-2016

Rudicell, R. S., Piel, A. K., Stewart, F., Moore, D. L., Learn, G. H., Li, Y., . . . Hahn, B. H. (2011). High prevalence of simian immunodeficiency virus infection in a community of savanna chimpanzees. *Journal of Virology*, *85*, 9918–9928.

Ruffo, C. K., Birnie, A., & Tenganäs, B. (2002). Edible wild plants of Tanzania: Technical handbook No. 27. Dar es Salaam: REMLA.

Russak, S. (2013). Ecological role of dry-habitat chimpanzees (*Pan troglodytes schweinfurthii*). Ph.D. Dissertation, Arizona State University.

Sanz, C., Call, J., & Morgan, D. (2009). Design complexity in termite-fishing tools of chimpanzees (*Pan troglodytes*). *Biology Letters*, *5*, 293–296.

Sanz, C., Morgan, D., & Gulick, S. (2004). New insights into chimpanzees, tools, and termites from the Congo Basin. *The American Naturalist*, *164*, 567–581.

Sanz, C. M., Deblauwe, I., Tagg, N., & Morgan, D. B. (2014). Insect prey characteristics affecting regional variation in chimpanzee tool use. *Journal of Human Evolution*, *71*, 28–37.

Sanz, C. M., & Morgan, D. B. (2009). Flexible and persistent tool-using strategies in honey-gathering by wild chimpanzees. *International Journal of Primatology*, *30*, 411–427.

Sanz, C. M., & Morgan, D. B. (2011). Elemental variation in the termite fishing of wild chimpanzees (*Pan troglodytes*). *Biology Letters*, *7*, 634–637.

Schick, K., & Toth, N. (2000). Origin and development of Tool-making behavior in Africa and Asia. *Human Evolution*, *15*, 121–128.

Schick, K., & Toth, N. (2006). An overview of the Oldowan industrial complex: the sites and the nature of their evidence. In N. Toth & K. Schick (Eds.), *The Oldowan: Case Studies into the Earliest Stone Age* (pp. 3–42). Gosport: Stone Age Institute Press.

Stewart, F. A., & Piel, A. K. (2014). Termite fishing by wild chimpanzees: new data from Ugalla, western Tanzania. *Primates*, *55*, 35–40.

Stewart, F. A., Piel, A. K., & McGrew, W. C. (2011). Living archaeology: Artefacts of specific nest site fidelity in wild chimpanzees. *Journal of Human Evolution*, *61*, 388–395.

Tan, K. K., & Wiart, C. (2014). Botanical descriptions, ethnomedicinal and non-medicinal uses of the genus Artabotrys R.BR. *International Current Pharmaceutical Journal*, *6*, 34–40.

Teleki, G. (1974). Chimpanzee subsistence technology: Materials and skills. *Journal of Human Evolution*, *3*, 575–594.

Toth, N., & Schick, K. (2009). The Oldowan: The tool making of early hominins and chimpanzees compared. *Annual Review of Anthropol*, *38*, 289–305.

Uehara, S. (1982). Seasonal changes in the techniques employed by wild chimpanzees in the Mahale Mountains, Tanzania, to feed on termites (*Pseudocanthotermes spiniger*). *Folia Primatol*, *37*, 44–76.

Whiten, A., Goodall, J., McGrew, W. C., Nishida, T., Reynolds, V., Sugiyama, Y., . . . Boesch, C. (1999). Cultures in chimpanzees. *Nature*, *399*, 682–685.

Whiten, A., Goodall, J., McGrew, W. C., Nishida, T., Reynolds, V., Sugiyama, Y., & Wrangham, R. W. (2001). Charting cultural variation in chimpanzees. *Behaviour*, *138*, 1481–1516.

Whiten, A., Schick, K., & Toth, N. (2009). The evolution and cultural transmission of percussive technology: Integrating evidence from palaeoanthropology and primatology. *Journal of Human Evolution*, *57*, 420–435.

Wilkins, J., Schoville, B. J., Brown, K. S., & Chazan, M. (2012). Evidence for early hafted hunting technology. *Science*, *338*, 942–946.

WoldeGabriel, G., White, T. D., Suwa, G., Renn, P., de Heinzelin, J., Hart, W. K., & Heiken, G. (1994). Ecological and temporal placement of early Pliocene hominids at Aramis, Ethiopia. *Nature*, *371*, 330–333.

Wondra, E. M., van Casteren, A., Pascual-Garrido, A., Stewart, F. A., & Piel, A. K. (2016). A new report of chimpanzee ant-fishing from the Issa Valley, Tanzania. *African Primates*, *11*, 1–18.

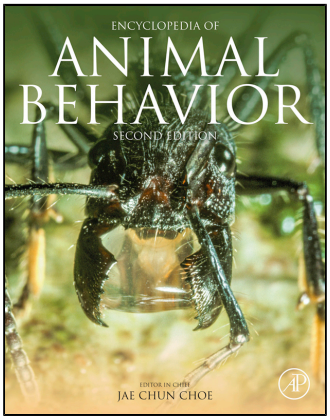
Wrangham, R. W. n.d. Kibale NP - Flora. Available at: http://pages.ucsd.edu/~jmoore/apesites/Kibale/KibaleFlora.html. Last accessed, 15–04-2016.

How to cite this article: Almeida-Warren K, Sommer V, Piel AK, Pascual-Garrido A. Raw material procurement for termite fishing tools by wild chimpanzees in the Issa valley, Western Tanzania. *Am J Phys Anthropol*. 2017;00:1–13. https://doi.org/10.1002/ajpa.23269

Author's personal copy

Provided for non-commercial research and educational use.
Not for reproduction, distribution or commercial use.

This article was originally published in Encyclopedia of Animal Behavior, published by Elsevier, and the attached copy is provided by Elsevier for the author's benefit and for the benefit of the author's institution, for non-commercial research and educational use including without limitation use in instruction at your institution, sending it to specific colleagues who you know, and providing a copy to your institution's administrator.



All other uses, reproduction and distribution, including without limitation commercial reprints, selling or licensing copies or access, or posting on open internet sites, your personal or institution's website or repository, are prohibited. For exceptions, permission may be sought for such use through Elsevier's permissions site at:
https://www.elsevier.com/about/our-business/policies/copyright/permissions

From Carvalho, S., Almeida-Warren, K. (2019). Primate Archaeology. In: Choe, J.C. (Ed.), Encyclopedia of Animal Behavior, (2nd ed.). vol. 1, pp. 397–407. Elsevier, Academic Press.
ISBN: 9780128132517
Copyright © 2019 Elsevier Ltd. All rights reserved.
Academic Press

Author's personal copy

Primate Archaeology

Susana Carvalho and Katarina Almeida-Warren, University of Oxford, Oxford, United Kingdom

© 2019 Elsevier Ltd. All rights reserved.

Glossary

Assemblage In archaeological terms, it refers to a collection of archaeological material and artefacts (e.g., tools, ceramics, coins etc…) that have accumulated in one location over time.

Chaîne opératoire In archaeological terms, it refers to a method employed to reconstruct the making of a tool, that can include the complete operational sequence of a technological activity, from raw material selection, to object modification, utilization, and, eventually, discard.

Clinometer Or inclinometer, is an instrument used to measure vertical angles (tilt), between two objects.

GIS Geographic Information System. It is a digital framework or program, specialised in collecting, visualizing, managing, and processing geographic and spatial information.

GNSS Global Navigation Satellite System. It is an umbrella term for satellite navigation systems that provide autonomous geospatial positioning at a global scale. Examples of GNSS systems include: GPS, Galileo, and GLONASS.

Hominin Also Hominini is a taxonomic group that refers to our species, *Homo sapiens*, and all our ancestors (e.g., *H. habilis*, *H. erectus*, *H. neanderthalensis*). *H. sapiens* is the only Hominin species alive today.

In-situ In archaeological terms, it refers to archaeological remains that are found in their original location (i.e., where they were last used), without any evidence of displacement by taphonomic processes.

Material culture Represents the physical evidence (e.g., objects, resources, buildings, spaces) that define the culture of a population.

Micro-wear Defines microscopic abrasion, wear, polishing, left on the surface of artefacts, such as tools, as a result of their use in particular activities.

Morphometric Refers to the quantitative analysis of the dimensions and shape of an object and its features.

Plumb bob Or plummet, is a weight with a pointed tip which is suspended from a string and is used as a vertical reference line.

Use-wear Defines the surface modification on an object or artefact, as a result of its use in a particular activity.

Abstract

Primate Archaeology is a novel field of research that has had transformed our knowledge about the origins and evolution of technology. It expanded the focus of traditional archaeological studies from humans to all primates that are tool-users. Research in this area focuses on present and past processes of tool-making, use and site formation in extant and extinct primates, such as chimpanzees and monkeys. The discipline is flourishing and is at the forefront of key scientific developments in the fields of primatology, archaeology and palaeoanthropology. In this article, we provide an historical overview of the discipline, describe main methodological tools, highlight key case studies and discuss implications of recent findings and future research directions.

Keywords

Behavioral evolution; Capuchins; Chimpanzees; Cognition; Extractive foraging; Human evolution; Macaques; Non-human artefacts; Nut-cracking; Pliocene archaeology; Primate archaeology; Primate heritage; Technological Origins; Termite-fishing; Tool-making; Tool-use

Introduction

Primate Archaeology is a recently created, and burgeoning, field of research at the inter-section of Primatology and Archaeology (Carvalho *et al.*, 2008, 2009; Haslam *et al.*, 2009, 2017). The sub-discipline focuses on the study of the technological behavior of extant (and extinct) non-human primates and its material record. Research in this field typically combines archaeological methods with ethological approaches by studying the material evidence of technology in tandem with the behavioral evidence, whether directly or indirectly observed, associated with tool-use and tool-making in the Primate order.

The need to establish a new discipline that considers non-human primate tools, *and behavior*, as critical to further understand how humans developed such complex technology (Carvalho *et al.*, 2008; Haslam *et al.*, 2009) emerged as a natural consequence of milestone, first time developments during the last decade: archaeologists went to West Africa to study chimpanzee stone tools (e.g., Joulian, 1994, 1996; Mercader *et al.*, 2002; Mercader *et al.*, 2007), and primatologists applied archaeological methods to infer

Encyclopedia of Animal Behavior, Second Edition, 2019, 397–407

Author's personal copy

invisible behavior from chimpanzee tools (see Hernandez-Aguilar *et al.*, 2007; Carvalho *et al.*, 2007). Primate Archaeology provided a novel framework to investigate the origins of technological behavior using a cross-species, evolutionary approach (Haslam *et al.*, 2009, 2017).

The growing research operating within this paradigm has recently brought researchers to suggest that the variation we see today in the tool-use of the primate order indicates that: (1) Tool-use in humans and chimpanzees may be a shared, primitive trait, thus the Last Common Ancestor between humans and chimpanzees (ca. 7 million years ago) was likely a tool-user; (2) Tool-use in the more distant related primates, like monkeys, may be better explained by convergence, i.e., parallel evolution (see also Campbell and Carvalho, 2017 for an extensive review on tool-use and manufacture in the Last Common Ancestor of *Pan* and *Homo*).

The foundation of Primate Archaeology has had wide scientific implications, leading to important re-interpretations of past archaeological records (see Proffitt *et al.*, 2016; Roche, 2016). It has opened the way to the new "Pliocene Archaeology" and the acknowledgement that archaeological assemblages pre-dating 2.6 million years should exist in Africa (Carvalho and McGrew, 2012; Harmand *et al.*, 2015). It is illuminating variables that can explain the loss of technological traditions (Luncz *et al.*, 2017b), and is challenging the old premise that hominins must have manufactured *all* of the artefacts found in the archaeological record. This new paradigm suggests that in the past, as is the case today, a variety of primate species generated material culture.

Primate archaeology also encapsulates ethoarchaeology, a branch of archaeology which studies, in effect, living archaeology and the relationships between observed behaviors and the active archaeological signatures they produce on a daily basis (e.g., McGrew *et al.*, 2007). The study of this living archaeology, enables an in-depth understanding of contemporary primate technology and the associated cognitive, social and cultural mechanisms.

Thus, in using the same methodological framework of traditional archaeology, Primate Archaeology is producing a wealth of information that can be directly translated into the archaeological record of our earliest ancestors and is becoming a vital asset to Paleolithic archaeologists for understanding the functional and cognitive contexts of early hominin technology, as well as reconstructing patterns of resource exploitation and landscape use associated to the earliest archaeological assemblages (Toth *et al.*, 2006; Toth and Schick, 2009). It can help identify the evolutionary origins of hominin tool-use and provided tools for identifying currently archaeologically invisible behaviors (Panger *et al.*, 2002; Carvalho *et al.*, 2009).

Non-human primate tool-use itself, has been known for over 60 years, when Jane Goodall witnessed, for the first time, chimpanzee termite-fishing at the wild chimpanzee field site now known as The Gombe Stream National Park. She provided the first scientific account of tool-use in a species other than our own (Goodall, 1963). This ground-breaking discovery defied the long-standing anthropocentric view that technology was a uniquely human trait (Carvalho and McGrew, 2012; Carvalho and Beardmore-Herd, in press).

However, despite decades of primatological studies focusing on primate material culture (McGrew, 2002, 2004), and the awareness that tool-using primates could be useful models for hominin technological evolution (Wynn and McGrew, 1989; Sakura and Matsuzawa, 1991; Marchant and McGrew, 2005), archaeology continued to be synonymous of 'human' until 2002, when the first excavation of a non-human archaeological site was published, in a groundbreaking study in *Science* (Mercader *et al.*, 2002). The excavations took place at three wild chimpanzee nut-cracking sites in the Taï National Park, Cote d'Ivoire, and yielded several buried tree roots used as anvils with associated hammerstone fragments and nutshell debris. The earliest remains dated back to 4,300 years ago, revealing that, much like our hominin ancestors, chimpanzees too are leaving behind durable archaeological records (Mercader *et al.*, 2007). It was this excavation that would open the way for the establishment of a field of non-human Primate Archaeology. A re-assessment of the original Taï chimpanzee assemblage is being published as we write this piece (Proffitt *et al.*, in press).

In 2008, a team of researchers published a milestone study combining ethological and archaeological methods, including direct and indirect records of tool-use at several stone tool sites by the wild chimpanzees of Bossou, Guinea (Carvalho *et al.*, 2008). It was described soon after as 'so far the most comprehensive study bringing archaeological methodology to the study of primate tools, applying the theoretical concept of operational sequences to chimpanzee nut cracking and highlighting variability in tool function and regional diversity in tool use.' (Haslam *et al.*, 2009: 344). Interdisciplinary training in archaeology and primatology was then highlighted as a pre-requisite for the field of Primate Archaeology to emerge. A follow-up conference aiming to bridge these fields (*Palaeoanthropology meets Primatology*, Ling *et al.*, 2009) led to a review 'manifesto' urging the establishment of this field of research (Haslam *et al.*, 2009).

Today, primate technology encapsulates a range of different tool-using behaviors from Western chimpanzee (*Pan troglodytes verus*) nut-cracking with stone or wood hammers and anvils, to the use of stones by Burmese long-tailed Macaque (*Macaca fascicularis aurea*) to extract sea-snails and other marine invertebrates from their hard shells (Sugiyama and Koman, 1979; Malaivijitnond *et al.*, 2007). It also includes the Brazilian bearded capuchin (*Sapajus libidinosus*) stone-on-stone percussion for extracting minerals, chimpanzee and orangutan (*Pongo sp.*) honey dipping with sticks, and nest-building in several ape species (Sept, 1992; Stewart *et al.*, 2011; van Schaik *et al.*, 2003; Sanz and Morgan, 2009; Hernandez-Aguilar, 2009; Proffitt *et al.*, 2016).

But, how can archaeological theory and methods enhance our knowledge about primate technology? For example, an excavation of a primate tool site, such as a chimpanzee nut-cracking assemblage, can help determine the age of the behavior at that location (Mercader *et al.*, 2007; Haslam *et al.*, 2016a,b). It can also reveal whether the behavior has remained consistent or has changed over time, and can help identify the timing of technological innovations or loss of them (Haslam *et al.*, 2017; Luncz *et al.*, 2017b). From an active assemblage, it is possible, when analyzed within the broader ecological context, to assess whether a primate population is targeting specific raw materials that they use for tools (Carvalho *et al.*, 2008; Almeida-Warren *et al.*, 2017). Analysis of the mechanical properties of the tools used can also provide information about the knowledge and expertise acquired by individuals in order to be successful and proficient tool-users (Visalberghi *et al.*, 2009). Lastly, comparison with assemblages from other populations can

Author's personal copy

help determine whether there is technological conformity or variation of the behavior and which variables may be determining the variation (Carvalho *et al.*, 2008; Luncz *et al.*, 2018), which in turn, when combined with genetic evidence, can provide insight into past dispersal patterns, networks of information transmission, and the evolutionary origins of technology throughout the primate lineage.

Perhaps expectedly, primate archaeology, has largely focused on the primate species that use stone tools, particularly stone tools used for extractive foraging via percussive activities. Studies on stone tool-use by chimpanzees (*Pan troglodytes*), capuchins (*Sapajus libidinosus*), and long-tailed macaques (*Macaca fascicularis aurea*) predominate the literature between 2008 and 2018, with a behavioral focus on nut-cracking and shellfish pounding. Lithic technology comprises the vast majority of the early archaeological records (Hovers and Braun, 2009; Shea, 2016) - together with fossil bones, these are the most durable materials that can last for millions of years. Because archaeologists have had to infer past behavior mostly from lithic artifacts, they have well-established methodologies for its study. However, re-constructions of early hominin evolution continue seriously hampered by this limited evidence and the low number of early archaeological sites (Hovers and Braun, 2009; McPherron *et al.*, 2010; De la Torre, 2011; Harmand *et al.*, 2015).

Thus, the opportunity to focus on invisible records, i.e., tools made of perishable materials that are unknown to the oldest archaeological records, is another important area of studying extant primate technology. Making use of this 'living archaeology', the field has been expanding towards the study of ephemeral technologies, such as nest building, ant-dipping and termite fishing (Stewart *et al.*, 2011; Almeida-Warren *et al.*, 2017; Pascual-Garrido *et al.*, 2012). While the lifespan of perishable tools is relatively short compared to stone tools, there are many archaeological methods that are applicable, such as the selection, re-use and spatial distribution of nesting locations, as well as the selection and transport of raw materials for insect predation. Plant-based technology is the most common and, arguably, the most diverse and complex manifestation of primate tool-use (Whiten *et al.*, 1999; Wynn *et al.*, 2011). Thus, such studies hold the key for obtaining a comprehensive understanding of primate technology as a whole (**Fig. 1**).

At a broader, evolutionary level, the study of perishable technology through an archaeological lense is providing a framework for reconstructing archaeologically invisible aspects of hominin behavior. It is offering information on selection and use of plant-based technology and on landscape use and foraging patterns based on the location and exploitation of resources. This will be crucial to contextualize the currently known archaeological sites and to re-think ranging patterns and locations of potential unknown sites (Almeida-Warren *et al.*, 2017; Stewart *et al.*, 2011; Panger *et al.*, 2002; Pascual-Garrido *et al.*, 2012).

Not all primate species use tools in the wild, however. In fact, tool use in the animal kingdom is rare (Beck, 1980). Thus, primate archaeological research has largely focused on the most studied primate of all, the chimpanzee (*Pan troglodytes sp.*), or in other versatile tool-users: bearded capuchins (*Sapajus libidinosus*), and Burmese long-tailed macaques (*Macaca fascicularis aurea*). Chimpanzee tool-use is unique in that it is a generalized feature of all studied populations, includes tool-use that is *not* for extractive foraging (e.g., hygiene, comfort, see Whiten *et al.*, 1999), and encompasses lengthy tool-kit repertoires of more than 20 different tool-types in a single community (Carvalho and McGrew, 2012; McGrew, 2004, 2010; Campbell and Carvalho, 2017). Nevertheless, the fact that tool use is not widespread in the primate order, but occurs in apes, New World and Old World monkeys poses in itself and interesting evolutionary and behavioral conundrum.

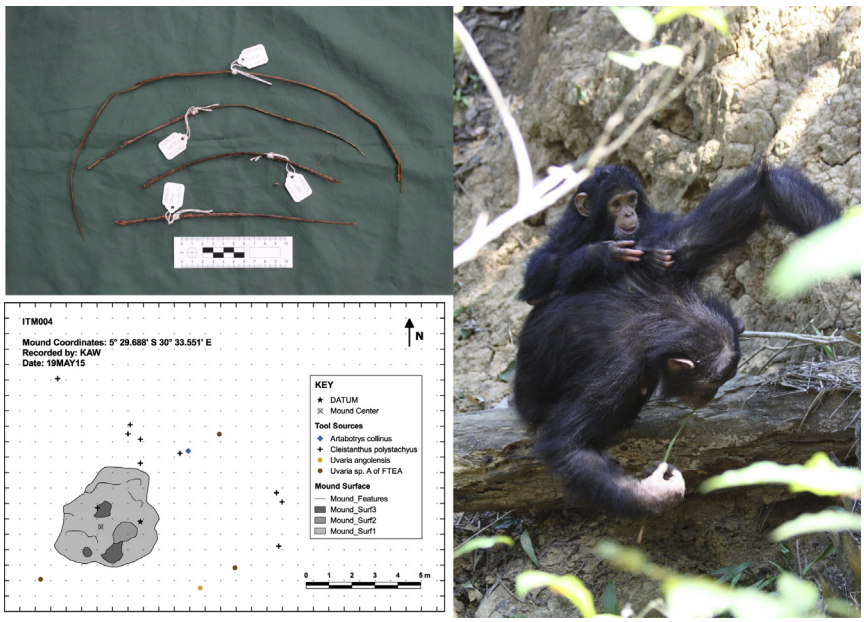


Fig. 1 Chimpanzee plant tool-use. Top left, chimpanzee termite fishing tools from the Issa valley (Tanzania); bottom left, map of raw material sources at a chimpanzee termite-fishing site in the Issa valley (Tanzania); right, chimpanzee termite fishing.

Author's personal copy

Further research operating within the framework of primate archaeology will no doubt begin to tap into the foundations and nuances of primate technological behaviors, gradually building an evolutionary tree of primate technology (Haslam *et al.*, 2017; Campbell and Carvalho, 2017).

In the following sections, we discuss the main methodological approaches of primate archaeology and present some of the key findings revealed thus far.

Methods in Primate Archaeology

There is a wide selection of archaeological methods that have been applied in primatology, ranging from full scale excavations, surveys and surface documentation of tools and raw material sources, *chaînes operatóires* (behavioral sequences during tool-use or tool-making), analysis of use-wear (tool damage), analyses of density and distribution of tools at sites, mechanical properties of raw materials used and etc. The methods chosen for a particular study will rely largely on the research question and the type of information the investigation seeks to obtain. Here we summarize the main approaches and their applications.

Archaeological Excavations and Surface Surveys

Ultimately, excavation and surface surveys deal with the distribution of artefacts in space and time within a technological assemblage. Archaeological excavations are a vital and important component of traditional archaeological approaches: they provide *in-situ* material, stratigraphic and depositional contexts, time depth, and chronology through absolute (e.g., radio-carbon, OSL, Ar/Ar) and relative (e.g., biochronology or via diagnostic tool morphologies) dating. Essentially, they help date the behavior, trace its history, track changes over time, and reconstruct the possible social and ecological contexts of the fossilized activity (Renfrew and Bahn, 2015).

In primate archaeology, the excavation of tool sites is useful for dating the earliest evidence of a technological behavior, and investigating how the behavior may have changed over time (Mercader *et al.*, 2007; Mercader *et al.*, 2002; Haslam *et al.*, 2016b). Excavation protocols vary widely between archaeological projects and largely depend on the geological context, the nature of the evidence (e.g., what materials will be excavated), and the resolution that the research question demands. Nevertheless, all include a methodology for systematic excavation (e.g., grid-system or trenches, by spits or stratigraphic layers), spatial data collection, as well as documenting and labelling all the collected material. There are several archaeology manuals, textbooks and online material that describe the different methods, some of which we have included in further reading at the end of this article.

While an archaeological excavation has its merits in primatology, it requires time, manpower, and expensive, heavy, equipment. One must also consider the implications of disturbing, and potentially destroying, an active tool site and its impact on future activities by the tool-using population in that area.

A less invasive and less time-consuming approach is to carry out surface surveys. As mentioned previously, unlike human archaeology which deals with fossilized behaviors, primate archaeology studies the technological behaviors of a living population. Thus, while surface surveys cannot provide a date for the origin of the behavior *per se*, they can document how these living archaeological sites are formed and record the changes in archaeological signatures in real time (Carvalho *et al.*, 2008, 2011). This can be achieved by tracking, over time, the position and movements of tools, the appearance of new tools, the modification of tools, and their eventual discard.

In this way, surface surveys provide a life history of primate tools and the assemblages they are part of. Furthermore, studying these living assemblages generates important tools for the identification of fossilized tool sites, as well as their behavioral interpretations (Almeida-Warren *et al.*, 2018b).

Spatial data collection and GIS

Most archaeological research, whether of humans or non-humans, involves spatial data collection, map-making and subsequent spatial analysis. One of the reasons for this is that it allows the record of the exact location of an artefact, but also its relative position to other artefacts, raw material sources, and ecological features that may be associated to the behavior (e.g., nut-trees and watercourses in the case of the chimpanzee nut-cracking; shorelines in the case of long-tailed macaque sea-snail extraction/foraging). This provides rigorous data which is essential in the study of site formation and tool movement over time, raw material sourcing, but also the spatial relationships between technological behaviors and other activities.

There are several available tools and approaches for spatial data collection, which vary in cost, accuracy, and portability. To date, the most frequently used in Primate Archaeology research, is the traditional method which requires two measuring-tapes, string, water level, plumb bob and compass (digital or analog) (e.g., Carvalho *et al.*, 2008; Pascual-Garrido *et al.*, 2016; Almeida-Warren *et al.*, 2017). Known as the distance-azimuth method, one tape is used to measure the horizontal distance from a fixed Datum, the other for the vertical distance between the tape and the object, and the compass serves to determine the direction of the object from the Datum relative to North. The collected data can be converted into standard X, Y, Z coordinates using basic trigonometry.

While this method is the most affordable and portable, it is by far the least accurate or precise. While the tapes can provide millimetric resolution, the bowing of the tape at greater distances and the fact that vertical measurements are limited between ground level (measuring upslope) and the measurer's height (measuring downslope), can cause significant distortions to the data.

Author's personal copy

Furthermore, most compasses only have degree resolution, which causes greater error as the distance increases. This is augmented by the fact that all the relative measurements are taken manually, which leaves a lot of room for human error both in reading the measurements as well as recording. However, if the study in question does not require extremely detailed resolution, this is a good and practical option, especially suited to handle the complexities of surveying in the tropical rainforest.

Another method, which is the current state-of-the-art in archaeological work, and employed in a few primate studies, is the Total Station. The Total Station was originally built for use in construction and engineering, and provides highly accurate spatial measurements relative to a fixed Datum. This technology uses a laser-beam and integrated digital compass to measure distance, azimuth, vertical and horizontal angles, which are automatically converted into X, Y, Z coordinates. The output can be read directly from the device, or can be downloaded as a digital file. To date, this is the most accurate method of spatial data collection, but it is also the least portable, and the most expensive. While it is the best tool for large scale excavations, it is heavy and cumbersome equipment to carry in remote locations with difficult terrain and closed vegetation, particularly if the research requires data from multiple sites.

A very recently adopted, and less know option, is the so-called "paperless survey", i.e., the use of the Disto X2 (Almeida-Warren *et al.*, 2018b; Almeida-Warren *et al.*, 2018a; Almeida-Warren *et al.*, in prep). It is a portable hand-held laser distance measurer with an integrated digital compass and clinometer, which can be paired to an android device through the open-access software, TopoDroid. Originally developed for mapping cave systems to replace the traditional time-consuming and labor-intensive method of manual measurements and paper sketches (Heeb, 2008). This method started to gain recognition recently in archaeology for data collection of archaeological sites located in caves, where Total Stations are not viable, and GPS signals are absent (Trimmis, 2018, 2015). While it is less accurate as the Total Station method, it has the advantage of being highly portable and considerably more affordable (Redovniković *et al.*, 2016). Current empirical work comparing the results of using the three described methods, suggests the DistoX2 as the optimal choice, overall, for the most common Primate Archaeological surveys (Almeida-Warren *et al.*, in prep).

The methods above describe several options of relative spatial data collection. Absolute coordinates, for global geographic mapping in GIS, can be determined with the help of a GPS/GNSS device. The GPS/GNSS device is used to provide the geographic coordinates of the Datums, which are then used to translate the relative X, Y, Z distances of points into actual geographic coordinates.

There is a wide variety of GPS/GNSS devices available on the market. GPS technology is advancing at a fast pace, with some commercial GNSS systems boasting sub-cm accuracy (e.g., Arrow series by EOS; Trimble R-Series), and even the average smartphone or tablet can now provide GIS data with a five-meter accuracy under open sky (van Diggelen and Enge, 2015). The choice of which to use will largely depend on project budget, and the accuracy required for data collection. However, due to its versatility and portability most Primate Archaeology research uses hand-held GPS devices (e.g., Garmin, Magellan), which typically have an absolute accuracy of three meters under optimal conditions (e.g., minimal canopy cover), although the use of tablets is becoming increasingly popular.

To map and analyze the data there are several GIS software applications available, such as ArcGIS and the open source equivalent QGIS. Both provide tools for generating site maps, as well as performing refined analysis of potential spatial relationships between individual artefacts, between assemblages, and other associated features.

Raw Material Studies

Raw material studies primarily serve to investigate evidence of selectivity, i.e., if individuals in a population are targeting specific types of materials for their tools. There are two main approaches that can help answer this question. The first is to compare the raw material of the tools that are being used relative to their general availability in the surrounding ecological habitat. This can be achieved by documenting proportions of the different types of materials used, and comparing them to the natural proportions of available materials collected from the tool-site vicinity and/or sample areas (Almeida-Warren *et al.*, 2017; Carvalho *et al.*, 2008; Braun *et al.*, 2008; Braun *et al.*, 2009; Stout *et al.*, 2005). If the proportions are different, it is a good indication that certain raw materials are being sourced over others.

The second is to look at the physical and mechanical properties of the raw materials. For primate stone tools these may include size, weight, hardness, friability (Carvalho *et al.*, 2008; Visalberghi *et al.*, 2009). For plant tools these may include length, width, pliability (Almeida-Warren *et al.*, 2017). Typically, this involves taking quantitative measurements of material dimensions and other relevant properties, and experimentally testing the performance of the materials used as tools, relative to other available materials that have not been used. Another form of experimental testing can be achieved by artificially supplying a selection of raw materials, of known physical properties, to a tool-use location and documenting, through observation, which types of materials are most frequently selected by the tool-users for the activity (see Carvalho *et al.*, 2008; Carvalho *et al.*, 2012; Visalberghi *et al.*, 2009). This can not only help determine whether individuals are targeting specific material properties, but also assess cognitive skills, technological performance, and social learning mechanisms (**Fig. 2**).

When the raw material source is known, another useful indicator is the distance between source and tool-site. This may be recorded through direct behavioral observation, or in the case of plant materials it is often possible to identify source plants from removal scarification (see Pascual-Garrido *et al.*, 2012; Almeida-Warren *et al.*, 2017). If raw materials for tools are sourced some distance away from the activity area when other types of suitable materials are available nearby, it suggests that individuals are travelling further afield to search for the best or preferred materials.

Author's personal copy



Fig. 2 Chimpanzee stone tool-use. Left, chimpanzee nut-cracking at the experimental outdoor lab in Bossou (Guinea); middle, weighing stone tools used by chimpanzees for nut-cracking in Bossou (Guinea); right, chimpanzee nut-cracking tools and nut shell debris from a site in Bossou (Guinea).

Raw material studies like these can not only help understand the underlying cognitive framework of a tool-based activity, but can also help uncover potential cultural traits of a primate population (Almeida-Warren *et al.*, 2017).

Use-Wear

The study of use-wear of tools is useful for understanding the techniques and manual/manipulative skills (e.g., action, precision, grips) involved in the technological behavior (Haslam *et al.*, 2013). Furthermore, in the absence of direct behavioral observation, it can also help isolate the diagnostic features of a tool, which in turn can provide a protocol for identifying materials that have been used as tools from those which have not (Haslam *et al.*, 2013; Caruana *et al.*, 2014; Benito-Calvo *et al.*, 2015).

Use-wear can be studied at a macroscopic (macro-wear) or microscopic (micro-wear) level. This can be achieved through producing 3D-models (via photogrammetry or 3D-scanning) of the tools and analyzing their virtual surfaces through morphometric analysis (see Benito-Calvo *et al.*, 2015). In the case of tools used in pounding activities, such as nut-cracking or processing marine invertebrates, this involves documenting pitting, crushing and fracture wear on the tool surface (Proffitt *et al.*, 2018). For plant-based tools such as termite-fishing or ant-dipping, this would involve documenting features like fraying and clipping, although this has yet to be explored.

Refined quantitative methods like these are providing the first building-blocks that allow for technological comparisons between different primate species, including hominins.

Tool Modification

The ability to modify an object and the way in which this object is modified in order to produce a tool, is often used in Paleolithic archaeology as a measure of technological and cognitive complexity (Shea, 2016). One measure, for example, would be the number of flake detachments that are successfully removed from a cobble to achieve the desired tool (Delagnes and Roche, 2005). While primates only use stone tools that are modified by use, not prior to use, and do not intentionally flake stones in the wild, they do present several instances of tool modification, particularly in chimpanzee plant technology. Plant materials are often curated prior to use by removing leaves and off-shoots, and in some populations the functional ends of termite-fishing tools are modified to produce a brush tip that increases the surface catchment area of the tool, thus making the tool more efficient (e.g., Sanz *et al.*, 2009). As with human archaeology, studying the processes of primate tool modification, can provide valuable insight into the cognitive frameworks of primate technology.

Case Studies

While still in its infancy, Primate Archaeology is developing at a very fast pace. In the past decade, the field has been extremely prolific, expanding from chimpanzee archaeology, to studies including capuchins and macaques, and new populations of non-human primates have been reported to use tools. A wealth of information has been uncovered, which is continuously building our knowledge on primate technological repertoires and cognitive abilities, but also providing valuable insight into our evolutionary past.

Here we present some of the key findings of these studies.

Chimpanzees (*Pan Troglodytes*)

Chimpanzee populations throughout Africa use stone and plant materials for extractive foraging, social interactions and self-maintenance (McGrew, 2004; Whiten *et al.*, 1999). They use stones and hardwoods as hammers and anvils to crack open nuts;

Author's personal copy

wads of chewed-up leaves as sponges to soak up drinking water; and long twigs and strips of bark to harvest social insects (ants, termites, bees) and their products (e.g., honey) (Boesch and Boesch, 1984; McGrew, 2004; Sanz and Morgan, 2010; Whiten *et al.*, 1999). They present the largest and most diverse repertoire compared to any other non-human species (Carvalho *et al.*, 2013).

The first non-human archaeological excavations were conducted at a chimpanzee nut-cracking field site where it was found that this behavior dated back to at least 4,300 years (Mercader *et al.*, 2007). This provided the first evidence that chimpanzees, like our human ancestors, are also capable of producing a durable and archaeologically recognizable record. A recent study on use-wear analysis has further supported this, by revealing that stones used by chimpanzees for nut-cracking are quantitatively distinguishable from stone natural damage, and can, therefore, be identified without direct observation of the activity, i.e., in the archaeological record (Benito-Calvo *et al.*, 2015).

Subsequent research at the two long-term sites for wild chimpanzee nut-cracking, Taï (Cote d'Ivoire) and Bossou (Guinea), revealed that chimpanzees are selective of the rocks they use as tools (Sirianni *et al.*, 2015; Carvalho *et al.*, 2008) and show preference for re-using the same pair of stones (Carvalho *et al.*, 2009). Furthermore, research on transport distances at a landscape-wide scale in Taï, suggests that hammerstone transport by chimpanzees follows a distance-decay model akin to that of some early hominin sites, in which the weight of the tool decreases with the increase in distance from the nearest raw material sources (Luncz *et al.*, 2016). This pattern was also found in the spatial analysis of the excavated material from Noulo, suggesting that this strategy has probably remained unchanged in the last 4,300 years.

Thus, selection for nut-cracking tools, seems to be conditioned by a combination of the physical properties of the raw material (e.g., size, weight, type), the ecology of the technology (e.g., availability and density of the resource), and the energetics of the behavior (costs of sourcing and transportation versus energetic gains) demonstrating that chimpanzees have an in-depth understanding of the physical and mechanical properties of different materials, and are also able to weigh up a series of complex information in order to achieve an optimal foraging strategy (Sirianni *et al.*, 2015; Carvalho *et al.*, 2008).

This does not appear to be a universal condition of nut-cracking technology, however, as a recent study comparing different chimpanzee communities of Taï have revealed that there is considerable intra-specific variation in nut-cracking efficiency (Luncz *et al.*, 2018). This variation occurs due to the differential selection of raw materials for tools and differences in the manual techniques used between communities, despite the availability of the same raw materials throughout the forest. These so-called cultural differences persist even with the transfer of immigrant individuals from neighboring communities, who adopt the technological norms of the new group, regardless of its efficiency (Luncz *et al.*, 2018). This suggests, that although chimpanzees may have intimate technical knowledge, their technology is bounded by pressures imposed by the social norms of the community they belong to.

While most studies have focused on stone tool use, interest has gradually been expanding towards the use of plant-based tools. Research into chimpanzee termite fishing in the Issa Valley (Tanzania), has also revealed that chimpanzees are targeting specific plant species and plant materials, where bark is the only material used, despite the greater abundance of other types of suitable raw materials (Almeida-Warren *et al.*, 2017). The fact that other populations elsewhere use several kinds, provides tentative evidence of a cultural tradition by the chimpanzees of Issa. Studies of transport distances combined with resource availability data, also suggests that there is some degree of forward planning, in which chimpanzees may source raw materials for tools on the way to the targeted mound (Almeida-Warren *et al.*, 2017). Similar evidence has also been found in the plant-based ant-dipping and honey-dipping technologies of the chimpanzees at Gashaka-Kwano (Nigeria) (Pascual-Garrido *et al.*, 2012).

Beyond extractive foraging technologies, researchers have also started studying the ethoarchaeology of chimpanzee nesting patterns (Hernandez-Aguilar, 2009; Stewart *et al.*, 2011). Nest-building is the only technological behavior that manifests in all ape and all chimpanzee populations (Stewart *et al.*, 2011). It's study, both in terms of architecture, re-use, and spatial distribution may hold important clues for understanding the evolution of spatial cognition, as well as reconstructing the evolution of hominin shelter.

Bearded Capuchins (*Sapajus Libidinosus*)

Capuchins are the most encephalized of the New World monkeys and range Central and South America (Fragaszy *et al.*, 2004). They are known for their manipulative skills and are the only New World monkeys known to use tools, and, out of all capuchin species, only the bearded capuchin (*S. libidinosus*) is a habitual tool-user (Ottoni and Izar, 2008). This species lives predominantly in the dry savannah-like habitats of Brazil, and engages in a variety of technological activities including cashew nut-cracking with stones, and using plant tools to access small prey (insects, lizards) from tree hollows and rock-cracks, and for honey extraction (Ottoni and Izar, 2008). The also practice stone-on-stone percussion, possibly to access mineral dietary supplements (Proffitt *et al.*, 2016).

Recent excavations of capuchin nut-cracking sites in Serra da Capivara (Brazil) have begun to tap into the capuchin archaeological record, revealing that this activity dates back to at least 700 years (Haslam *et al.*, 2016b). In Boa Vista (Brazil), studies on raw material selection in an experimental setting have provided evidence of hammerstone selection based on size, weight and friability (Visalberghi *et al.*, 2009). It also found that this community of capuchins was often able to assess the suitability of a raw material based on visual cues alone. When they were not able to do so (e.g., all tools were visually similar, but different weight), they would manually handle the stones before carrying one to the nut-cracking location. This suggest that capuchins engage in pre-tool-use planning and raw material selection, much like chimpanzees and our early ancestors (Visalberghi *et al.*, 2009).

More recently, it has been found that capuchins are capable of producing stone flakes as unintentional by-products of stone-on-stone percussion activities (Proffitt *et al.*, 2016). These flakes exhibit the same conchoidal fracturing characteristic of the Oldowan assemblages of our ancestors, which were long thought only possible through intentional and calculated knapping. This discovery

Author's personal copy

challenges current methods for identifying intentionality in the archaeological record, highlighting the potential for error when evaluating artefacts without further context. It also gives further support to the older hypothesis that early stone flaking may have first emerged as a bi-product of pounding activities, later developing into an intentional and systematic technology (Mora and De la Torre, 2005; Carvalho *et al.*, 2009).

To date, no primate archaeology studies have explored capuchin perishable technology. Plant tools-use by capuchins is often a one-off activity (e.g., flushing a lizard out of a crack in a rocky outcrop, using a nasal probe or toothpick), different from the intensive extractive foraging of chimpanzees' termite-fishing or ant-dipping in which chimpanzees may be engaged for hours at a time. It is perhaps more comparable to the use of sharpened sticks by the chimpanzees of Fongoli (Senegal) to immobilize and capture bushbabies sleeping in tree hollows (Pruetz and Bertolani, 2007). Nevertheless, the study of this more infrequent type of tool use can be beneficial to understand whether it also produces recognizable archaeological signatures and how the behavioral sequences compare to those of more intensive technological behaviors.

Burmese Long-Tailed Macaques (*Macaca Fascicularis Aurea*)

The newest of the non-human primate tool-users, is the long-tailed macaque. Tool-use has been mostly reported for one subspecies – *M. fascicularis aurea* – endemic to the coastal areas in southwestern Thailand and Myanmar (Gumert and Malaivijitnond, 2012). However, there are new reports adding the *Macaca fascicularis umbrosus* to this list (Pal *et al.*, 2008). Their marine-dependent ecological niche has shaped the development of unique behavioral adaptations for the extractive foraging of an impressive variety of different aquatic resources, such as oysters, snails, crabs, and sea-almonds, using stone tools (Gumert and Malaivijitnond, 2012; Falótico *et al.*, 2017). But inland, and like chimpanzees, they have also developed a lithic technology to crack oil palm nuts. Oil palms are not endemic to Thailand and were only introduced in the last decade. This demonstrates that the Burmese macaques have been able to quickly transfer their former technological skill-set, used in the foraging of marine resources, for the exploitation of novel resources located away from the shoreline (Luncz *et al.*, 2017a).

Their lithic technology comprises two main techniques: axe-hammering of sessile oysters, and pounding of unattached hard-shelled foods such as gastropods, crabs and nuts. For each technique, these macaques select tools with different morphological features and employ different manual skills, i.e., for prying oyster from rock, they use flat, axe-like tools held in a precision grip; for pounding, they use rounder and heavier stones held in a power grip (Gumert *et al.*, 2009).

A primate archaeology study on the use-wear patterns of the axes and hammer tools have revealed that these macaque technologies produce distinct damage patterns, and can be reliably identified through the analysis of impact marks left on the tools (Haslam *et al.*, 2013). This also means that this method can be used to study macaque surface tool assemblages and tool life-histories without direct observation, as well as interpret excavated remains.

Although transport distances of tools used in marine resource exploitation were recorded as far as 87 m, overall, stones were transported relatively short distances, and were mostly collected within one meter of the target resources (Haslam *et al.*, 2016c). Nevertheless, tools were often reused during sequential foraging bouts, and frequently transported between different prey items, indicating that individuals have a strong tendency to keep hold of a tool throughout a feeding session. Larger tools, such as hammers used for pounding, were transported much shorter distances and were often collected and abandoned within the immediate vicinity of the anvil stones. This behavior produces patterns of spatial association of hammers with anvils, as well as oyster-bearing rocks, which also increases the likelihood of tool re-use between individuals and foraging sessions (Haslam *et al.*, 2016c). As with chimpanzees and capuchins, these patterns of accumulation and re-use, produce a recognizable archaeological footprint.

The first excavated remains were uncovered in 2016, revealing an assemblage largely composed of axe-hammers used for processing mollusks, and one stone likely used for pounding activities (Haslam *et al.*, 2016a). While the remains were dated to only 65 years ago, the authors speculate, based on geological evidence and sea-level reconstruction, that sites found in the area may have been formed within the last 1,000 years or be older than 7,000 (Haslam *et al.*, 2016a). Future excavations will provide a clearer picture of the site formation processes in this area.

Future Directions

Primate archaeology is building a solid profile of tool-use and technology that transcends our anthropocentric existence. It has demonstrated that, like human populations in the past and present, other primates like chimpanzees, capuchins and long-tailed macaques produce a durable and recognizable archaeological record, and that processes of tool selection, reuse, tool-function, transport and accumulation in discrete locations are traits manifested amongst all of the major primate tool-users.

We now have comprehensive data on the stone tool behaviors and sites of three extant non-human primates, including dated archaeological records for all species (Haslam *et al.*, 2017). The field is now starting to expand to include analyses of perishable tools, which represents the most prevalent material used to make tools and is the only tool type that primates modify prior to use. In the future, it will be important to include studies of the perishable tools used by another great ape, the arboreal orangutan (*Pongo* sp.).

The unusual challenges of the primate environments, as well as the nature of the archaeological evidence have also spurred methodological innovations (e.g., using GIS to map tool surfaces, use of DistoX2 to map tool sites), which, in turn, are benefiting Paleolithic archaeological research by opening the way to standardized data collection across sites that will allow reliable

Author's personal copy

comparisons of technological records within the primate order (see Almeida-Warren *et al.*, in prep.). Likewise, ethoarchaeology of primate technology is providing valuable insights into how archaeological sites are formed and the dynamic processes shaping patterns of accumulation, and how these fit within the broader contexts of landscape use and resource exploitation (McGrew, 2010).

But Primate Archaeology is also pushing forward the studies of the Early Stone Age. Archaeologists focusing on the origins of technology started surveying Pliocene (>2.6 Ma) deposits in Africa by 2008. Based on a common denominator – pounding tools – the ubiquitous tool type shared by human and non-human primates and present across all chronological periods (Caruana *et al.*, 2014), parsimony suggested that the oldest assemblages would be composed, by large, of pounding tools. The finding of the Lomekian tools dating from 3.4 Ma (Harmand *et al.*, 2015) confirmed this premise and current work indicates that Pliocene Archaeology continues to expand (Tuosto *et al.*, 2017). As the earliest tool-makers moved from our genus *Homo* to earlier human ancestors, including the small brained Australopithecines, and archaeologists continue to excavate archaeological records of modern non-human primates, it becomes a real possibility to find (and recognize) records with millions of years that may belong to non-human primates. Moreover, with the contribution of Primate Archaeologists, paleoanthropologists are putting forward new hypotheses, challenging old queries about the origins of hunting and scavenging behavior (Thompson *et al.*, in press).

Importantly, the field of Primate Archaeology has also raised issues that can have an important effect on primate conservation. Recently, a call for studying threatned ape populations was made, urging the documentation and preservation of their cultural heritage (Hockings *et al.*, 2015).

Finally, while archaeological methods have so far only been applied within the primate order, they are by no means restricted to it. The goals of primate archaeology and the methodologies described in this article have equal potential in the study of many other tool-using species whether mammal, bird or fish. It will provide an invaluable tool to unveiling the true richness of animal cognitive, technological, and cultural behaviors, as well as the ecological contexts and evolutionary paths that have led to the emergence of technology throughout the animal kingdom.

References

Almeida-Warren, K., Sommer, V., Piel, A.K., Pascual-Garrido, A., 2017. Raw material procurement for termite fishing tools by wild chimpanzees in the Issa valley, Western Tanzania. American Journal of Physical Anthropology 164, 292–304.

Almeida-Warren, K., Braun, D.R., Matsuzawa, T., Carvalho, S., 2018a. Mapping primate archaeology: New tools for standardizing spatial data collection across the primate order. In: Proceedings of the XIVIlth Congress of the International Primatological Society, Nairobi.

Almeida-Warren, K., Braun, D.R., Regala, F.T., et al., 2018b. The ecology of chimpanzee technology: New approaches for modelling early hominin ranging patterns and resource exploitation. In: Proceedings of the XIVIlth Congress of the International Primatological Society, Nairobi.

Almeida-Warren, K., *et al.* in prep. The DistoX2 survey method: towards the standardisation of spatial data collection in primate archaeology.

Beck, B.B., 1980. Animal Tool Use: The Use and Manufacture of Tools by Animals. Garland, New York.

Benito-Calvo, A., Carvalho, S., Arroyo, A., Matsuzawa, T., De LaTorre, I., 2015. First GIS analysis of modern stone tools used by wild chimpanzees (*Pan troglodytes verus*) in Bossou, Guinea, West Africa. PLOS ONE 10, 1–22.

Boesch, C., Boesch, H., 1984. Possible causes of sex differences in the use of natural hammers by wild chimpanzees. Journal of Human Evolution 13, 415–440.

Braun, D.R., Plummer, T., Ditchfield, P., et al., 2008. Oldowan behavior and raw material transport: Perspectives from the Kanjera Formation. Journal of Archaeological Science 35, 2329–2345.

Braun, D.R., Plummer, T., Ferraro, J.V., Ditchfield, P., Bishop, L.C., 2009. Raw material quality and Oldowan hominin toolstone preferences: Evidence from Kanjera South, Kenya. Journal of Archaeological Science 36, 1605–1614.

Campbell, R., Carvalho, S., 2017. Tool use and manufacture in the last common ancestor of *Pan* and *Homo*. In: Muller, M., Wrangham, R., Pilbeam, D. (Eds.), Chimpanzees and Human Evolution. Harvard University Press, Harvard, pp. 602–644.

Caruana, M.V., Carvalho, S., Braun, D.R., et al., 2014. Quantifying traces of tool use: A novel morphometric analysis of damage patterns on percussive tools. PLOS ONE 9, 1–18.

Carvalho, S., Sousa, C., Matsuzawa, T., 2007. New nut-cracking sites in Diecké forest, Guinea: An overview of the etho-archaeological surveys. Pan African News 14 (1), 11–13.

Carvalho, S., Cunha, E., Sousa, C., Matsuzawa, T., 2008. Chaînes opératoires and resource-exploitation strategies in chimpanzee (*Pan troglodytes*) nut cracking. Journal of Human Evolution 55, 148–163.

Carvalho, S., Biro, D., McGrew, W.C., Matsuzawa, T., 2009. Tool-composite reuse in wild chimpanzees (*Pan troglodytes*): Archaeologically invisible steps in the technological evolution of early hominins? Animal Cognition 12, 103–114.

Carvalho, S., Cunha, E., Sousa, C., Matsuzawa, T., 2011. Extensive surveys of chimpanzee stone tools: From the telescope to the magnifying glass. In: Matsuzawa, T., Humle, T., Sugiyama, Y. (Eds.), The Chimpanzees of Bossou and Nimba, first ed. Springer Japan, Tokyo, pp. 145–155.

Carvalho, S.C., Braun, D.R., Harris, J.W.K., McGrew, W.C., Matsuzawa, T., 2012. Wild Chimpanzee (*Pan troglodytes*) and Pleistocene hominin raw material preference compared: Evidence from archaeological data and natural experiments. PaleoAnthropology 2012, A7–A8.

Carvalho, S., McGrew, W.C., 2012. The origins of the Oldowan: Why chimpanzees (*Pan troglodytes*) still are good models for technological evolution in Africa. In: Domínguez-Rodrigo, M. (Ed.), Stone Tools and Fossil Bones: Debates in the Archaeology of Human Origins. Cambridge University Press, Cambridge, pp. 222–244.

Carvalho, S., Matsuzawa, T., McGrew, W., 2013. From pounding to knapping: How chimpanzees can help us to model hominin lithics. In: Sanz, C.M., Call, J., Boesch, C. (Eds.), Tool Use in Animals: Cognition and Ecology. Cambridge University Press, Cambridge, pp. 225–241.

Carvalho, S., Beardmore-herd, M., in press. Technological origins: Primate perspectives and Early hominin tool use. Oxford Research Encyclopedia of African History.

Delagnes, A., Roche, H., 2005. Late Pliocene hominid knapping skills: The case of Lokalalei 2C, West Turkana, Kenya. Journal of Human Evolution 48, 435–472.

De la Torre, I., 2011. The origins of stone tool technology in Africa: A historical perspective. Philosophical Transactions of the Royal Society of London B: Biological Sciences 366, 1028–1037.

Falótico, T., Spagnoletti, N., Haslam, M., et al., 2017. Analysis of sea almond (*Terminalia catappa*) cracking sites used by wild Burmese long-tailed macaques (*Macaca fascicularis aurea*). American Journal of Primatology 79, 1–8.

Fragaszy, D., Izar, P., Visalberghi, E., Ottoni, E. B., De Oliveira, M. G. 2004. Wild capuchin monkeys (*Cebus libidinosus*) use anvils and stone pounding tools. *American Journal of Primatology*, 64(4), 359–366.

Goodall, J., 1963. Feeding behaviour of wild chimpanzees. Symposia of the Zoological Society of London 10, 39–48.

Author's personal copy

Gumert, M.D., Malaivijitnond, S., 2012. Marine prey processed with stone tools by burmese long-tailed macaques (*Macaca fascicularis aurea*) in intertidal habitats. American Journal of Physical Anthropology 149, 447–457.
Gumert, M., Kluck, M., Malaivijitnond, S., 2009. The physical characteristics and usage patterns of stone axe and pounding hammers used by Long-tailed Macaques in the Andaman Sea region of Thailand. American Journal of Primatology 608, 594–608.
Harmand, S., Lewis, J.E., Feibel, C.S., et al., 2015. 3.3-million-year-old stone tools from Lomekwi 3, West Turkana, Kenya. Nature 521, 310–315.
Haslam, M., Hernandez-Aguílar, A., Ling, V., et al., 2009. Primate archaeology. Nature 460, 339–444.
Haslam, M., Gumert, M.D., Biro, D., Carvalho, S., Malaivijitnond, S., 2013. Use-wear patterns on wild macaque stone tools reveal their behavioural history. PLOS ONE 8, 1–8.
Haslam, M., Hernandez-Aguilar, R.A., Proffitt, T., et al., 2017. Primate archaeology evolves. Nature Ecology and Evolution 1, 1431–1437.
Haslam, M., Luncz, L., Pascual-garrido, A., et al., 2016a. Archaeological excavation of wild macaque stone tools. Journal of Human Evolution 96, 134–138.
Haslam, M., Luncz, L.V., Staff, R.A., et al., 2016b. Pre-columbian monkey tools. Current Biology 26, R521–R522.
Haslam, M., Pascual-garrido, A., Malaivijitnond, S., Gumert, M., 2016c. Stone tool transport by wild Burmese long-tailed macaques (*Macaca fascicularis aurea*). Journal of Archaeological Science: Reports 7, 408–413.
Heeb, B., 2008. Paperless caving – An electronic cave surveying system. In: Proceedings of the IV European Speleological Congress. Lans-en-Vercors, France, pp. 130–133.
Hernandez-Aguilar, R.A., 2009. Chimpanzee nest distribution and site reuse in a dry habitat: Implications for early hominin ranging. Journal of Human Evolution 57, 350–364.
Hernandez-Aguilar, R.A., Moore, J., Pickering, T.R., 2007. Savanna chimpanzees use tools to harvest the underground storage organs of plants. Proceedings of the National Academy of Sciences of the United States of America 104 (49), 19210–19213.
Hockings, K.J., McLennan, M.R., Carvalho, S., et al., 2015. Apes in the Anthropocene: Flexibility and survival. Trends in Ecology and Evolution 30, 215–222.
Hovers, E., Braun, D.R., 2009. Interdisciplinary Approaches to the Oldowan. Springer, New York.
Joulian, F., 1994. Culture and material culture in chimpanzees and early hominids. In: Roeder, J.J., Thierry, B., Anderson, J.R., Herrenschmidt, N. (Eds.), In: Proceedings of the XIVth Congress of the International Primatological Society, Current Primatology Vol. II: Social Development, Learning and Behaviour. Universite Louis Pasteur, Strasbourg, pp. 404–497.
Joulian, F., 1996. Comparing chimpanzee and early hominid techniques: Some contributions to cultural and cognitive questions. In: Mellars, P., Gibson, K.R. (Eds.), Modelling the Early Human Mind. McDonald Institute for Archaeological Research, Cambridge, pp. 173–189.
Ling, V., Hernandez-Aguilar, A., Haslam, M., Carvalho, S., 2009. The origins of percussive technology: A smashing time in Cambridge. Evolutionary Anthropology 18, 48–49.
Luncz, L.V., Proffitt, T., Kulik, L., Haslam, M., Wittig, R.M., 2016. Distance-decay effect in stone tool transport by wild chimpanzees. Proceedings of the Royal Society B: Biological Sciences 283, 20161607.
Luncz, L.V., Svensson, M.S., Haslam, M., Malaivijitnond, S., 2017a. Technological response of wild macaques (*Macaca fascicularis*) to anthropogenic change. International Journal of Primatology 38, 872–880.
Luncz, L.V., Tan, A., Haslam, M., et al., 2017b. Resource depletion through primate stone technology. Elife 6, e23647.
Luncz, L.V., Sirianni, G., Mundry, R., Boesch, C., 2018. Costly culture: Differences in nut-cracking efficiency between wild chimpanzee groups. Animal Behaviour 137, 63–73.
Malaivijitnond, S., Lekprayoon, C., Tandavanittj, N., et al., 2007. Stone-tool usage by Thai long-tailed macaques (*Macaca fascicularis*). American Journal of Primatology 69, 227–233.
McGrew, W.C., 2004. The Cultured Chimpanzee: Reflections on Cultural Primatology. Cambridge University Press, Cambridge.
McGrew, W.C., Marchant, L.F., Hunt, K.D., 2007. Etho-archaeology of manual laterality: Well digging by wild chimpanzees. Folia Primatologica 78, 240–244.
McGrew, W.C., 2010. In search of the last common ancestor: New findings on wild chimpanzees. Philosophical Transactions of the Royal Society of London B 365, 3267–3276.
McPherron, S.P., Alemseged, Z., Marean, C.W., et al., 2010. Evidence for stone-tool-assisted consumption of animal tissues before 3.39 million years ago at Dikika, Ethiopia. Nature 466, 857–860.
Mercader, J., Barton, H., Gillespie, J., et al., 2007. 4300-year-old chimpanzee sites and the origins of percussive stone technology. Proceedings of the National Academy of Sciences of the United States of America 104, 3043–3048.
Mercader, J., Panger, M., Boesch, C., 2002. Excavation of a chimpanzee stone tool site in the African rainforest. Science 296, 1452–1455.
Mora, R., De la Torre, I., 2005. Percussion tools in Olduvai Beds I and II (Tanzania): Implications for early human activities. Journal of Anthropological Archaeology 24, 179–192.
Ottoni, E.B., Izar, P., 2008. Capuchin monkey tool use: Overview and implications. Evolutionary Anthropology 17, 171–178.
Pal A., Kumara H.N., Mishra P.S., Velankar A.D., Singh M., 2008. Extractive foraging and tool-aided behaviors in the wild Nicobar long-tailed macaque (*Macaca fascicularis umbrosus*). *Primates*, 59(2), 173–183.
Panger, M.A., Brooks, A.S., Richmond, B.G., Wood, B., 2002. Older than the Oldowan? Rethinking the emergence of hominin tool use. Evolutionary Anthropology 11, 235–245.
Pascual-Garrido, A., Buba, U., Nodza, G., Sommer, V., 2012. Obtaining raw material: Plants as tool sources for Nigerian chimpanzees. Folia Primatologica 83, 24–44.
Pascual-Garrido, A., Sommer, V., Almeida-Warren, K., 2016. Raw material procurement for termite fishing tools in wild chimpanzees. PeerJ Preprints 4, e1844v1.
Proffitt, T., Luncz, L.V., Falótico, T., et al., 2016. Wild monkeys flake stone tools. Nature 539, 85–88.
Proffitt, T., Luncz, V.L., Malaivijitnond, S., et al., 2018. Analysis of wild macaque stone tools used to crack oil palm nuts. Royal Society: Open Science 4, 171904.
Proffitt, T., Haslam, M., Mercader, J., Boesch, C., Luncz, L.V., in press. Revisiting Panda 100, the first archaeological chimpanzee nut cracking site. Journal of Human Evolution.
Pruetz, J.D., Bertolani, P., 2007. Savanna chimpanzees, *Pan troglodytes verus*, hunt with tools. Current Biology 17, 412–417.
Redovniković, L., Stančić, B., Cetl, V., 2016. Comparison of different methods of underground survey. In: Proceedings of the International Symposium on Engineering Geodesy. Varaždin, Croatia, pp. 465–472.
Renfrew, C., Bahn, P., 2015. Archaeology Essentials: Theories, Methods, and Practice, third ed. Thames & Hudson.
Roche, H., 2016. Behavioural biology: Stones that could cause ripples. Nature 539, 34–35.
Sakura, O., Matsuzawa, T., 1991. Flexibility of wild chimpanzee nut-cracking behavior using stone hammers and anvils: An experimental analysis. Ethology 87, 237–248.
Sanz, C., Call, J., Morgan, D., 2009. Design complexity in termite-fishing tools of chimpanzees (*Pan troglodytes*). Biology Letters 5, 293–296.
Sanz, C.M., Morgan, D.B., 2009. Flexible and persistent tool-using strategies in honey-gathering by wild chimpanzees. International Journal of Primatology 30, 411–427.
Sanz, C.M., Morgan, D.B., 2010. The complexity of chimpanzee tool-use behaviours. In: Lonsdorf, E.V., Ross, S.R., Matsuzawa, T., Goodall, J. (Eds.), The Mind of the Chimpanzee: Ecological and Experimental Perspectives. University of Chicago Press, Chicago, pp. 127–140.
Sept, J., 1992. Was there no place like home? A new perspective on early hominid archaeological sites from the mapping of chimpanzee nests. Current Anthropology 33, 187–207.
Shea, J.J., 2016. Stone Tools in Human Evolution: Behavioral Differences Among Technological Primates. Cambridge University Press, Cambridge.
Sirianni, G., Mundry, R., Boesch, C., 2015. When to choose which tool: Multidimensional and conditional selection of nut-cracking hammers in wild chimpanzees. Animal Behaviour 100, 152–165.
Stewart, F.A., Piel, A.K., McGrew, W.C., 2011. Living archaeology: Artefacts of specific nest site fidelity in wild chimpanzees. Journal of Human Evolution 61, 388–395.
Stout, D., Quade, J., Semaw, S., Rogers, M.J., Levin, N.E., 2005. Raw material selectivity of the earliest stone toolmakers at Gona, Afar, Ethiopia. Journal of Human Evolution 48, 365–380.
Sugiyama, Y., Koman, J., 1979. Tool-using and -making behavior in wild chimpanzees at Bossou, Guinea. Primates 20, 513–524.
Thompson, J., Carvalho, S., Marean, C., Alemseged, Z., in press. The origins of the human predatory pattern: The transition to large animal exploitation by early hominins. Current Anthropology.
Toth, N., Schick, K., 2009. The Oldowan: The tool making of early hominins and chimpanzees compared. Annual Review of Anthropology 38, 289–305.
Toth, N., Schick, K., Semaw, S., 2006. A comparative study of the stone tool-making skills of Pan, Australopithecus, and Homo sapiens. In: Toth, N., Schick, K. (Eds.), The Oldowan: Case Studies Into the Earliest Stone Age. Stone Age Institute Press, Gosport, IN, pp. 155–222.
Trimmis, K.P., 2015. Fear of the light: Mapping modern cave use strategies in Kythera Island caves. Ethnoarchaeology 7, 141–156.

Author's personal copy

Trimmis, K.P., 2018. Paperless mapping and cave archaeology: A review on the application of DistoX survey method in archaeological cave sites. Journal of Archaeological Science: Reports 18, 399–407.
Tuosto, K., Ascoli, S., Braun, D.R., et al., 2017. Selectivity among Early Pleistocene hominins: New evidence from the Koobi Fora Formation. PaleoAnthropology 2017, A7–A8.
van Diggelen, F., Enge, P., 2015. The world's first GPS MOOC and worldwide laboratory using smartphones. In: Proceedings of the 28th International Technical Meeting of the Satellite Division of the Institute of Navigation (ION GNSS+ 2015). Tampa, Florida, pp. 361–369.
van Schaik, C.P., Ancrenaz, M., Borgen, G., et al., 2003. Orangutan cultures and the evolution of material culture. Science 299, 102–105.
Visalberghi, E., Addessi, E., Truppa, V., et al., 2009. Selection of effective stone tools by wild bearded capuchin monkeys. Current Biology 19, 213–217.
Whiten, A., Goodall, J., McGrew, W.C., et al., 1999. Cultures in chimpanzees. Nature 399, 682–685.
Wynn, T., McGrew, W.C., 1989. An ape's view of the Oldowan. Man 383–398.
Wynn, T., Hernandez-Aguilar, R.A., Marchant, L.F., McGrew, W.C., 2011. "An ape's view of the oldowan" revisited. Evolutionary Anthropology 20, 181–197.

Further Reading

Biro, D., Haslam, M., Rutz, C., 2013. Tool use as adaptation. Philosophical Transactions of the Royal Society of London B Biological Sciences 368 (1630). https://doi.org/10.1098/rstb.2012.0408.
Biro, D., Inoue-Nakamura, N., Tonooka, R., et al., 2003. Cultural innovation and transmission of tool use in wild chimpanzees: Evidence from field experiments. Animal Cognition 6, 213–223.
Buchanan, B., O'Brien, M.J., Eren, M.I., 2018. Convergent Evolution in Stone-Tool Technology. MIT Press, Cambridge, MA.
Marchant, L.F., McGrew, W.C., 2005. Percussive technology: Chimpanzee baobab smashing and the evolutionary modeling of hominid knapping. In: Roux, V., Bril, B. (Eds.), Stone Knapping: The Necessary Conditions for a Uniquely Human Behaviour. McDonald Institute for Archaeological Research, Cambridge, pp. 341–350.
Matsuzawa, T., 2011. Field experiments of tool-use. In: Matsuzawa, T., Humle, T., Sugiyama, Y. (Eds.), The Chimpanzees of Bossou and Nimba, first ed. Springer Japan, Tokyo, pp. 145–155.
Mercader, J., 2002. Under the Canopy: The Archaeology of Tropical Rain Forests. Rutgers University Press, New Jersey.
Muller, M.N., 2017. Chimpanzees and Human Evolution. Harvard University Press, Harvard.
Renfrew, C., Bahn, P., 2012. Archaeology: Theories, Methods, and Practice, sixth ed. Thames and Hudson, London.
Toth, N., Schick, K., 2006. The Oldowan: Case Studies into the Earliest Stone Age. Stone Age Institute Press, Gosport, IN.
Sanz, C.M., Call, J., Boesch, C., 2013. Tool Use in Animals: Cognition and Ecology. Cambridge University Press, Cambridge.

Relevant Websites

http://www.oum.ox.ac.uk/visiting/current.htm–O.U.M.N.H. Exhibitions –Oxford University Museum of Natural History.
https://primobevolab.web.ox.ac.uk–Primate Models for Behavioural Evolution Lab.
https://www.scientificamerican.com/article/ancient-stone-tools-force-rethinking-of-human-origins/–Scientific American –Ancient Stone Tools Force Rethinking of Human Origins.
https://www.sciencenews.org/article/aping-stone-age–Science News –Aping the Stone Age.

Journal of Archaeological Science: Reports 35 (2021) 102688

Contents lists available at ScienceDirect

Journal of Archaeological Science: Reports

journal homepage: www.elsevier.com/locate/jasrep

The DistoX2: A methodological solution to archaeological mapping in poorly accessible environments

Katarina Almeida-Warren [a,b,1,*], David R. Braun [c,2], Susana Carvalho [a,b,d,e,2]

[a] Primate Models for Behavioural Evolution Lab, Institute of Cognitive and Evolutionary Anthropology (ICEA), University of Oxford, Oxford, UK
[b] Interdisciplinary Center for Archaeology and Evolution of Human Behaviour (ICArEHB), Universidade do Algarve, Faro, Portugal
[c] Center for the Advanced Study of Human Paleobiology, Anthropology Department, George Washington University, Washington, DC, USA
[d] Centre for Functional Ecology (CEF), Coimbra, Portugal
[e] Gorongosa National Park, Sofala, Mozambique

ARTICLE INFO

Keywords:
Low-cost spatial mapping
Point provenience
Archaeological recording
Surveying
Field methods

ABSTRACT

Spatial information is crucial to archaeological field research. From the plane-table to the total station, recent technological advances have enabled data collection to become fully digital and highly accurate. Nevertheless, the recent expansion of archaeological expeditions to novel environments often incompatible with modern mapping equipment, e.g. tropical forests or ephemeral shorelines, calls for further methodological innovations. Such projects, as well as those under logistic or financial limitations, are still largely reliant on more time consuming, less accurate, traditional approaches, e.g. offset or tape and compass methods. The DistoX2 is a digital, highly portable, and versatile hand-held instrument originally developed for speleological surveys where total stations and DGPSs are not feasible. However, the potential of the DistoX2 system as a spatial mapping tool in above-ground contexts has been surprisingly overlooked. Here, we present a first assessment of the applicability of the DistoX2 for archaeological mapping in non-speleological environments. We investigate precision and accuracy in controlled above-ground settings relative to two common methods of data collection – total station, and tape and compass. We test the relative precision of the DistoX2 when mounted on a tripod or operated in hand-held mode and discuss its applicability, and potential combined used, in the context of other increasingly popular methods – GNSS and SfM photogrammetry. With a mean error of ≈5.00 cm for horizontal readings and ≈2.00 cm for vertical readings, the DistoX2 is considerably more accurate than the tape and compass method (μ ≈ 67.00 cm horizontal; μ ≈ 3.00 cm vertical). While the DistoX2 exceeds the error thresholds of projects that require high spatial sensitivity (e.g. Palaeolithic excavations), it provides a reliable, low-cost and more accurate alternative to many projects that resort to more traditional methods. This fills an existent methodological and financial gap amongst the growing diversity of archaeological expeditions.

1. Introduction

Spatial mapping has been a key component of archaeological research and documentation for over 100 years (Wheatley and Gillings, 2002). It helps determine the spatial relationships between archaeological objects and features, and the stratigraphic contexts in which they are found, crucial for the interpretation of an archaeological site or assemblage and its possible relationship to others (McPherron, 2005).

While mapping techniques in accessible urban or open environments are well established, it is not standardized throughout all archaeological settings – ranging from highly accurate total station systems, to analogue tape and compass methods. The pursuit of a universal methodology, compatible with all archaeological environments, has become more urgent in the last decades, as archaeological research expands to the exploration of cave sites, tropical forests and non-human primate records (Haslam et al., 2009; Mercader, 2002a,b, Trimmis, 2015, 2018; Carvalho and Almeida-Warren, 2019). The challenges of these new environments, particularly in terms of accessibility, have made the

* Corresponding author at: Primate Models for Behavioural Evolution Lab, Institute of Cognitive and Evolutionary Anthropology (ICEA), University of Oxford, 64 Banbury Rd., Oxford, OX1 6PN, UK.
E-mail address: katarina.almeida-warren@anthro.ox.ac.uk (K. Almeida-Warren).
[1] This is the main author and contributor.
[2] These authors contributed equally to this work.

https://doi.org/10.1016/j.jasrep.2020.102688
Received 26 June 2020; Received in revised form 9 November 2020; Accepted 20 November 2020
Available online 28 December 2020
2352-409X/© 2020 The Authors. Published by Elsevier Ltd. This is an open access article under the CC BY-NC-ND license (http://creativecommons.org/licenses/by-nc-nd/4.0/).

implementation of many modern archaeological mapping methods unfeasible, thus limiting the potential of comparison across different datasets.

Mapping in the pre-digital era was achieved using a variety of methods and tools such as the plane table, the manual theodolite, or varying combinations of measuring tapes, levelling aids, and a compass (Dibble, 1987; Historic England, 2017; Wheatley and Gillings, 2002). While some of these methods are still used today, technological developments in engineering and Global Navigation Satellite Systems (GNSS) in the last decades have revolutionized the speed, accuracy and automation of mapping techniques, evolving from simple analogue approaches, to fully digital total station theodolite (TST) systems, and, more recently, to Real-Time Kinematic (RTK) GNSS, terrestrial laser scanning (TLS), and photography-based surveys, such as Structure from Motion (SfM) photogrammetry (Dibble, 1987; Jo and Hong, 2019; Kjellman, 2012; Martínez-Fernández et al., 2020; McPherron, 2005; Pearson et al., 2015; Roosevelt, 2014; Willis et al., 2016).

However, archaeology in extreme or poorly accessible environments, such as underground cave systems with narrow passages and densely forested landscapes with difficult terrain, has until recently been largely limited to the tape and compass method (Almeida-Warren et al., 2018; Trimmis, 2018). Also known as the distance-azimuth method, it typically involves the use of one measuring tape to measure the horizontal distance between a fixed reference point (datum) and the object of interest, a second tape to measure the vertical distance between the first tape and the object, and a compass to determine the direction of the object from the datum relative to North (Carvalho and Almeida-Warren, 2019). An alternative method (tape-compass-clinometer) measures the direct distance between the datum and the object, replacing the second tape with a clinometer to determine the inclination of the first tape (Ballesteros et al., 2013; Redovniković et al., 2014). While highly portable and effective, these methods lack the precision of more contemporary archaeological methods and are more time consuming both at the data collection level, recorded by hand, as well as data entry from paper to a digital format.

The limitations of such methods are particularly acute in primate archaeological research where standardized methods are needed to make meaningful comparisons between human and non-human primate records within an evolutionary context. Primate archaeologists study living non-human primates often in remote environments, such as densely vegetated high-canopy forests requiring daily travel of several kilometres on foot, and ephemeral shorelines where data collection is conditioned by the tides (Carvalho et al., 2008; Carvalho and Almeida-Warren, 2019; Haslam et al., 2016). They also face the additional challenge of working at 'living sites', which are still visited by the study species, often requiring minimal disturbance and rapid removal of equipment when subjects appear (Carvalho et al., 2011).

While a critical part of primate archaeology research deals with extant technological behaviour, the research questions mirror many of the spatial queries of traditional archaeology: how are archaeological objects spatially related to each other? How do assemblages change over time? Is there inter and intra-site variation? (Carvalho et al., 2008; Carvalho and Almeida-Warren, 2019; Falótico et al., 2019). Thus, like with traditional archaeology, precision in these contexts is essential for accurate mapping of archaeological objects and features.

The DistoX is a customized hand-held electronic laser distance measurer (e.g. Leica Disto A3; Leica Disto X310) retrofitted with a compass and clinometer. It was developed for mapping cave systems to replace the traditional time-consuming and labour-intensive method of manual measurements and paper sketches (Heeb, 2008). It is a compact (55 × 31 × 122 mm), light-weight instrument (150 g), which can be paired with an Android or Windows device, making it a highly versatile fully digital system for spatial data collection (Heeb, 2014). Further technical information including assembly instructions can be found here: https://paperless.bheeb.ch/.

Performance tests in cave settings have revealed that the DistoX system (X1 model) is considerably more accurate than the tape and compass method, and presents readings more comparable to total station measurements (Ballesteros et al., 2013; Redovniković et al., 2014). More recently, the DistoX1 has successfully been used to document archaeological remains found in caves on Kithera Island and Kastoria in Greece (Trimmis, 2018, 2015).

Nevertheless, while the DistoX has been adopted as one of the main speleological tools for mapping cave systems (see Trimmis, 2018), its potential in archaeological settings has yet to be fully explored. The portable and relatively affordable nature of the DistoX system make it a suitable candidate to replace the tape and compass method, with the potential to bring archaeological data collection in challenging environments to a similar level and quality as that seen in major archaeological research projects around the world. The DistoX system could also benefit those archaeological projects with a limited budget, where a total station or other modern alternative equipment, although viable in practice, may be too costly financially (Table 1).

To date, very little empirical literature exists on the performance of the DistoX method for capturing spatial provenience information. All equipment tests have, so far, been restricted to cave settings, and have provided limited statistical assessments (see Ballesteros et al., 2013; Redovniković et al., 2014, 2016). Here we test the latest model of the DistoX – DistoX2 – in controlled open-air settings. We assess performance in terms of precision, as well as accuracy relative to two common methods of spatial data collection – total station, and tape and compass.

Table 1
Practical details of common mapping methods compared to the DistoX2.

Method	Weight	North	Functionality	Cost
Tape and compass	1–3 Kg	Magnetic North	Analogue or Semi-digital	$20–200[1]
Total station	4–10 Kg	Programmed by user	Fully digital	$4,000–10,000
GNSS/RTK GNSS	2–10 Kg	True North	Fully digital	$1,500–20,000
Photogrammetry	1–8 Kg	Programmed by user	Fully digital	$200–1,500
DistoX2	0.5–3[2] Kg	Magnetic North	Fully digital	$280–500[2]

[1] if using a digital compass
[2] depending on digital accessories chosen (e.g. mobile or tablet device), and whether tripod is included



Fig. 1. DistoX2 and accessories: a) DistoX2 instrument (Photo: F. Tátá Regala); b) Disto calibration block (Photo: F. Tátá Regala); c) Custom-made tripod adapter (Photo: K. Almeida-Warren).

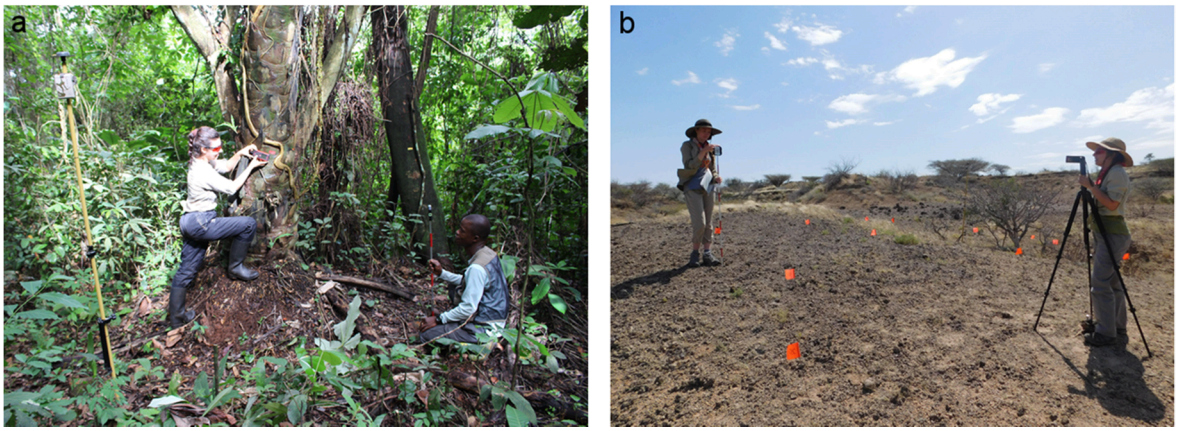


Fig. 2. DistoX2 setup options: a) Hand-held mode (Photo: V. Mamy); b) Tripod mode (Photo: C. Daniel).

1.1. The DistoX2

1.1.1. Technical summary

The DistoX2 is the latest model of the DistoX system (Fig. 1a). It is a hand-held electronic measuring device composed by a Leica DistoX310 laser distance meter retrofitted with a tilt-compensated (3D) digital compass, clinometer, and a Bluetooth module for wireless data transfer (Heeb, 2014). It was originally developed in 2008 as a paperless alternative to mapping the internal structures of caves, where more typical digital spatial mapping instruments, such as GPS/GNSS modules and total stations, are not viable (Heeb, 2008; Redovniković et al., 2014; Trimmis, 2018). Spatial mapping in forested environments, presents similar challenges to the cave settings – total stations are too heavy and bulky to carry manually in dense vegetation over large distances, and canopy cover is often too dense to achieve GPS readings at a sufficiently low resolution for accurate spatial mapping.

The DistoX2 provides instantaneous distance, inclination and azimuth readings. It can be used as a hand-held device without other supporting accessories or mounted on a tripod for additional stability; and measurements can be taken directly towards the target object or aimed at a reflector of fixed height placed on the target location (Fig. 2). It can function as a stand-alone instrument, but its performance is optimal when used in tandem with an external mobile device such as a phone or tablet (Redovniković et al., 2016). Data can be uploaded via Bluetooth connection onto a compatible data management application (Heeb, 2014). The currently available applications, both open-access, are PocketTopo for Windows OS (Heeb, 2008), and TopoDroid for Android OS (Corvi, 2016), which allow data management and organisation by project, data visualisation, and export in a variety of formats including .csv and .klm. These applications were designed for mapping speleological contexts, but can be adapted to archaeological settings (e.g. Trimmis, 2015, 2018), although a tailor-made application that integrates common archaeological data collection specifications (e.g. grid systems, digital finds/feature forms, conversion between angle readings and XYZ measurements) would help make the data collection process more streamlined. General DistoX2 technical specifications are presented in Table 2.

Table 2
Disto X2 technical specifications as per Heeb (2014).

	Range	Resolution	Precision
Distance	0.05 – >100 m	Magnetic North	0.2 cm[1]
Azimuth	0 – 360°[2]	0.1°	0.5° RMS[3]
Inclination	±90°	0.1°	0.5° RMS[3]

[1] up to 10 m.
[2] relative to magnetic North.
[3] after successful calibration.

In order to achieve the best results, regular calibration of the DistoX2 is essential to correct for spatial and temporal magnetic shifts, particularly when starting a project in a different geographic location or after long periods of inactivity (Heeb, 2013). Calibration is possible free-hand or with a calibration block (Fig. 1b) and the calibration function available on the Android or Windows software interface (Heeb, 2013; Regala, 2016, 2015).

It is important to note that azimuth readings are always relative to magnetic North and need to be corrected for magnetic declination (deviation from true North) (Redovniković et al., 2014). Magnetic declination fluctuates over time and is different depending on geographic location. Historic and current magnetic declination data can be consulted by coordinate location on the National Centers for Environmental Information website (https://www.ngdc.noaa.gov/geomag-web/).

1.1.2. Previous tests

Performance tests of the DistoX1 system in cave settings relative to the tape, compass and clinometer (TCC) method, and the total station revealed that, although less accurate than the total station, the DistoX1 is considerably more accurate than the TCC method (Ballesteros et al., 2013; Redovniković et al., 2014). Tests in El Pindal Cave (Spain), demonstrated that the DistoX1 measurements deviated from the total station readings by 0.72 m ± 0.04%, while the TCC measurements deviated by 9.18 m ± 11.64% (Ballesteros et al., 2013). Tests in cave Veternica (Croatia) mapping out a series of points along a 565.44 m traverse showed TCC deviations of up to 2.06 m in vertical distance from the total station baseline, while the DistoX1 only diverged by a maximum of 0.56 m (Redovniković et al., 2014). Horizontal distance error presented more exaggerated results, with TCC error ranging 0 – 30 m, and the DistoX1 error remaining consistently under 0.5 m. While not specified in the paper, the wide range for TCC error is likely due to the fact that the effect of angle measurement error and resolution (i.e. from compass and clinometer) is exacerbated as the distance from the measuring station increases, whereby at 0 m angle error would be negligible, but at 500 m the divergence from the true position would be considerable. One would expect a similar effect on the DistoX1, albeit to a lesser degree due to greater instrument accuracy and precision. However, data of these measurements were not provided in the publication.

Only one article has been published so far on the performance of the latest model of the DistoX – DistoX2 – where it was compared to the total station using two different post-processing applications (Redovniković et al., 2016). Both tests revealed similar results, with DistoX2 error ranging 0.07 – 0.24 m for horizontal measurements, and 0.00 – 0.03 m for vertical measurements. However, the test was only conducted on 14 physical control points, 8 of which were included in the study. The remainder of the publication focuses on comparing point clouds

generated from photogrammetry using the 8 control points taken with the DistoX2, with points clouds produced from the equivalent total station data. In this case, for the 900 000 common generated points, measurement deviation between the DistoX2 and the total station point clouds was found to be largely under 0.04 m (Redovniković et al., 2016).

While previous empirical work has gone some way in testing the DistoX performance, and providing evidence supporting the DistoX as a better system than the tape and compass method for spatial mapping in cave settings, it has relied on small sample sizes (between 2 and 38 test points) and all have used different methodological protocols, which limits the potential/feasibility of collating and homogenizing the various results. Given the potential of the DistoX system as a spatial mapping method in above-ground scenarios we conduct a series of tests in controlled outdoor settings to assess the DistoX2 performance relative to the total station and tape and compass methods. We also test the relative precision of the DistoX2 when mounted on a tripod, as compared to when operated in hand-held mode. This data will not only complement the current literature on the performance of the DistoX system, but will also assess its capacity for spatial data collection across all non-aquatic environments, and for bridging the gap in methodological discrepancies between the optimal and the most challenging archaeological settings.

2. Methods

We tested the DistoX2 at two main levels: precision in both hand-held and tripod modes; and accuracy relative to the total station and to the tape and compass method. Tests were conducted in three geographically distinct open-air settings: Bossou, Guinea (L1); Koobi Fora Base camp, East Turkana, Kenya (L2); and University Parks, Oxford, United Kingdom (L3). L1 and L2 are field sites where the DistoX2 has been used for recording modern wild chimpanzee tool-use sites and Plio-Pleistocene archaeological surface assemblages, respectively. All DistoX2 measurements were taken with the aid of a reflector to avoid interference caused by low-lying vegetation or other foreground objects obstructing line of sight. Test points were allocated to cover a range of distances and location within a 15-metre radius of the DistoX2 position and were marked with numbered pin-flags. The DistoX2 was calibrated with a calibration block at each measurement location prior to tests. Data was imported and processed on a Samsung Android tablet using the TopoDroid application (Corvi, 2016).

2.1. Precision

The precision test served to determine variation between successive measurements taken of the same point. This helps establish the level of relative error a single measurement might have. While the technical specifications of the DistoX2 provide information regarding instrument precision, we wanted to verify this data in a real-world scenario, and to compare results between the two different device setups. Test data were collected from a total of 100 points – 50 points were documented in L1 using hand-held setup whereby the researcher was manually holding the DistoX2 positioned on the established datum; the other 50 points were documented in L3 using the tripod setup whereby the DistoX2 mounted on a tripod and set on a 5-second timer so the researcher could release their hands from the device before the measurement was taken. Each of the 100 points was recorded successively 5 times to determine device precision.

We designed a custom-made tripod mount with the help of Science Oxford, composed of a 3D-printed piece and non-magnetic bolts for fixing (Fig. 1c). See Appendix A for details on the design and a link to the 3D-model where downloads for printing are freely available.

2.2. Accuracy

Accuracy tests served to assess the performance and measurement errors of the DistoX2. In this case we use the total station measurements as a baseline and statistically compared the deviation in measurements (absolute error) of the DistoX2 with that of the tape and compass method in relation to a total station system. The DistoX2 accuracy relative to the total station was tested at L2 and L3. At L2 we collected 50 test points using a Leica Builder 505 (angular accuracy = 5″; distance accuracy = 2.0 mm) with a CPR111 True-Zero prism (constant = 0.0 mm; centring accuracy: 2.0 mm). At L3 we collected another 50 test points using a Leica TS06 (angular accuracy = 2″; distance accuracy = 1.5 mm), paired with a GPR111 prism (constant = 0.0 mm; centring accuracy: 2.0 mm). All total station points were recorded using the prism except for the datum and Disto position which were recorded by direct laser. Because control points with precise coordinate data were unavailable at either of the locations, the total station North was set to the magnetic North readings of the DistoX2, to avoid introducing further error from an additional measuring device. For this reason, we did not have to correct the DistoX2 readings for magnetic declination.

Tape and compass data were only collected for the 50 test points established at L3. We used a standard 30 m tape (resolution = 0.2 cm) to measure horizontal distance, a 5 m retractable tape (resolution = 0.1 cm) to measure vertical distance, and the in-built 3D digital compass of a Garmin Oregon 700 (resolution = 1.0°; reported accuracy = 2.0°, calibrated before use) to measure azimuth. The north reference was set to the default – true north – and azimuth readings were converted to a magnetic north reference based on declination information for the date of recording (Magnetic Model EEM2017 version 0.914, Declination = −0.752 decimal degrees). A string, plumb-bob and spirit level were used to keep the horizontal tape level to the datum. Although we recognize that using a digital compass with greater resolution and accuracy would directly improve the accuracy of this method, we wanted to reproduce a realistic scenario, using the equipment that is typically employed.

2.3. Statistical analyses

All statistical analyses were calculated in RStudio Version 1.1.383 (R Studio Team, 2017, 2017). We employed non-parametric tests as most data distributions were returned as not normal following a Shapiro-Wilk tests in R ('shapiro.test()' function). For the precision tests we calculate the average deviation from the mean for each set of five measurements taken for each test point. Comparisons of average deviation between the two methods were computed using a two-sample Wilcoxon signed-rank test (non-parametric equivalent to the two-sample *t*-test). For accuracy tests, comparison of errors between the different methods was computed with paired Wilcoxon tests. Errors were calculated as the absolute difference ($|\Delta|$) between each pair of measurements being compared. 3D error values were calculated as the Euclidean distance between test and reference XYZ coordinates for each test point.

Raw angular and distance errors between methods were also compared using paired Wilcoxon tests. Here, total station XYZ coordinate outputs were converted to angular and distance measurements to serve as a baseline for the comparison of raw errors (angles and distances) between the two methods; and inclination values from the DistoX2 were converted to vertical distance (Z) to enable direct comparison with the tape and compass method.

Angular and distance measurements recorded by the DistoX2 were converted into XYZ coordinates in R using the following trigonometric equations:

$$X = \sin\alpha \times (\cos\beta \times d)$$

$$Y = \cos\alpha \times (\cos\beta \times d)$$

$$Z = \sin\beta \times d,$$

where α = *azimuth*, β = *inclination* and d = *distance*

Angular and distance measurements recorded using the tape and

Table 3
Raw DistoX2 precision results in hand-held and tripod modes. Values calculated from the average deviation.

	Hand-held mode				Tripod mode			
Measurement	mean	median	IQR	95% CI	mean	median	IQR	95% CI
Azimuth (°)	0.069	0.048	0.046	0–0.284	0.023	0.032	0.032	0–0.048
Distance (m)	0.006	0.005	0.003	0–0.014	0.002	0.003	0.003	0–0.005
Inclination (°)	0.023	0.032	0.048	0–0.048	0.009	0.000	0.000	0–0.048

Table 4
DistoX2 precision results in hand-held and tripod modes converted into XYZ format. Values in metres, calculated from the average deviation.

	Hand-held mode				Tripod mode			
Axes	mean	median	IQR	95% CI	mean	median	IQR	95% CI
X	0.005	0.005	0.005	0–0.011	0.002	0.003	0.002	0–0.005
Y	0.006	0.005	0.004	0–0.016	0.002	0.003	0.002	0–0.006
Z	0.002	0.001	0.003	0–0.007	0.001	0.000	0.000	0–0.007

compass method were converted into XYZ coordinates using the following trigonometric equations:

$$X = \sin\alpha \times d$$

$$Y = \cos\alpha \times d$$

$$Z = h,$$

where α = *azimuth*, d = *distance* and h = *height*

For the conversion of total station XYZ coordinates to angular and distance measurements, azimuths were calculated in R: unsigned angles between the vectorized coordinates and a fixed point (x = 0, y = 1) representing North, were computed using the 'angle.calc' function of the Morpho package (version 2.8; Schlager et al., 2020); then converted from radians to degrees using the 'rad2deg' function of the REdaS package (version 0.9.3; Maier, 2015); finally, angles were converted to a 360° format by subtracting the output from 360 where the original X coordinate was negative. Horizontal distance between the datum and each test point was calculated in QGIS (version 2.18.4) using the inbuilt Distance Matrix tool.

Major outliers for all data were defined as outliers that fell below the first quartile (Q1) subtracted by three times the interquartile range (IQR) or above three times the IQR added to the third quartile (Q3). Level of significance was set at $p < 0.05$.

3. Results

3.1. Precision

Overall, the precision test of the DistoX2 using the raw data output (angles and distance) yielded, on average, sub-degree and sub-centimetre precision for both hand-held and tripod modes (Table 3). Nevertheless, comparison between modes revealed that the average deviation values of the tripod mode were significantly lower than the reported values for the hand held mode, demonstrating that the tripod mode yields greater precision (Wilcoxon signed-rank test, Az: $z = 4.63$, $w = 1905.5$, $p < 0.01$; Dist: $z = 5.84$, $w = 2078.5$, $p < 0.01$; Inc: $z = 3.36$, $w = 1678.5$, $p < 0.01$).

For ease of interpretation we also converted the data into linear XYZ measurements, where the DistoX2 in tripod mode was found to be two-times more precise than the hand-held alternative with an average deviation of < 0.75 cm (95% CI) for all axes (Wilcoxon signed-rank test, X: $z = 4.78$, $w = 1943.5$, $p < 0.01$; Y: $z = 5.30$, $w = 2019.0$, $p < 0.01$; Z: $z = 4.19$, $w = 1854.0$, $p < 0.01$) (Table 4; Fig. 3).

3.2. Accuracy

The accuracy tests of the DistoX2 relative to the total station system were performed at two different locations. At L2 the DistoX2 errors

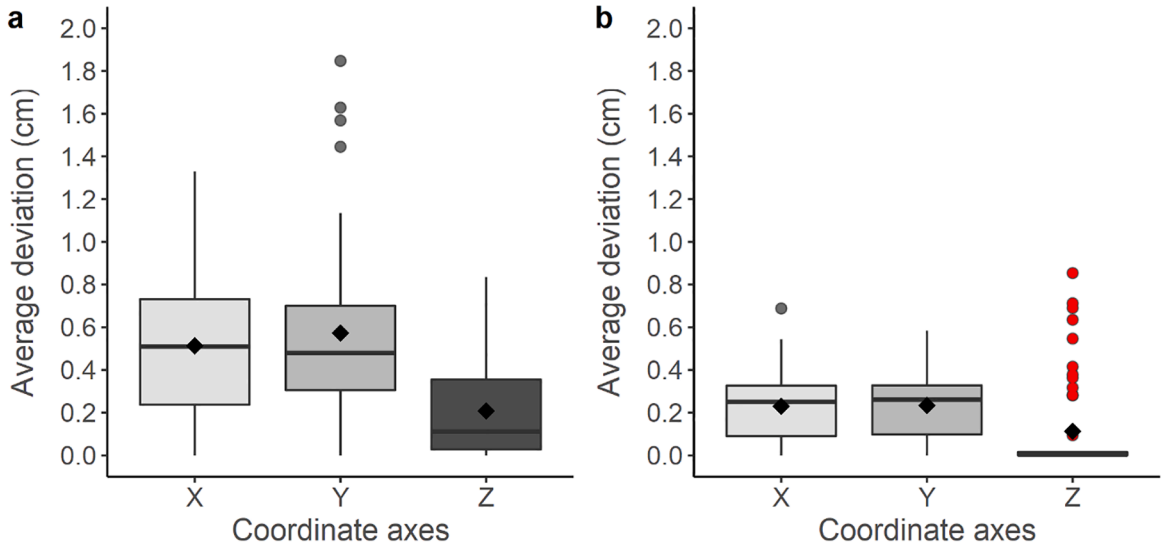


Fig. 3. DistoX2 precision: a) Hand-held mode; b) Tripod mode. Mean values represented by the diamond symbol, and major outliers indicated in red. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 5
DistoX2 accuracy relative to the total station at the two different test locations: L2 (Koobi Fora, Kenya) and L3 (Oxford, UK). Values in metres, calculated from the absolute error; 3D error calculated as Euclidean distance.

	Disto X2 – L2				Disto X2 – L3			
Axes	mean	median	IQR	95% CI	mean	median	IQR	95% CI
X	0.041	0.038	0.022	0.011–0.078	0.054	0.039	0.046	0.001–0.175
Y	0.025	0.022	0.022	0.001–0.061	0.051	0.048	0.059	0.002–0.130
Z	0.022	0.019	0.020	0.001–0.059	0.023	0.021	0.023	0.001–0.061
3D	0.057	0.055	0.024	0.028–0.093	0.089	0.073	0.064	0.018–0.184

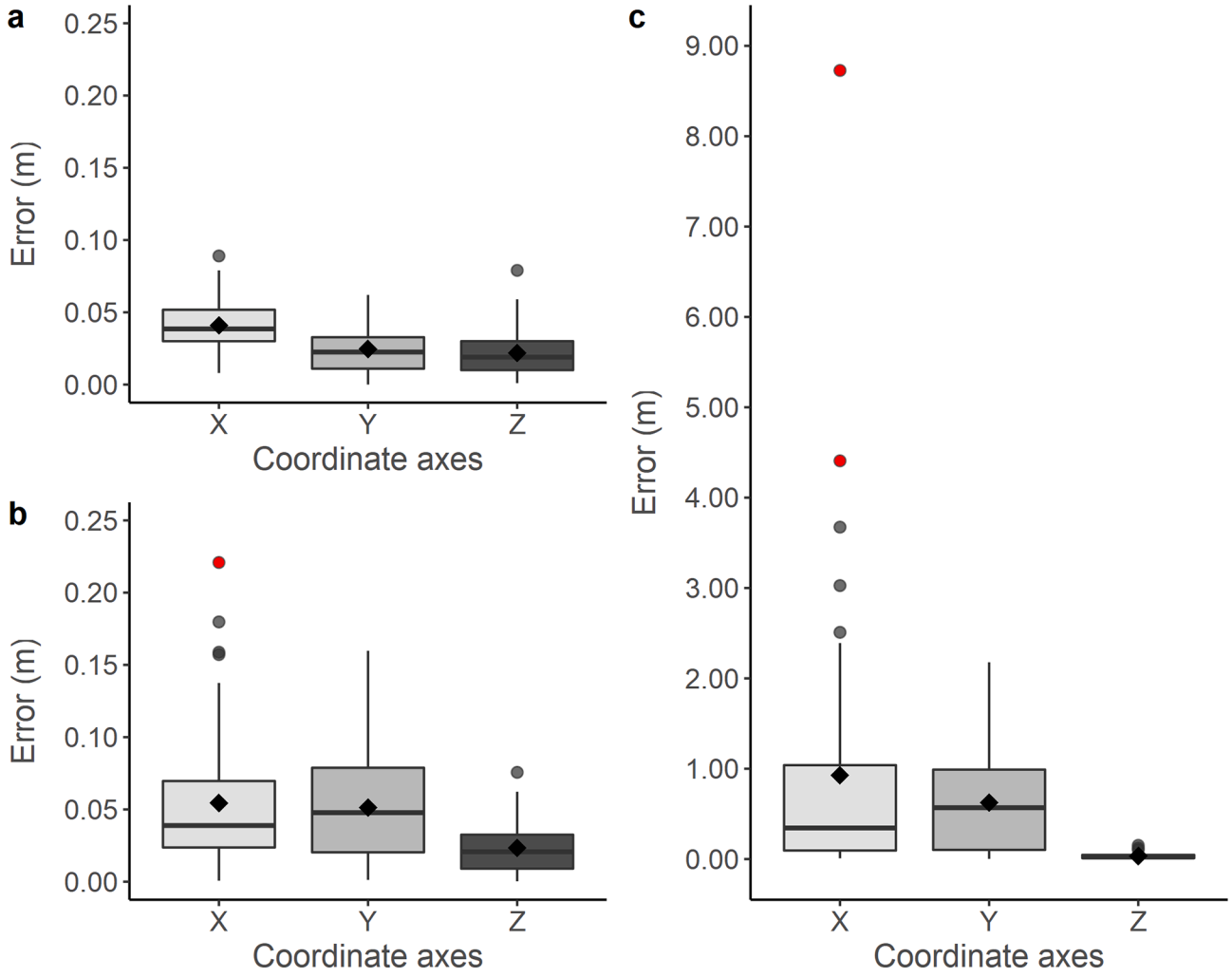


Fig. 4. Accuracy of the tested methods: a) DistoX2 at L2; b) DistoX2 at L3; c) Tape and compass method at L3. Values reported as absolute errors. Mean values represented by the diamond symbol, and major outliers highlighted in red. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 6
Tape and compass accuracy relative to the total station with and without major outliers. Values in metres, calculated from the absolute error; 3D error calculated as Euclidean distance.

	TC – all data				TC – excluding major outliers			
Axes	mean	median	IQR	95% CI	mean	median	IQR	95% CI
X	0.928	0.344	0.945	0.012–4.242	0.693	0.332	0.795	0.011–2.936
Y	0.626	0.568	0.888	0.003–1.837	0.637	0.602	0.908	0.003–1.852
Z	0.034	0.023	0.036	0.001–0.117	0.034	0.022	0.034	0.001–0.118
3D	1.277	0.834	1.367	0.032–4.287	1.056	0.799	1.100	0.032–3.07

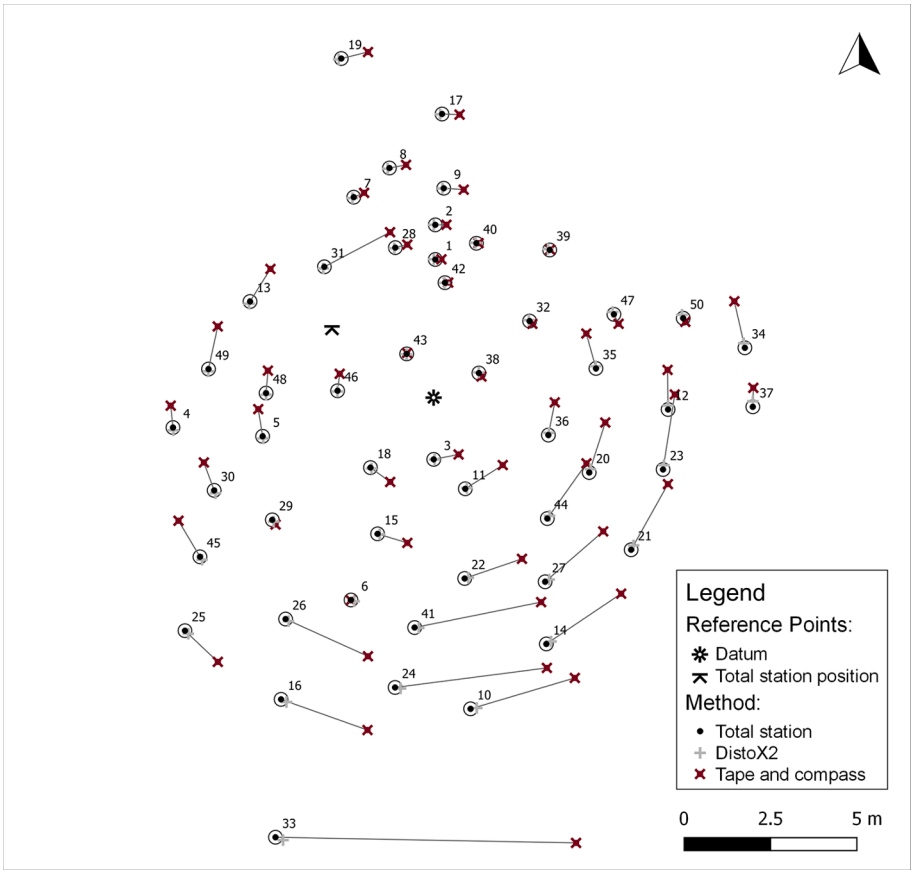


Fig. 5. 2D-plan of the test points at L2 mapped using the three different methods: total station, DistoX2, and tape and compass. Open circles represent a 20-cm buffer around the total station measurements. Lines illustrate the linear error between the tape and compass and total station methods where error is greater than 20 cm.

ranged 0–0.10 m for all axes (Table 5, Fig. 4a). At L3 the DistoX2 presented somewhat higher errors, ranging 0–0.20 m for the X and Y axes, 0–0.10 for the Z axis, and 0.02–0.20 for the overall 3D error (Table 5; Fig. 4b). However, these results were only significantly different for the Y axis and the composite 3D error (Wilcoxon signed-rank test, X: $z = -0.32$, $w = 1203$, $p = 0.75$; Y: $z = -3.37$, $w = 760$, $p < 0.01$; Z: $z = -0.46$, $w = 1183$, $p = 0.64$; 3D: $z = -3.28$, $w = 773$, $p < 0.01$).

Accuracy tests of the tape and compass relative to the total station conducted at L3 produced sub-metre average errors for the X and Y axes, with several points exceeding the one-metre error threshold, while error values for the Z axis were largely within the 0–0.1 m range (Table 6).

Paired comparisons between the error values of the two methods tested at L3, demonstrated that the DistoX2 is significantly more accurate than the tape and compass method (Paired Wilcoxon test, X: $z = -5.96$, $v = 20$, $p < 0.01$; Y: $z = -5.88$, $v = 28$, $p < 0.01$; Z: $z = -2.52$, $v = 376$, $p < 0.01$; 3D: $z = -6.06$, $v = 9$, $p < 0.01$). The level of significance was maintained even when the most extreme outliers were removed (Paired Wilcoxon test, X: $z = -5.82$, $v = 20$, $p < 0.01$; Y: $z = -5.74$, $v = 28$, $p < 0.01$; Z: $z = -2.63$, $v = 331$, $p < 0.01$; 3D: $z = -5.93$, $v = 9$, $p < 0.01$; Table 6, Fig. 4c). Fig. 5 shows a map of the coordinate positions of each test point taken with the three different methods.

Comparison of raw angle and distance errors between the DistoX2 and the tape and compass methods provides some insight into the nature of the stark discrepancy in accuracy (Table 7). While statistical significant differences were apparent for all measurement (Paired Wilcoxon test, Az: $z = -6.06$, $v = 9$, $p < 0.01$; Dist: $z = -5.75$, $v = 41$, $p < 0.01$; Z: $z = -3.53$, $v = 271$, $p < 0.01$), it is clear that the higher values and variance of the azimuth error of the tape an compass method is the principal contributor, suggesting that the compass used is a driving cause of the lower accuracy of this approach. While resolution and reported accuracy of the compass accounts for this in part, additional random error was likely introduced by the general imprecision of the whole system – compass orientation is done by hand and relies on the visual aptitude of the human eye for alignment with the measuring tape, with the compass changing location between each measurement. By comparison, the DistoX2 and total station are in fixed positions and use exact guides (e.g. reflector, prism) and visual aids (e.g. laser, magnifier) to record orientation. Thus, even with the highest attention to detail, the tape and compass method is more prone to extrinsic errors that could result in a higher incidence and range of erroneous measurements.

Angular errors translate into linear errors that increase with distance. This effect is particularly apparent for the tape and compass method, which also demonstrates high variance in error values reflecting the inconsistent nature of this method (Fig. 6). While the DistoX2

Table 7
Raw measurement accuracy of the DistoX2 and tape and compass methods relative to the total station baseline. Values calculated from the absolute errors.

	DistoX2				Tape and Compass			
Measurement	mean	median	IQR	95% CI	mean	median	IQR	95% CI
Azimuth (°)	0.769	0.761	0.364	0.386–1.146	11.323	8.824	14.389	0.21–31.989
Horizontal distance (m)	0.007	0.006	0.008	0–0.017	0.015	0.015	0.005	0.008–0.024
Vertical distance (m)	0.016	0.014	0.014	0.001–0.045	0.034	0.022	0.036	0.001–0.117

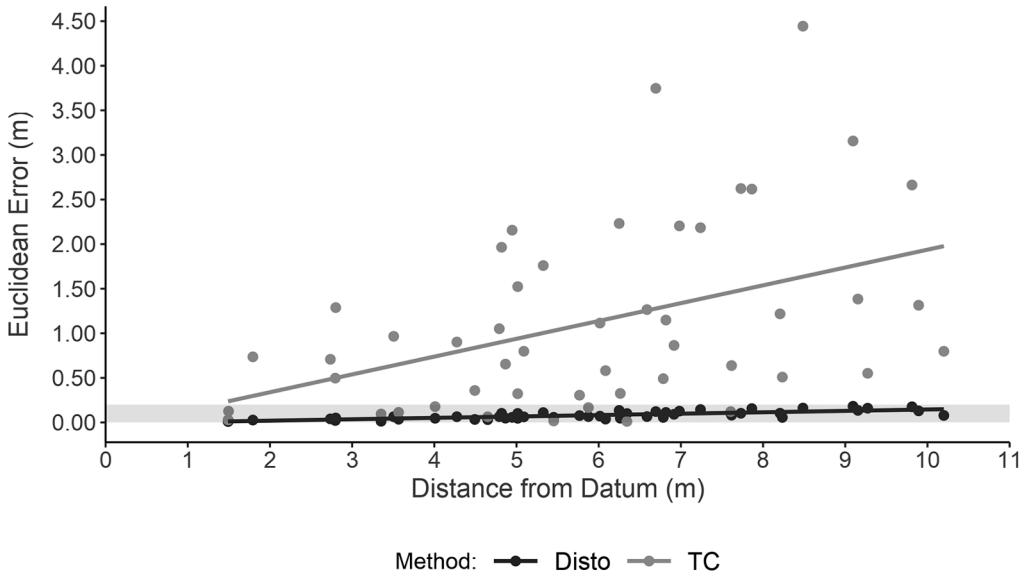


Fig. 6. 2D linear distance error between each test method and the total station baseline relative to distance from datum. Grey bar indicates the 0.0 – 0.2 m error range.

measurements ae also affected by this trend, the effect is far less extreme due to its higher precision, accuracy, and corresponding lower error dispersal.

4. Discussion

4.1. Observations on overall performance

In addition to the current study, the authors have had extensive experience in using all three survey methods in a range of real-world archaeological settings. KAW and SC have previously used the tape and compass method during primate archaeological fieldwork at wild chimpanzee sited in Tanzania and Guinea. SC also used the total station to record several chimpanzee nut-cracking sites in Guinea, and DRB uses it extensively for documenting Plio-Pleistocene excavations throughout Africa. More recently, KAW has used the DistoX2 to map chimpanzee tool sites in Guinea, as well as document surface material from Plio-Pleistocene deposits in Kenya. The following observations are a reflection on our collective experiences.

The DistoX2 system proved to be an easy to use, highly versatile instrument. While initial calibration required time and often several attempts before reaching acceptable calibration levels, the spatial data collection itself was fast and extremely efficient, and to a similar degree to the total station. It was only less so, in bright sunlight conditions when it was difficult to see the laser beam for targets beyond ~10 m, although laser enhancement glasses help mitigate this. The fact that data was recorded automatically in digital format and could be viewed in real time on a tablet was another major advantage of this system. Exporting and loading the data to a computer was also easy and intuitive.

Another major advantage of the DistoX2 was that it uses magnetic north as point of reference, and, once calibrated, it is ready to use anywhere within an approximately 100 km radius. This, combined with its small size and portability, enables mapping of several sites consecutively and instantaneously in a short period of time. In contrast, a total station generally needs to be "told" where North is, usually with the aid of a minimum of two fixed geo-referenced points. This means every site needs at least two geo-reference points, and every mapping session requires the total station to be setup and referenced relative to the known points. For multi-site projects covering large areas, the whole process from setup to completion of data collection can take up a considerable amount of research time (Fitts, 2005), although the use of a self-tracking (robotic) total station can help overcome the more nuanced logistical challenges of large-scale surveys (Holdaway and Fanning, 2008). While we did not document the exact recording times for each of the discussed methods, previous tests in cave settings have reported that a survey with the total station took a total of 48 h and three people, while the same survey was achieved with the DistoX in five hours by two people (Redovniković et al., 2014). Lastly, learning to use the DistoX2 system was relatively easy and took less than a day of training. In contrast, the total station often requires extensive training and a high level of expertise, which may pose additional limitations for archaeological projects with logistic and financial constraints.

Spatial mapping using the tape and compass method was the most time consuming, often requiring readjustments of the tape and levelling string. Between two people measuring and recording, where each person was handling multiple objects at the same time, it was also necessary to confer and redo measurements on several occasions to ensure accurate recording. The compass was also highly sensitive to movement and could display divergent readings for any given target point, providing greater potential for erroneous measurements. These factors, combined with the high range of error uncovered during data analysis, indicate that the tape and compass method is the least reliable and most prone to random human and instrument errors. While the addition of a third person dedicated solely to recording the measurements, the application of tension, sag and temperature corrections to distance measurements, and the use of a more accurate digital compass would have improved data quality and collection efficiency, this would not have been a realistic representation of most archaeological operations that use this method.

Total station real-world accuracy under field conditions is estimated at around ±0.05 – 0.10 cm (Sapirstein, 2016). This not only allows for highly accurate provenience data, but also enables the detailed recording of object orientation and slope required for high-profile excavations, such as those in Palaeolithic contexts (McPherron, 2005; Peng et al., 2017). While the DistoX2 observes a much higher error threshold (around ±0.10 – 15.00 cm), it can be considered a suitable method for archaeological projects that do not demand sub-cm accuracy – e.g. surface surveys, recovery excavations, community projects. It could also complement the total station and other current methods in large-scale projects where both excavations and surface surveys are taking place

Table 8
Summary of specifications and practical information of current and novel mapping methods.

	Tape and compass	Total station	RTK GNSS	Ground-based photogrammetry	DistoX2
Accuracy[1]	0–300 cm	< 0.5 cm	0–2 cm	0–5 cm	0–15 cm
Distance range	~ 20 m	~ 4 km	~ 15 km (Base and Rover RTK) ~ 100 km (RTK network)	~ 300 m	~ 100 m[2]
Weight	1–3 Kg	4–10 Kg	2–10 Kg	1–8 Kg	0.5–3[3] Kg
Speed	Slow	Moderate	Moderate	Slow	Fast
Operating time	10–26 hrs[4]	8–30 hrs	8–30 hrs	4–15 hrs	2–3 days[5]
Expertise required	Low	High	Moderate-High	Moderate-High	Moderate
Optimal conditions	Any	Open spaces	Overground with open sky	Any	Overground, underground
Practical limitations	Not suitable in locations with steep terrain unless used in tandem with a clinometer	Not suitable in underground settings with restrictive access	Not suitable in forested conditions. Requires a Base and Rover system or access to an RTK network with good cell service	Not suitable in locations with many vertical obstacles, dense vegetation or contrasting light conditions	Not suitable in locations with very strong sunlight or high magnetic interference
Cost	$20–200[6]	$4,000–10,000	$1,500–20,000[7]	$200–1,500[7]	$280–500[3]

[1]Reported as absolute error.
[2]Up to 10–15 m in bright sunlight.
[3]Depending on digital accessories chosen (e.g. mobile or tablet device), and whether tripod is included.
[4]Unlimited if using a fully analogue system.
[5]Up to two weeks for low to moderate usage.
[6]If using a digital compass.
[7]Depending on additional accessories, and whether a subscription to software and/or correction service is needed.

over a large geographic area.

Nevertheless, the DistoX2 would be of most benefit to projects for which modern mapping techniques are incompatible, whether due to site characteristics, or logistical and budgetary limitations. Worldwide, there are many expeditions that, due to such conditions, still rely on older provenience techniques (Peng et al., 2017), including the tape and compass method tested here. The DistoX2 presents an affordable and versatile alternative to such methods while providing a tenfold improvement in accuracy as well as other benefits such as digital recording, speed and consistency. Thus, the DistoX2 narrows the error thresholds between the diverse range of archaeological projects, bringing those that would typically rely on traditional methods closer to the total station standard.

4.2. Other methods

While the focus of the present research was to test the performance of the DistoX2, we also consider two of the latest methods that are becoming increasing commonplace in archaeological research – photogrammetry, and high-accuracy GNSS. Extensive literature now exists on the performance of these approaches in open archaeological settings, many reporting high levels of accuracy and precision comparable to the total station (Fitts, 2005; Hill et al., 2019; Peng et al., 2017; Roosevelt, 2014; Sapirstein, 2016; Tripcevich and Wernke, 2010; Willis et al., 2016). Conditions permitting, at least one of these methods may be feasible for archaeological mapping in poorly accessible environments. Close-range photogrammetry, for example, has been successful in both underground and underwater settings, albeit to varying degrees (Chang et al., 2019; Jordan, 2017; Lee, 2018; Yamafune et al., 2017); and has been implemented for generating 3D-models of both natural and archaeological features in these environments (Dabove et al., 2019; Figueira et al., 2015; Unhammer, 2016; Yamafune et al., 2017; Perfetti et al., 2020). One of the great advantages of photogrammetry is that the core equipment required – a digital camera – is already part of the archaeologist's toolkit. Additional elements, such as tripods, access to SfM software, as well as material for identifying ground control points, can be acquired at relatively low cost. It is a great visual tool for complementing traditional excavation recording methods, reconstructing archaeological objects, and providing immersive 3D-visualisation for preservation and dissemination of cultural heritage. It can be implemented in almost all archaeological settings, except for forested environments (Willis et al., 2016), where low-lying vegetation and many vertical obstacles (trees) could greatly impact the feasibility of this method unless it is possible to clear large areas of vegetation.

Archaeological studies investigating accuracy of SfM photogrammetry have reported errors as low as 0.20 cm, ranging ~0.0–5.0 cm (Peng et al., 2017; Sapirstein, 2016; Willis et al., 2016). However, we highlight that most of these studies have scaled their SfM models with ground control points that were georeferenced using a total station or real-world coordinates, and very few tested the accuracy of point provenience data directly (i.e. compared the total station coordinates of predefined points with those yielded from photogrammetric data). Nevertheless, accuracy and precision of photogrammetry-generated models can be extremely variable as it is dependent on a variety of factors, including: the scale and texture of the subject, the image quality and degree of overlap among photos, the number of ground control points, the camera used, the accuracy of the scaling method (e.g. georeferenced control points, measurements between known points, object of known scale), and whether coded targets are included (Peng et al., 2017; Sapirstein, 2016). Thus, in order to achieve reliably consistent results requires expertise and strict protocols (Sapirstein and Murray, 2017). This is even more crucial when no other methods of spatial data collection are being used. In most fieldwork scenarios, SfM composites cannot be generated *in situ* in real-time, consequently failure to take sufficient overlapping photos covering the whole area of interest could result in complete loss of valuable data if the area is under active

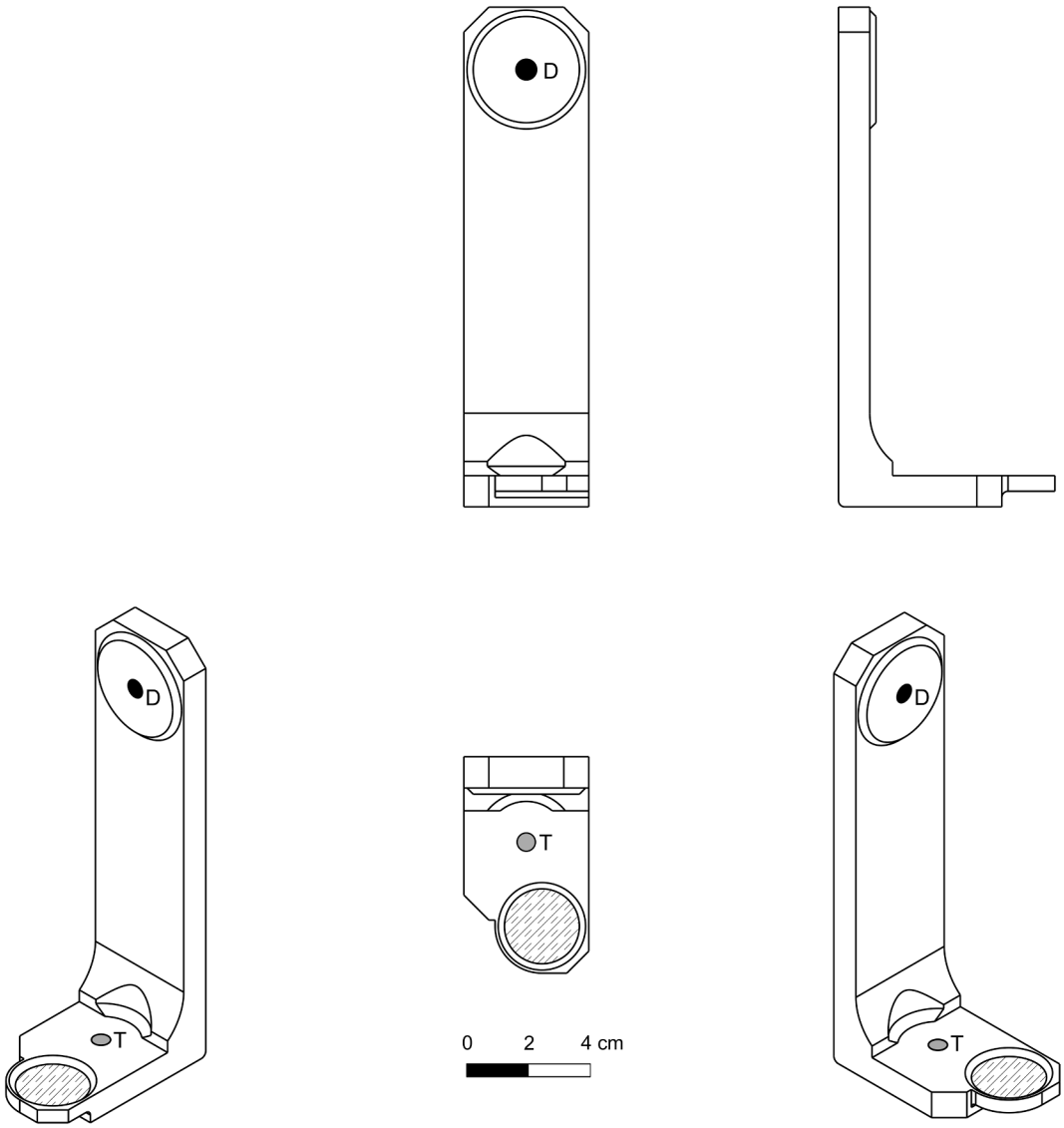


Fig. A1. Blueprint of DistoX2 custom-made tripod mount (Original composite by P. Riggs; with modifications by K. Almeida-Warren). Solid fill areas indicate screw attachments and connections to the DistoX2 (D), and tripod head (T). Hatch fill areas indicate surface for fitting a small circular spirit level.

excavation or a site of modern activity (e.g. an active chimpanzee nut-cracking site).

At a practical level, extracting spatial provenience of archaeological artefacts and features using SfM photogrammetry without the aid of a total station or a GNSS device, requires precise measurements of the distances between multiple ground control points or the inclusion of an object of known dimensions. It may also require the use of a camera boom to enable greater surface coverage and a shade to diffuse strong sunlight and reduce shadows. While the whole process, from taking the photographs, to generating the 3D-models, to extrapolating the desired spatial data, can be time-consuming and labour-intensive (Sapirstein and Murray, 2017), SfM photogrammetry may be a good alternative to the total station in archaeological projects that implement photogrammetry as part of the recording practices whether for digital archives or public outreach.

High-accuracy GNSSs technology is rapidly advancing, and such devices may well replace the total station in open-air settings in the coming decades, if not years. Currently, most RTK GNSSs range from sub-cm to 2 cm horizontal accuracy in optimal conditions (e.g. good satellite coverage, clear sky) (EOS Positioning Systems Inc., 2017; Hill et al., 2019; Pearson et al., 2015). However, this system requires connection to an RTK network (via cell signal) or nearby base station (Pearson et al., 2015), which are not always available or feasible in remote field sites. As an alternative, some GNSS companies offer subscription access to differential correction services (e.g. Atlas^{TM}; CenterPoint^{TM} RTX) that can provide base-station free corrections at accuracies as low as two centimetres (Ames et al., 2020; EOS Positioning Systems Inc., 2017). Nevertheless, the accuracy of such systems is still heavily conditioned by access to open sky and clear satellite geometry. One of the authors (KAW), who used an EOS Arrow Gold with Atlas H10 correction extensively during fieldwork in the Bossou (Guinea), found that the system performed very poorly under forested conditions. Often the device struggled to reach a reliable measurement (Fix solution frequency = 2.5%, n = 1324), with data outputs returning error values of ≈ 2.13 m HRMS and ≈ 4.00 m VRMS (Appendix B), despite observing each point for several minutes to half an hour. Battery life may also be a limitation if there is no daily access to a power source. In the case of the Emlid Reach RTK, battery autonomy is approximately 30 h (Hill et al., 2019), while for the EOS Arrow Gold it caps at around 8 h (EOS Positioning Systems Inc., 2017). In contrast, the DistoX2 can last 2–3 days of intensive data collection to approximately two weeks of low to moderate usage. While the cost of commercially available GNSS instruments is

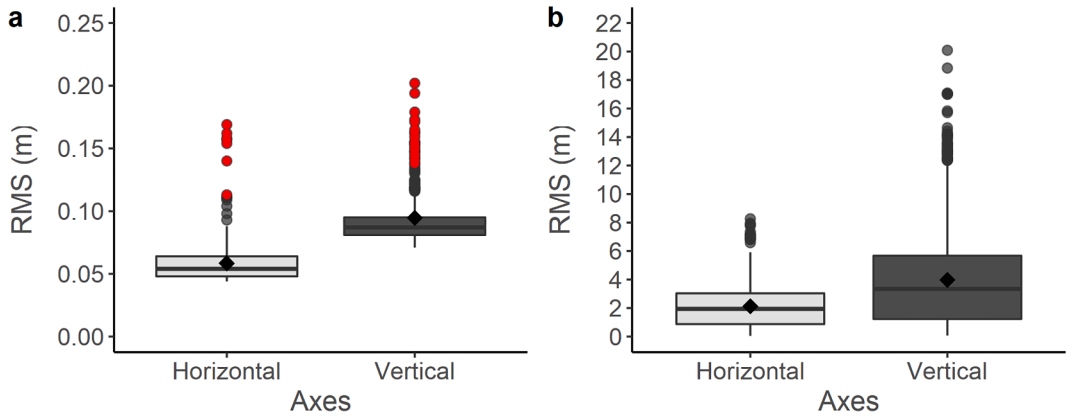


Fig. B1. Accuracy of the Arrow Gold GNSS Receiver as reported by the device during field surveys under two canopy conditions: a) open canopy; b) closed canopy. Values indicated as root mean square (RMS). Mean values represented by the diamond symbol, and major outliers highlighted in red.

becoming more and more affordable, a complete survey kit even at the lower end of the spectrum will range between $1,500 and $2,500. In projects with a limited budget, a GNSS device especially if requiring the added cost of periodic subscriptions to correction services may not be economically feasible (Ames et al., 2020).

Ultimately, the method used for collecting spatial provenience data is a decision that depends on the nature of the project – from the characteristics of the site (location, environment, scale, accessibility), archaeological significance/importance, funding available, and project duration, to the team size and the amount of logistical support. In some cases, the total station will be the only compatible option, while for others, practical or budgetary limitations will require the use of alternative methods. For ease of comparison, we provide a summary of key information as well as some practical limitations regarding each of the survey methods discussed in this study (Table 8).

While the current research has mainly focused on assessing the DistoX2 as a stand-alone data collection method, we would like to highlight that the DistoX2 could equally be used in tandem with other methods. Currently several archaeological projects employ a combination of total station, GNSS and/or photogrammetry, including expeditions directed by one of the authors – DRB – in Koobi Fora, Kenya. The DistoX2 system constitutes a new addition to the archaeologist's toolkit that can complement and facilitate the tailoring of spatial mapping strategies to the specific goals of an archaeological project.

5. Conclusions

Today, archaeological expeditions are becoming increasingly diverse, and the data collection methods used will depend on the requirements and limitations of the project at hand. While the total station should be the primary choice in most instances, especially when very high accuracy is required, many projects may not meet the conditions or means required to implement such a method, or other current alternatives. Yet, other projects may also seek to combine several mapping methods to fit their needs. The DistoX2 provides a methodological solution to those projects that would still typically resort to more traditional, analogue methods, but also constitutes a novel system that complements other commonly used methods in projects that benefit multiple approaches.

The DistoX2 presents a good level of precision both in hand-held and tripod modes. However, it is most precise when mounted on a tripod, where the mean precision is ≈ 2.00 cm for the X and Y axes and ≈ 1.00 cm for Z.

The conservative estimate for DistoX2 accuracy relative to the total station is ≈ 5.00 cm for 2D dimensions and ≈ 2.00 cm for the Z axis (≈ 6.00 cm for 3D composite). These values are better than the previously published results, although the errors fall under the same upper boundary (see Redovniković et al., 2016).

In contrast, the tape and compass method, with a mean error of ≈ 69.00 cm for the X axis, ≈ 64.00 cm for the Y axis, and ≈ 3.00 cm for the Z axis, is considerably less accurate than the DistoX2, particularly with respect to the X and Y axes. The fact that the analogue or digital compass used in the tape and compass method cannot be calibrated to the same rigour nor have the same resolution as the DistoX2, is a major disadvantage to this approach. Furthermore, unlike the DistoX2, data collection using this method is not an automated process, and therefore has greater propensity for human errors at the reading, recording, and data-entry levels. Despite being the most affordable, its high level of measurement error makes this method a poor option for spatial data collection and should only be used when alternative methods (including the DistoX2) are not viable options.

In sum, the DistoX2 presents several features that make it a suitable and affordable alternative to the more commonly used digital spatial mapping methods in archaeology, and to the tape and compass method: 1) small, light-weight and highly-portable device; 2) can be calibrated, ensuring more accurate readings than standard analogue or digital compasses; 3) more accurate and more efficient than the tape and compass method; 4) records measurements instantaneously onto a digital interface, that can be exported and uploaded to a laptop for analysis.

The DistoX2 combines the portability and affordability of the tape and compass method with the speed, accuracy and digital features of the total station. Its applicability in poorly accessible field-sites fills a critical gap in archaeological mapping methods, and enables greater standardization of spatial data collection across all human and non-human archaeological records.

CRediT authorship contribution statement

Katarina Almeida-Warren: Conceptualization, Methodology, Investigation, Formal analysis, Data curation, Visualization, Writing - original draft. **David R. Braun:** Conceptualization, Resources. **Susana Carvalho:** Conceptualization, Supervision, Resources.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We are grateful to V. Mamy, L. Goigbe, B. Zogbila, G. Zogbila, A. Curley, C. Costa, C. Daniel, N. Mann, N. Gitaw, K. O'Brien, Dr. J. Reeves and Dr. M. Bluteau for support during the data collection process; to F.

Tátá Regala, L. Meira Paulo and M. J. Pinto at AESDA (Associação de Estudos Subterrâneos e Defesa do Ambiente) for DistoX2 training, suggestions and technical support. We thank P. Riggs at Science Oxford for producing a custom-made tripod adaptor; Dr. L. Luncz and the Institute of Archaeology (University of Oxford) for kindly loaning their survey equipment during testing in Oxford. We also thank the Direction Nationale de la Recherche Scientifique, the Institut de Recherche Environmentale de Bossou (Guinea), Kyoto University Primate Research Institute, National Museums of Kenya, and the National Commission for Science, Technology and Innovation (Kenya), and the Koobi Fora Field School for research permissions and logistical support overseas.

This work was funded by the Fundação para a Ciência e Tecnologia (FCT) [grant number: SFRH/BD/115085/2016] to KAW, with support from the Programa Operacional Capital Humano (POCH) and the European Union; ICArEHB with support from FCT [grant number: UIDB/04211/2020]; the Boise Trust Fund (University of Oxford) to KAW; the National Geographic Society [grant number: EC-399R-18] to KAW; and a Philip Leverhulme Prize to SC.

Appendix A – Custom-made tripod mount

The DistoX2 tripod mount was conceptualized by KAW and Paul Riggs (Science Oxford), to enable a setup more in line with the total station system and standard archaeological data collection protocols. The piece is designed so that the DistoX2 can be mounted on a standard camera tripod over a fixed point and rotated along vertical and horizontal planes, covering all directions except for the area within the tripod legs. The rotation axes align with the origin of the laser (at the base of the DistoX2) and over the fixed point at the base of the tripod, so that the DistoX2 can be rotated while maintaining the fixed position of the laser source. The build is sturdy and lightweight, with a space at the base to fit a small circular spirt-level to aid with setup (Fig. A.1). The 3D file is freely available for download and printing through Thingivese (https://www.thingiverse.com/thing:4367548) where print instructions and related information can be found.

The connections with the tripod and the DistoX2 are made using common photography tripod adaptor components available from eBay and other sources:

– 1/4″ male to 1/4″ female screw adaptor for camera tripod flash bracket

– 1/4″ dual nuts tripod mount screw and camera flash hot shoe adapter

These pieces need to be non-magnetic (e.g. aluminium) so as not to interfere with the DistoX2's internal compass.

Appendix B – Arrow Gold GNSS Receiver

Fig. B1.

References

Almeida-Warren, K., Braun, D.R., Matsuzawa, T., Carvalho, S., 2018. Mapping primate archaeology: new tools for standardizing spatial data collection across the primate order. Proceedings of the XXVIIth Congress of the International Primatological Society.

Ames, C.J.H., Shaw, M., O'Driscoll, C.A., Mackay, A., 2020. A multi-user mobile GIS solution for documenting large surface scatters: an example from the Doring River, South Africa. J. F. Archaeol. 45, 394–412. https://doi.org/10.1080/00934690.2020.1753321.

Ballesteros, D., Domínguez-Cuesta, M.J., Jiménez-Sánchez, M., González- Pumariega, P., 2013. Tape-compass-clinometer, DistoX or total station, what is the best method to elaborate a cave survey? A case study in El Pindal Cave, Spain, in: 8th International Conference (AIG) on Geomorphology, 27-31 August, Paris.

Carvalho, S., 2011. Diécké Forest, Guinea: Delving into Chimpanzee Behavior Using Stone Tool Surveys. In: Matsuzawa, T., Humle, T., Sugiyama, Y. (Eds.), The Chimpanzees of Bossou and Nimba. Springer Japan, pp. 301–312. https://doi.org/10.1007/978-4-431-53921-6_31.

Carvalho, S., Almeida-Warren, K., 2019. Primate Archaeology, in: Chun Choe, J. (Ed.), Encyclopedia of Animal Behavior. Elsevier, pp. 397–407. https://doi.org/10.1016/B978-0-12-809633-8.90156-0.

Carvalho, S., Cunha, E., Sousa, C., Matsuzawa, T., 2008. Chaînes opératoires and resource-exploitation strategies in chimpanzee (*Pan troglodytes*) nut cracking. J. Hum. Evol. 55, 148–163. https://doi.org/10.1016/j.jhevol.2008.02.005.

Chang, A., Jung, J., Um, D., Yeom, J., Hanselmann, F., 2019. Cost-effective framework for rapid underwater mapping with digital camera and color correction method. KSCE J. Civ. Eng. 23, 1776–1785. https://doi.org/10.1007/s12205-019-1891-3.

Corvi, M., 2016. TopoDroid v.2.7.

Dabove, P., Grasso, N., Piras, M., 2019. Smartphone-based photogrammetry for the 3D modeling of a geomorphological structure. Appl. Sci. 9, 3884. https://doi.org/10.3390/app9183884.

Dibble, H.L., 1987. Measurement of artifact provenience with an electronic theodolite. J. F. Archaeol. 14, 249–254. https://doi.org/10.1179/009346987792208457.

EOS Positioning Systems Inc., 2017. Arrow Gold [WWW Document]. URL https://eos-gnss.com/wp-content/uploads/2017/11/eos-arrow-gold-revC-v4.pdf (accessed 3.12.20).

Falótico, T., Proffitt, T., Ottoni, E.B., Staff, R.A., Haslam, M., 2019. Three thousand years of wild capuchin stone tool use. Nat. Ecol. Evol. 3, 1034–1038. https://doi.org/10.1038/s41559-019-0904-4.

Figueira, W., Ferrari, R., Weatherby, E., Porter, A., Hawes, S., Byrne, M., 2015. Accuracy and precision of habitat structural complexity metrics derived from underwater photogrammetry. Remote Sens. 7, 16883–16900. https://doi.org/10.3390/rs71215859.

Fitts, W.R., 2005. Precision GPS surveying at Medieval Cottam, East Yorkshire. England. J. F. Archaeol. 30, 181–190. https://doi.org/10.1179/009346905791072387.

Haslam, M., Hernandez-Aguilar, A., Ling, V., Carvalho, S., De La Torre, I., Destefano, A., Du, A., Hardy, B., Harris, J., Marchant, L., Matsuzawa, T., McGrew, W.C., Mercader, J., Mora, R., Petraglia, M., Roche, H., Visalberghi, E., Warren, R., 2009. Primate archaeology. Nature 460, 339–344. https://doi.org/10.1038/nature08188.

Haslam, M., Luncz, L., Pascual-Garrido, A., Falótico, T., Malaivijitnond, S., Gumert, M., 2016. Archaeological excavation of wild macaque stone tools. J. Hum. Evol. 96, 134–138. https://doi.org/10.1016/j.jhevol.2016.05.002.

Heeb, B., 2014. The next generation of the DistoX cave surveying instrument. Cave Radio Electron. Gr. J. 88, 5–8.

Heeb, B., 2013. DistoX2 Calibration Manual [WWW Document]. URL https://paperless.bheeb.ch/download/DistoX2_CalibrationManual.pdf (accessed 5.30.19).

Heeb, B., 2008. Paperless Caving - An Electronic Cave Surveying System. Proc. IV Eur. Speleol. Congr. 130–133.

Hill, A.C., Limp, F., Casana, J., Laugier, E.J., Williamson, M., 2019. A New Era in Spatial Data Recording: Low-Cost GNSS. Adv. Archaeol. Pract. 7 (2), 169–177. https://doi.org/10.1017/aap.2018.50.

Historic England, 2017. Understanding the Archaeology of Landscapes: A Guide to Good Recording Practice, 2nd ed. Historic England, Swindon.

Holdaway, S., Fanning, P., 2008. Developing a landscape history as part of a survey strategy: a critique of current settlement system approaches based on case studies from Western New South Wales, Australia. J. Archaeol. Method Theory 15, 167–189. https://doi.org/10.1007/s10816-008-9051-y.

Jo, Y., Hong, S., 2019. Three-dimensional digital documentation of cultural heritage site based on the convergence of terrestrial laser scanning and unmanned aerial vehicle photogrammetry. ISPRS Int. J. Geo-Information 8, 53. https://doi.org/10.3390/ijgi8020053.

Jordan, J.H., 2017. Modeling Ozark Caves with Structure-from-Motion Photogrammetry: An Assessment of Stand-Alone Photogrammetry for 3-Dimensional Cave Survey. BSc Thesis. University of Arkansas.

Kjellman, E., 2012. From 2D to 3D: a photogrammetric revolution in archaeology? MSc Thesis University of Tromsø.

Lee, T.O., 2018. An Examination of Close-Range Photogrammetry and Traditional Cave Survey Methods for Terrestrial and Underwater Caves for 3-Dimensional Mapping. MSc Thesis. University of Southern California.

Maier, M.J., 2015. Package "REdaS.".

Martínez-Fernández, A., Benito-Calvo, A., Campaña, I., Ortega, A.I., Karampaglidis, T., Bermúdez de Castro, J.M., Carbonell, E., 2020. 3D monitoring of Paleolithic archaeological excavations using terrestrial laser scanner systems (Sierra de Atapuerca, Railway Trench sites, Burgos, N Spain). Digit. Appl. Archaeol. Cult. Herit. 19, e00156 https://doi.org/10.1016/j.daach.2020.e00156.

McPherron, S.J.P., 2005. Artifact orientations and site formation processes from total station proveniences. J. Archaeol. Sci. 32, 1003–1014. https://doi.org/10.1016/j.jas.2005.01.015.

Mercader, Julio, 2002a. Excavation of a Chimpanzee Stone Tool Site in the African Rainforest. Science (80-). 296, 1452–1455. https://doi.org/10.1126/science.1070268.

Mercader, J. (Ed.), 2002b. Under the canopy: the archaeology of tropical rain forests, Under the canopy: the archaeology of tropical rain forests. Rutgers University Press, New Brunswick.

Pearson, T., Ainsworth, S., Thomason, B., 2015. Where on Earth Are We? The Role of Global Navigation Satellite Systems (GNSS) in Archaeological Field Survey. Historic England, Swindon.

Peng, F., Lin, S.C., Guo, J., Wang, H., Gao, X., 2017. The application of SfM photogrammetry software for extracting artifact provenience from palaeolithic excavation surfaces. J. F. Archaeol. 42, 326–336. https://doi.org/10.1080/00934690.2017.1338118.

Perfetti, L., Fassi, F., Rossi, C., 2020. Low-cost digital tools for archaeology, in: Aste, N., Della Torre, S., Talamo, C., Adhikari, R., Rossi, C. (Eds.), Innovative Models for Sustainable Development in Emerging African Countries. Research for Development. Springer, Cham, pp. 137–148. https://doi.org/10.1007/978-3-030-33323-2_12.

R Studio Team, 2017. RStudio: Integrated Development for R.

Redovniković, L., Ivković, M., Cetl, V., Sambunjak, I., 2014. Testing DistoX Device for Measuring in the Unfavourable Conditions. In: 6th International Conference on Engineering Surveying, 3–4 April 2014. Czech republic, Prague, pp. 269–274.
Redovniković, L., Stančić, B., Cetl, V., 2016. Comparison of Different Methods of Underground Survey. In: International Symposium on Engineering Geodesy, 20–22 May 2016. Varaždin, Croatia, pp. 465–472.
Regala, F.T., 2016. AESDA - Calib: a calibrator for DistoX/X2 [WWW Document]. URL https://www.aesda.org/wp-content/uploads/2016/09/Calibrator-EuroSpeleo2016-adapted.pdf (accessed 10.2.19).
Regala, F.T., 2015. AESDA Calib - um calibrador para DistoX/X2, in: Proceedings of the 6th National Congress of Speliology. Alvados, Portugal, pp. 77–82. https://doi.org/10.1017/CBO9781107415324.004.
Roosevelt, C.H., 2014. Mapping site-level microtopography with Real-Time Kinematic Global Navigation Satellite Systems (RTK GNSS) and Unmanned Aerial Vehicle Photogrammetry (UAVP). Open Archaeol. 1, 29–53. https://doi.org/10.2478/opar-2014-0003.
Sapirstein, P., 2016. Accurate measurement with photogrammetry at large sites. J. Archaeol. Sci. 66, 137–145. https://doi.org/10.1016/j.jas.2016.01.002.
Sapirstein, P., Murray, S., 2017. Establishing best practices for photogrammetric recording during archaeological fieldwork. J. F. Archaeol. 42, 337–350. https://doi.org/10.1080/00934690.2017.1338513.
Schlager, S., Jefferis, G., Dryden, I., 2020. Package "Morpho.".
Trimmis, K.P., 2018. Paperless mapping and cave archaeology: a review on the application of DistoX survey method in archaeological cave sites. J. Archaeol. Sci. Reports 18, 399–407. https://doi.org/10.1016/j.jasrep.2018.01.022.
Trimmis, K.P., 2015. Fear of the light: mapping modern cave use strategies in Kythera Island Caves. Ethnoarchaeology 7, 141–156. https://doi.org/10.1179/1944289015Z.00000000031.
Tripcevich, N., Wernke, S.A., 2010. On-site recording of excavation data using mobile GIS. J. F. Archaeol. 35, 380–397. https://doi.org/10.1179/009346910X12707321242511.
Unhammer, O.F., 2016. Methodological evaluation of digital photogrammetry in a Middle Stone Age cave context. A case study from Blombos Cave, South Africa. MSc Thesis. The University of Bergen.
Wheatley, D., Gillings, M., 2002. Archaeology, space and GIS. In: Spatial Technology and Archaeology: The Archaeological Applications of GIS. Taylor & Francis, New York, pp. 1–18.
Willis, M.D., Koenig, C.W., Black, S.L., Castañeda, A.M., 2016. Archaeological 3D mapping: the structure from motion revolution. J. Texas Archaeol. Hist. 3, 1–36.
Yamafune, K., Torres, R., Castro, F., 2017. Multi-Image Photogrammetry to Record and Reconstruct Underwater Shipwreck Sites. J. Archaeol. Method Theory 24, 703–725. https://doi.org/10.1007/s10816-016-9283-1.

Archaeology of the Perishable

Ecological Constraints and Cultural Variants in Chimpanzee Termite Fishing

Alejandra Pascual-Garrido and Katarina Almeida-Warren

Selection and transport of materials for tools is ubiquitous throughout our species' evolutionary history. Yet our understanding of early human material culture is heavily skewed toward lithic technology. This poses challenges when reconstructing our technical origins, as organic raw materials, especially plants, likely played a significant role despite their absence from the record until 300 kya. Studies of plant-tool use by living apes can serve as a proxy to reconstruct such aspects of human behavior. Employing archaeological methods, we investigated raw material procurement for termite-fishing tools by three chimpanzee (*Pan troglodytes schweinfurthii*) populations in Tanzania: Gombe, Issa, and Mahale. All communities exploited plant sources from the immediate vicinity of termite mounds, as well as farther away, and reused them. However, at Issa, more parts were sourced per plant, with the number of removals decreasing as distance from the mound increased. These disparities are likely caused by environmental differences. Issa apes might try to minimize transport costs in what is a comparably more open and drier habitat with fewer suitable sources available near mounds. Despite similar raw material types being available, Issa and Mahale chimpanzees exclusively used bark for tool manufacture, while at Gombe, various materials were employed; these differences may reflect cultural variants. Our study highlights how environmental and cultural factors shape chimpanzee technology and identifies similarities to raw material selection processes inferred for Oldowan tool users. The archaeology of the perishable, even if at its infancy, is providing a new framework for reconstructing archaeologically invisible aspects of early human behavior and our own technological origins.

Online enhancements: supplemental tables.

The selection of raw materials for tool manufacture is ubiquitous throughout our evolutionary history stretching back to the earliest stages of stone technology (Braun et al. 2008, 2009; Goldman-Neuman and Hovers 2012). This included the use of flexible procurement strategies involving the targeting of locally available material to keep the energy costs low (Kimura 1999) but that may also have encompassed extensive energy investment in long-distance transport as a result of selective raw material sourcing (Braun et al. 2008). Such strategies are considered key aspects of Plio-Pleistocene hominin adaptations and reflect awareness of technically desirable material, bipedal carrying abilities, and the technocultural traditions of the tool users (Kimura 1999; Schick 1987; Stout et al. 2005, 2010). Furthermore, their long-distance raw material transport indicates foresight, planning, and other cognitive abilities unseen in any technological nonhuman primate (Delagnes and Roche 2005; de la Torre et al. 2003; Schick 1987; Shea 2016; Stout et al. 2010). Yet it is possible that some of the characteristics attributed to the Oldowan were in place long before. All modern nonindustrialized human societies as well as nonhuman primate species use plant materials for implements far more often than bones or stone (Carvalho and Almeida-Warren 2019; González-Ruibal, Hernando, and Politis 2011; Hoffecker and Hoffecker 2018). Thus, while plant-based artifacts are completely absent from the early archaeological record until 300 kya (Conard et al. 2015; Richter and Krbetschek 2015; Thieme 1997), it is unlikely that our early ancestors overlooked the potential value of this material as a tool (Conard et al. 2015; Dominguez-Rodrigo et al. 2001; Wynn and McGrew 1989). This suggests that current archaeological data are missing a substantial component of ancient technology (Panger et al. 2002).

The emerging discipline of primate archaeology compares material records across monkeys and apes and is enriching our understanding of human evolution (Carvalho and Almeida-Warren 2019; Carvalho and Beardmore-Herd 2019; Haslam et al. 2009, 2017; McGrew et al. 2019). For example, we now know that stone tool use and transport by monkeys and chimpanzees generate landscape patterns of raw material acquisition and artifact deposition similar to inferred (archaeologically invisible)

Alejandra Pascual-Garrido is a Postdoctoral Fellow in the Primate Models for Behavioural Evolution Lab of the School of Anthropology and Museum Ethnography of the University of Oxford (Oxford OX2 6PN, United Kingdom [alejandra.pascual-garrido@anthro.ox.ac.uk]). **Katarina Almeida-Warren** is a Doctoral Student in the Primate Models for Behavioural Evolution Lab of the School of Anthropology and Museum Ethnography of the University of Oxford (Oxford OX2 6PN, United Kingdom) and the Interdisciplinary Center for Archaeology and Evolution of Human Behaviour of the Universidade do Algarve (Faro, Portugal). This paper was submitted 14 I 19, accepted 10 II 20, and electronically published 30 IV 21.

Current Anthropology, volume 62, number 3, June 2021. © 2021 by The Wenner-Gren Foundation for Anthropological Research. All rights reserved.
0011-3204/2021/6203-00XX$10.00. DOI: 10.1086/713766

aspects of early human behavior (Boesch and Boesch 1984; Carvalho et al. 2008; Luncz et al. 2016; McGrew et al. 2019; Mercader, Panger, and Boesch 2002; Mercader et al. 2007; Proffitt et al. 2016), including affinities to the Oldowan (Carvalho et al. 2008; McGrew et al. 2019; Toth and Schick 2009). Furthermore, as described for Oldowan technological behaviors (Braun et al. 2008, 2009; Goldman-Neuman and Hovers 2012; Kimura 1999; Stout et al. 2005, 2010), those of nonhuman primates are influenced not only by the local environment but also by their technocultural traditions (Carvalho et al. 2008; Koops, McGrew, and Matsusawa 2013; Luncz, Mundry, and Boesch 2012; Luncz, Wittig, and Boesch 2015; Luncz et al. 2016; McGrew et al. 2019; van Schaik et al. 2003).

But, perhaps as expected, primate archaeology has largely focused on lithic technology, even when plant-based technology is the most common and arguably the most diverse and complex form of primate tool use, as well as the only form involving manufacture (Whiten et al. 1999; Wynn et al. 2011). The opportunity to focus on ephemeral records remains another important asset of studying primate technology, providing a unique framework for reconstructing invisible aspects of hominin behavior (Hernandez-Aguilar 2009; Hernandez-Aguilar, Moore, and Pickering 2007; Hicks et al. 2019; McBeath and McGrew 1982; Sanz et al. 2014; Sept 1992; Stewart, Piel, and McGrew 2011). These studies hold the key for obtaining a comprehensive understanding of primate technology as a whole (Carvalho and Almeida-Warren 2019).

Studies of chimpanzees (*Pan troglodytes*), with whom humans shared a last common ancestor 8–7 mya (Langergraber et al. 2012), are particularly promising. Their prolific use and manufacture of various types of tools (McGrew 1992; Whiten et al. 1999) make chimpanzees key living models for understanding the emergence of technology in our own lineage (Carvalho and Beardmore-Herd 2019; McGrew 1992, 2004; Rolian and Carvalho 2017; Teleki 1974; Toth and Schick 2009; Wynn and McGrew 1989; Wynn et al. 2011).

The first scientifically described mode of chimpanzee tool use was "termite fishing," a skillful technique that makes use of slim and pliable plant probes to extract the nutritious insects from their mounds (Goodall 1964). This technology has gained considerable attention from the paleoanthropology community (Lesnik 2011, 2014) since Backwell and d'Errico (2001) published their paper suggesting the use of bone tools for termite foraging by *Paranthropus* (*Australopithecus*) *robustus*, followed by the discovery of 3.7-mya *Macrotermes* termite mounds at Laetoli in Tanzania (Darlington 2005), roughly synchronous in time and space with *Australopithecus afarensis* (Leakey and Hay 1979; Leakey et al. 1976). That the consumption of termites by chimpanzees and present-day modern humans is a well-documented phenomenon poses the hypothesis that early humans also made use of this resource (Lesnik 2014; Nonaka 1996; O'Malley and McGrew 2014).

The manufacture of termite-fishing tools by wild chimpanzees includes the use of a variety of plant parts and materials, such as bark, grass, leaves, twigs, vines, petioles, and palm fronds (Fay and Carroll 1994; McGrew and Collins 1985; McGrew, Tutin, and Baldwin 1979; Sanz, Morgan, and Gulick 2004). Materials are usually obtained from near the termite mounds but also from farther away when they are locally unavailable. Distances of transport vary between a few meters and more than a kilometer (McGrew, Tutin, and Baldwin 1979; Sanz, Morgan, and Gulick 2004; Teleki 1974), and recovered assemblages indicate a preference for the materials and plant species employed (Bermejo and Illera 1999; Fay and Carroll 1994; Sanz, Morgan, and Gulick 2004; Sanz et al. 2014; Stewart and Piel 2014). However, without a detailed record of the raw material available, it is difficult to assert through artifacts alone whether plant species or materials were used (and thus selected) because of their physical characteristics or were simply used because they were more abundant in the environment (McBeath and McGrew 1982). Recent research has made a start in this respect, providing unequivocal evidence of tool material transport and selection for termite-fishing tools, including cultural preferences for material types used across groups (Almeida-Warren et al. 2017; Pascual-Garrido 2018, 2019; Sanz and Morgan 2007; Sanz, Morgan, and Gulick 2004). However, while a combination of ecological and social factors is known to shape primate material culture (Carvalho et al. 2008; Gruber et al. 2012; Hobaiter et al. 2014; Humle, Snowdon, and Matsuzawa 2009; Koops, Visalberghi, and van Schaik 2014; McGrew et al. 2019; Nishie 2011; Sanz and Morgan 2013; Schuppli and van Schaik 2019), including that of hominins (Andrefsky 1994; Braun et al. 2008, 2009; Goldman-Neuman and Hovers 2012; Harmand 2009; Kimura 1999; Stout et al. 2005, 2010, 2019), the extent to which these factors dictate raw material use for termite-fishing tools by our closest living relatives still remains largely unexplored (Almeida-Warren et al. 2017; Koops, McGrew, and Matsuzawa 2013; McBeath and McGrew 1982; Musgrave et al. 2016, 2020; Sanz and Morgan 2007; Sanz et al. 2014).

Chimpanzee termite fishing offers a unique opportunity to investigate raw material procurement for tools: First, unlike the nomadic characteristic of other social insects habitually harvested with implements by these apes (Pascual-Garrido et al. 2013), *Macrotermes* termites reside in the same conspicuous mounds for decades (Sanz and Morgan 2013) and possibly for much longer (Darlington 2005). This allows not only the easy recovery of artifacts at their place of discard (termite mounds; Jones and Sabater Pi 1969; McGrew and Collins 1985; Suzuki 1966) but also the systematic study of raw material availability and use near tool use sites (Almeida-Warren et al. 2017; McBeath and McGrew 1982; Pascual-Garrido 2019).

With the aim of more precisely defining the determinants that may influence raw material use for termite-fishing tools by wild chimpanzees (McBeath and McGrew 1982; Sanz et al. 2014), we extended our study conducted at the Issa Valley and compared it (Almeida-Warren et al. 2017) with two other genetically related termite-fishing communities living in different habitats in western Tanzania: Gombe and Mahale (Inoue et al. 2013; Piel et al. 2013). Previous studies indicate differences in

raw material use and transport among these sites (Almeida-Warren et al. 2017; Pascual-Garrido 2018). In this ethoarchaeological study, we evaluate the influence of environmental and cultural factors on raw material procurement for termite-fishing tools by chimpanzees by addressing the following questions: How are chimpanzees using sources of raw material for the manufacture of termite-fishing tools? Are sources used once or multiple times? How does this compare with the general abundance of the source species and its location (distance) in relation to the targeted mound?

Given that raw material availability and type, distance from the source, and cultural processes influence stone technology in chimpanzees (Carvalho et al. 2008; Luncz, Mundry, and Boesch 2012; Luncz, Wittig, and Boesch 2015; Luncz et al. 2016) and early humans (Andrefsky 1994; Braun et al. 2008, 2009; Kimura 1999; Stout et al. 2005, 2010), we expect these variables to also be determinants of chimpanzee termite-fishing technology. We also discuss implications for our understanding of the origins of human technology.

Background

Our study took place in three populations of *Pan troglodytes schweinfurthii* living in different habitats in western Tanzania (fig. 1). Study sites include (1) Gombe Stream National Park (S 4.67, E 29.65; 772–1,500 m in altitude), set on the eastern shore of Lake Tanganyika (fig. 1). The 35-km^2 national park is characterized by thicket woodland and vine tangle interspersed with small patches of open woodland and deep valleys falling from the rift escarpment to the lake. A wet season (November–April) is followed by a dry one (May–October), with an average annual rainfall of 1,495 mm (Collins and McGrew 1988). (2) Issa Valley (S 5.50, E 30.56; 900–1,800 m in altitude) is one of the driest, most open, and most seasonal habitats where chimpanzees reside. It is located 81 km inland and east of Lake Tanganyika (fig. 1), and its vegetation is mainly miombo woodland, dominated by *Brachystegia* and *Julbernardia* (Fabaceae) and interspersed with swamp, dry grassland, wooded grassland, woodland, gallery forest, thicket forest, and hill forest (Hernandez-Aguilar 2009). As in Gombe, a wet season (November–April) is followed by a dry one (May–October), with an average annual rainfall of 1,200 mm (Stewart and Piel 2014). (3) Mahale Mountains National Park (S 6.02, E 29.45; 772–2,462 m in altitude) is located on the eastern shore of Lake Tanganyika (fig. 1). Our study took place in Bilenge (Collins and McGrew 1987), located approximately 9 km to the north of the long-term Japanese research camp (Nakamura et al. 2013; Nishida and Uehara 1980). The terrain is mostly rugged and hilly and is dominated by the Mahale Mountains chain, which runs from the northwest to the southeast across the western part of the park. Bilenge is largely an open grassy forest woodland of *Brachystegia*, with narrow strips of vine tangle and forest along the valley. As at Gombe and Issa, a wet season (November–April) is followed by a dry period (May–October), with an average annual rainfall of 1,400 mm (Collins and McGrew 1988).

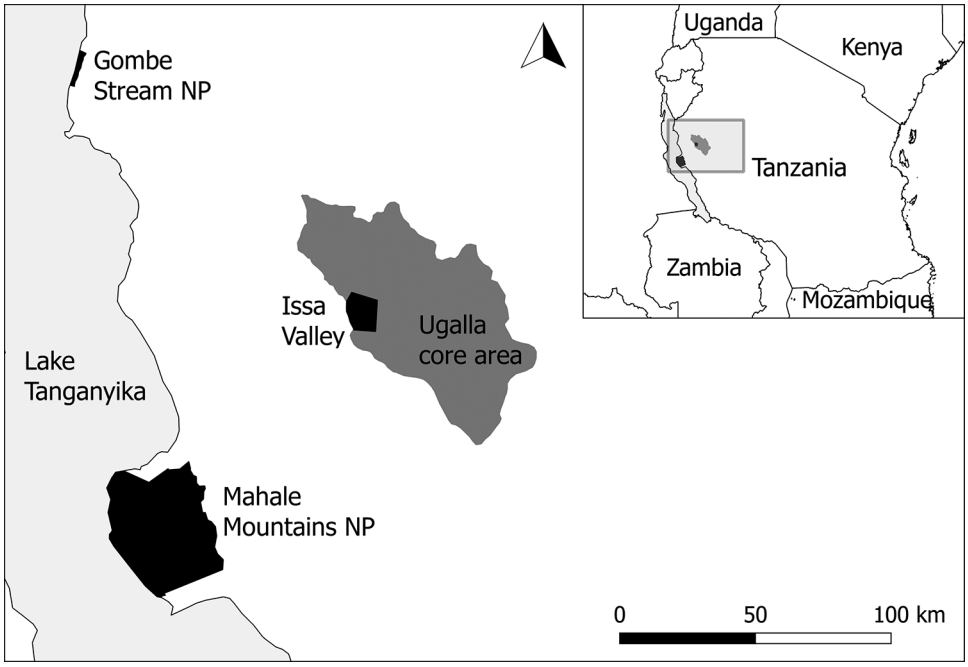


Figure 1. Map of western Tanzania indicating the three study sites. Map credit: Katarina Almeida-Warren. NP = National Park.

Study Communities

Study communities included the habituated community of Kasekela of Gombe Stream National Park (Goodall 1986), the partly habituated community of the Issa Valley (Stewart and Piel 2014), and the unhabituated Bilenge group of the Mahale Mountains National Park (McGrew and Collins 1985; Nishida and Uehara 1980; Uehara 1982). While these three populations are currently, but possibly not entirely, isolated from each other because of habitat fragmentation, genetic evidence suggests a history of gene flow between the Issa and Mahale populations and possibly also with Gombe (Inoue et al. 2013; Piel et al. 2013).

Chimpanzees at the three sites habitually termite fish at *Macrotermes* mounds. While apes at Gombe and Mahale are known to employ a wide variety of materials obtained from different plant species to manufacture their implements (McGrew 1992; McGrew and Collins 1985; Nishida and Uehara 1980; Uehara 1982), Issa chimpanzees specialize only in bark (Stewart and Piel 2014). Chimpanzees at Gombe termite fish year-round, though efforts are most frequent at the start of the rainy season from October to December (Goodall 1986). At Issa and Mahale, termite fishing is limited to the rainy months, with the most productive period being at the onset of the first rains (October–November; McGrew and Collins 1985; Stewart and Piel 2014; Uehara 1982). While direct observation of the behavior was possible only at Gombe (Lonsdorf 2005), at all study sites, research focused on the recovery of artifacts and other remnants left by chimpanzees as a result of their termite-fishing activities. This ensured a better standardization of the data collected and an unbiased cross-site comparison.

Methods

Data Collection

Data were collected by Alejandra Pascual-Garrido and Katarina Almeida-Warren, assisted by experienced Tanzanian research assistants, over 285 days from 2014 to 2016. This included a total of 117 days at Gombe (Pascual-Garrido: October 12–November 12, 2014; November 14–December 14, 2015; October 13–November 12, 2016; Almeida-Warren: April 16–May 12, 2015), 53 days at Mahale (Pascual-Garrido: November 25–December 14, 2014; October 20–November 8, 2015; November 21–December 8, 2016), and 115 days at Issa (Pascual-Garrido: January 9–February 9, 2015; Almeida-Warren: May 17–June 27, 2015; November 2–December 15, 2015).

Research focused on 29 *Macrotermes* termite mounds that had been targeted by chimpanzees for termite fishing: 7 at Gombe, 8 at Issa, and 14 at Mahale. Because of time constraints and the need to collect sufficient data for each mound, chosen mounds constitute a subset of mounds at which termite fishing occurred. A mound was considered to have been targeted if one or more of the following criteria applied: (1) apes were seen fishing, (2) artifacts, fragments, debris, or raw materials modified as a result of the manufacture process were present, and (3) plants from which raw material was sourced were detected (source plants; Almeida-Warren et al. 2017; Pascual-Garrido 2018). At each of these mounds, a site datum was assigned to a nail placed on a tree near the center of the mound to allow measurements in a standardized coordinate system, to map the relative positions of sources, and to measure their distances to the targeted mound (Almeida-Warren et al. 2017; Carvalho et al. 2008). Mounds were visited every one to three days so that abandoned artifacts and sources could be recorded.

Raw Material Availability

The availability of raw material for termite-fishing tools (i.e., living plants) was recorded for each targeted mound once ($n = 29$). Employing cardinal orientations (north-south, east-west), we divided the mound vicinity into four quadrants and arbitrarily selected the northwest 90° quadrant of a 5-m circle around the mound for scrutiny (Almeida-Warren et al. 2017; Koops, McGrew, and Matsuzawa 2013; McBeath and McGrew 1982). For each surveyed quadrant, we counted the number of plants suitable for tool making by species and material class (bark, twig, vine, grass). Material types were determined on the basis of previous research (McGrew and Collins 1985; McGrew, Tutin, and Baldwin 1979; Stewart and Piel 2014). Suitable sources were defined as plants that could provide long, thin, flexible pieces from which a functional termite-fishing implement could be made (Almeida-Warren et al. 2017).

Source Plants

Previous research at these sites indicates that chimpanzees obtain their tool material from plants close to targeted termite mounds but also from meters away (Almeida-Warren et al. 2017; Pascual-Garrido 2018). Thus, we surveyed for vegetation that chimpanzees had used for tool making (source plants) within a 20-m radius of the mound. Some materials may have occasionally been obtained from farther away (Pascual-Garrido 2018), but implementing a standardized search field allowed cross-site comparison and ensured data collection within a limited time frame.

We followed the criteria established by Pascual-Garrido (2018) for the identification of sources discernible by the following: (1) one or multiple removals (scars) were present as a result of apes removing material, (2) scars were located in specific parts of the specimen, (3) only a selected number of species showed signs of being sourced, (4) they were normally concentrated within the mound periphery, (5) they included species represented in the tool assemblage, and (6) chimpanzees were directly observed detaching the material. For each source identified, we recorded the distance from the targeted mound, the species, the type of material procured (i.e., twigs, bark), and the number of scars—the latter as an indicator of the intensity of use. Each source was marked and assigned a number to avoid recording it twice during repeated visits to the mounds. Samples from all plants recorded were collected and

curated in camp with a dryer for future identification by Frank Mbago, Department of Botany, University of Dar es Salaam, Tanzania.

Statistical Analyses

Given that all data in this study had a nonnormal distribution ($P < .05$), nonparametric statistics were implemented. To investigate potential differences among materials used, their availability, and the differences between them (i.e., raw material classes, species) both within and between sites, we conducted tests for the equality of proportions using the prop.test function in R with Yates's continuity correction. To test whether pairs of proportions were different within and between sites, we calculated individual *P* values of paired groups via pairwise post hoc proportion tests with the "Bonferroni" adjustment method. Kruskal-Wallis tests were employed as a nonparametric version of one-way analysis of variance (ANOVA) to compare continuous variables (i.e., number of scars per individual source) between sites. To assess differences between pairs of sites, we employed post hoc pairwise Wilcoxon rank sum tests. To examine whether the distance of a source from the targeted mound and relative species abundance in the vicinity of the mound influenced the number of times a plant was procured and whether there were site-specific differences, we applied generalized linear mixed models (GLMMs; Zuur et al. 2009) with the number of parts removed per individual plant (scars) as the response variable. As predictor variables with fixed effects, we included the site, the distance from the source to target mound, and mound-specific sourced species abundance relative to known sourced species, as well as their possible interactions (three-way and two-way). To control for possible between-mound variation, we included mound ID as a random effect. Additionally, before fitting the model, we *z* transformed the distance from the mound (mean = 6.57 m, SD = 5.42) and species abundance (mean = 0.40, SD = 0.32). Because the response variable was zero-truncated (minimum value = 1) and there was evidence of moderate overdispersion (dispersion ratio = 3.2, $P < .01$), we applied a zero-truncated Poisson-lognormal model with the addition of plant ID as an observation-level random effect (Harrison 2014). This was achieved using the glmmTMB (ver. 0.2.3) package in R. To test whether the predictors had a collective effect on the number of removals, we first conducted full null model comparison using a likelihood ratio test (R function ANOVA); the null model excluded all fixed effects but was otherwise identical to the full model (Dobson 2002; Schielzeth and Forstmeier 2009). We tested the significance of three-way and two-way interactions by systematically dropping them from the model one at a time and comparing the resulting reduced models with the respective full model using the drop1 function in R. Individual effects' *P* values were based on the likelihood ratio test results from the drop1 function (Dobson 2002). Collinearity between predictor variables, calculated by applying the vif function of the R package car (Fox and Weisberg 2011) to a linear model lacking the random effects and interactions, was not an issue (maximum variance inflation factor = 1.36). All analyses were performed in R (R Core Team 2017). All tests were two-tailed, and the level of significance for all statistical analyses was set at $P < .05$.

Ethical Note

No data were collected from chimpanzee individuals for the purpose of this study. Data were recorded when chimpanzees were absent from the study mounds, with no direct contact with any of the individuals. Research was conducted under the permits of Tanzania National Parks (TANAPA), Tanzania Wildlife Research Institute (TAWIRI), and Tanzania Commission for Science and Technology (COSTECH).

Results

Chimpanzees at Gombe, Issa, and Mahale behaved similarly in that they sourced raw material from the immediate vicinity of termite mounds and also from farther away, selected materials and plant species to make their implements (Pascual-Garrido 2018), and reused sources (fig. 2). However, chimpanzees in Issa exploited sources more intensively (i.e., more plant parts were extracted per individual), possibly to save transport distance costs in what is a comparably more open and drier habitat with less available raw material nearby. Despite similar raw material types available at all sites, Issa and Mahale chimpanzees exclusively used bark for tool manufacture, while at Gombe, various materials were employed—differences that potentially reflect cultural variants (i.e., behaviors present in at least one site and absent elsewhere without clear ecological differences; van Schaik et al. 2003; Whiten et al. 1999, 2001).

Abundance of Raw Material versus Use

Regarding the abundance of suitable sources per mound (plants that could provide at least one type of raw material), Gombe had the highest, followed by Mahale and Issa (table 1). At all sites, there was a significant difference between the proportion of raw material classes available near mounds, with twigs being the most abundant, followed by bark. Grass was rare at all sites, while vines were present only at Gombe (table 1). Differences were maintained when pairs of material types for each site were compared, except between vines and grasses at Issa, where they were equally rare (table A1; tables A1–A5, B1, C1, C2 are available online). There were also significant differences between sites regarding abundance by material type (table A2). These differences were maintained when pairs of sites were compared, except between Issa and Mahale, where grasses and vines were equally available or absent, respectively (table A3).

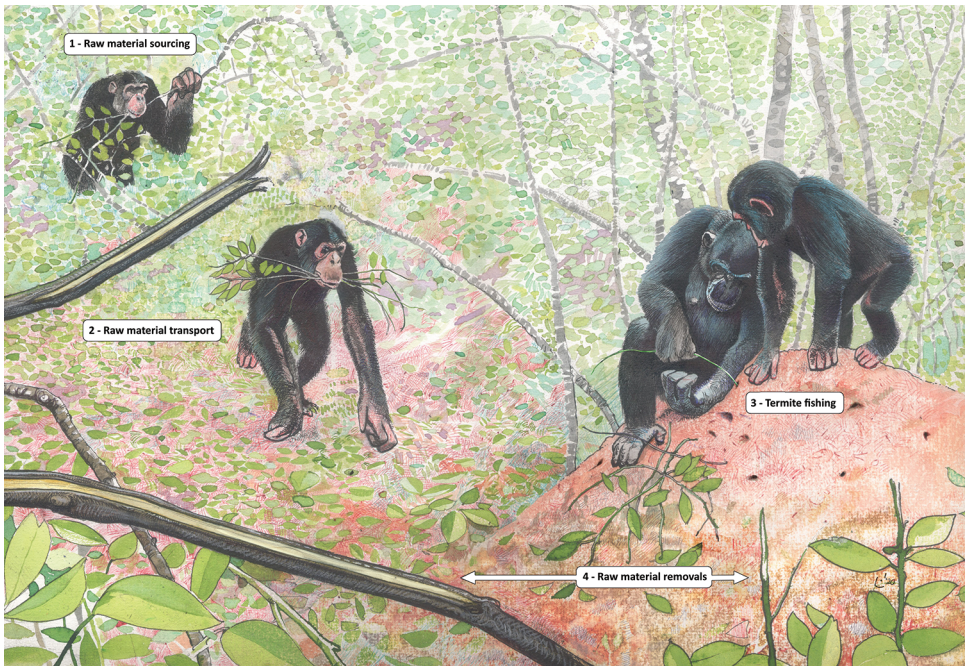


Figure 2. Raw material sourcing for termite-fishing tools by wild chimpanzees. 1, Tool material sourcing from the source plant. 2, Raw material transport to the tool use site (termite mound). 3, Tool manufacture and use. 4, Physical traces left on source plants as a result of chimpanzee tool material removal (*left*: bark removal; *right*: twig removal).

However, despite the availability of various materials at all sites, only Gombe chimpanzees procured different materials to make their implements (table 2). While Gombe chimpanzees used twig (44.0%) and bark (48.7%) in almost equal proportions, they manufactured only a small percentage of their utensils from vine (6.1%), while grass was used only rarely (1.2%). Only artifacts made from bark were recovered at Issa and Mahale (Pascual-Garrido 2018).

Suitable versus Sourced Plants

To test for species selection, we compared the proportion of plants from suitable versus sourced species. Results showed that chimpanzees at Gombe used 85.3% of the total suitable species available, while at Issa and Mahale, chimpanzees exploited only 12% (table A4). Pairwise tests between sites revealed significant differences in the proportion of plants of known source species used between Gombe and all sites ($P <$ .001). This indicates that chimpanzees at Mahale and Issa were more selective regarding their tool species. There was no significant difference in proportions between Mahale and Issa ($P = 1$; table A5).

Source Taxa

Species exploited for implements during this study included a total of 31 species from 15 families, with six species yielding more than one tool material type. Annonaceae and Tiliaceae were the most prevalent families, the latter represented exclusively by one genus: *Grewia* (table 3, adapted from Pascual-Garrido 2018). To test whether chimpanzees preferred some species over others, we compared for each source species the number of individuals exploited relative to their general abundance within the source species near mounds. Results showed that at Gombe, *Monanthotaxis poggei*, *Grewia* spp., and *Uvaria angolensis* were preferentially used (table B1; fig. 3), while at Issa and Mahale, source species were selected equally (except for *Azanza garckeana* at Issa). Interestingly, *Dicyophlena lucida* at Gombe and *A. garckeana* at Issa revealed a significant but inverse difference, with more individuals available than sourced, suggesting that these species, even if exploited for tool manufacture, were not preferred.

Table 1. Abundance of raw material types for each site

Site	Total	Mean per mound	Bark	Twig	Vine	Grass	χ^2	*P*
Gombe	457	65.3	.486	.871	.013	.116	892.925	<.001
Issa	264	33	.182	.936	0	.023	756.47	<.001
Mahale	639	45.6	.801	.983	0	.017	2,057.557	<.001

Note. The total was calculated based on the plants that could provide suitable raw material. The χ^2 and *P* values are a result of an equality of proportions test between raw material types for each site total.

Table 2. Proportion of raw material types available versus proportion of tool materials

Site, type	Raw material	Tools	χ^2	*P*
Gombe:				
Bark	.486	.487	0	1
Grass	.116	.012	35.75	<.001
Twig	.871	.44	178.644	<.001
Vine	.013	.061	12.944	<.001
Total (*n*)	457	411		
Issa:				
Bark	.182	1	242.873	<.001
Grass	.023	0	1.863	172
Twig	.936	0	333.13	<.001
Vine	0	0		
Total (*n*)	264	140		
Mahale:				
Bark	.801	1	4.926	.026
Grass	.017	0	0	1
Twig	.983	0	434.21	<.001
Vine	0	0		
Total (*n*)	639	25		

Note. Raw material was calculated based on the number of plants that could provide suitable raw material. Adapted from Pascual-Garrido (2018).

Reuse of Source Plants

The number of scars left as a result of chimpanzees removing tool material from an individual plant (Pascual-Garrido 2018) can function as a proxy for determining sourcing intensity (i.e., how often a plant is procured; fig. 4). At all sites, chimpanzees exploited sources once and multiple times; however, the intensity of use differed among sites.

At Gombe, chimpanzees sourced individual plants once (56.4%) and multiple times (43.6%) in almost equal proportions (χ^2: $\chi^2 = 2.3143$, df = 1, $P = .128$, $n = 140$). At Mahale, plants were mostly procured once (73.3%; $\chi^2 = 9.8$, df = 1, $P < .05$, $n = 45$), while at Issa, more than half (63.1%) of all recorded sources were used multiple times ($\chi^2 = 8.3934$, df = 1, $P < .05$, $n = 122$). Likewise, the average number of parts removed per plant differed significantly among sites (Kruskal-Wallis: $\chi^2 = 25.328$, df = 2, $P < .001$). The post hoc pairwise Wilcoxon rank sum test revealed that this difference was maintained among all sites (table A6). While Gombe chimpanzees removed, on average, 2.4 parts per individual plant (range = 1–22, SD = 2.85, $n = 140$), Mahale chimpanzees detached on average 1.3 parts (range = 1–3, SD = 0.55, $n = 44$), and at Issa, individual sources had the largest number of removals, with an average of 3.2 parts detached (range = 1–23, SD = 3.6, $n = 122$).

Use of Source Plants: Effects of Distance from Mound and Species Abundance on Number of Removals

If the number of removals per individual plant decreases the farther it is located from the targeted mound, it seems likely that a transport distance cost-benefit effect is at play, with apes reducing the costs of transport by preferentially exploiting sources closer to the mound rather than turning to those located farther away.

Overall, distance from the mound, species abundance, and study site influenced the number of removals (GLMM, full null model comparison: $\chi^2 = 90.03$, df = 11, $P < .001$). In the full model, the three-way interaction among site, distance

Table 3. Families and species of plants sourced for tool material types at Gombe, Issa, and Mahale

Family, species	Gombe	Issa	Mahale
Annonaceae:			
Artabotrys collinus		B	
Artabotrys monteiroae		B	
Annona senegalensis	B	B	
Monanthotaxis buchananii		B	B
Monanthotaxis poggei	B, T		
Uvaria angolensis	B, T	B	B
Uvaria sp. A of FTEA		B	B
Uvaria welwetschii		B	
Apocynaceae:			
Dicyophlena lucida	B, T		
Diplorhynchus condylocarpon	B, T		
Saba comorensis	B	B	B
Asclepiadaceae:			
Gymnema sylvestre	T		
Capparidaceae:			
Maerua holstii			B
Combretaceae:			
Combretum zeyheri	T		
Connaraceae:			
Byrsocarpus orientalis	T		
Euphorbiaceae:			
Cleistanthus polystachyus		B	
Gramineae:			
Grass	G		
Guttiferae:			
Garcinia buchananii			B
Malvaceae:			
Azanza garckeana		B	
Rubiaceae:			
Rothmannia urcelliformis		B	
Sabicea orientalis	V		
Sapindaceae:			
Allophylus congolanus	B, T		B
Paullinia pinnata			B
Sapotaceae:			
Mimusops kummel			B
Sterculiaceae:			
Dombeya burgessiae		B	
Tiliaceae:			
Grewia sp.		B	
G. forbesii	B, T		
G. platyclada	B		
G. mollis	B		
G. rugosifolia		B	
G. stolzii			B

Note. Adapted from Pascual-Garrido (2018). B = bark; FTEA = Flora of Tropical East Africa; G = grass; T = twig; V = vine.

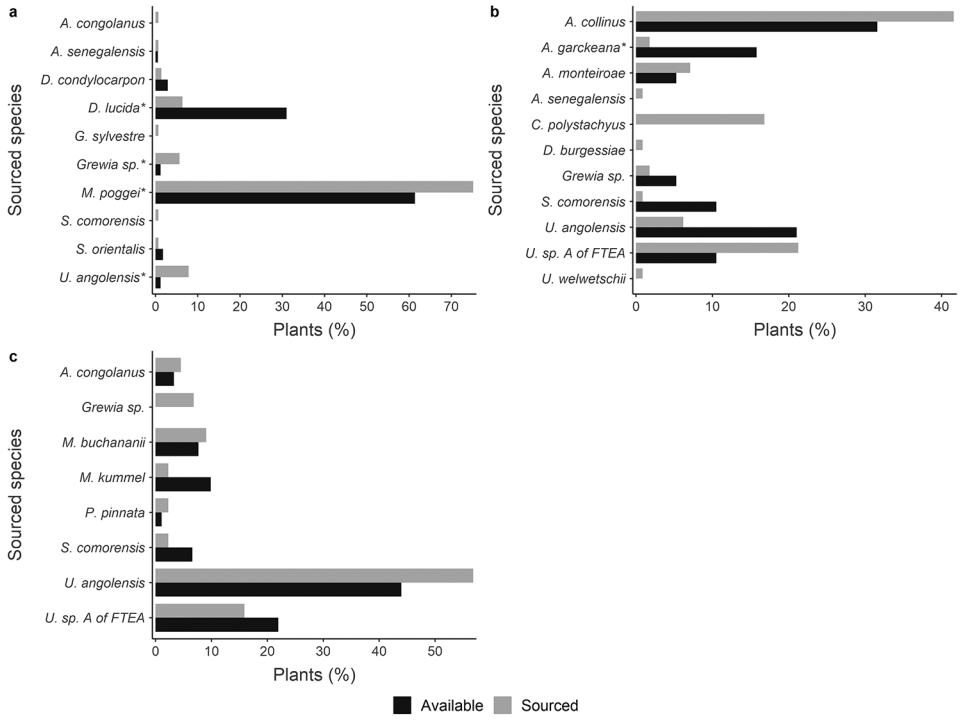


Figure 3. Percentage of plants sourced for tools by species (sourced; gray) compared with the species' general availability among exploited species (available; black). *a*, Gombe. *b*, Issa. *c*, Mahale. An asterisk indicates a significant difference between proportions where $P < .05$. Plants of the genus *Grewia* were combined into a *Grewia* sp. taxon, as it was not always possible to identify individual species.

from the mound, and species abundance appeared nonsignificant ($P = .208$; table C1), as did the two-way interaction between distance from the mound and species abundance ($P = .207$; table C2).

After the nonsignificant interactions were removed, the resulting reduced model revealed that the influence of distance from the mound and species abundance on the number of removals differed among the three study sites (table 4; fig. 5).

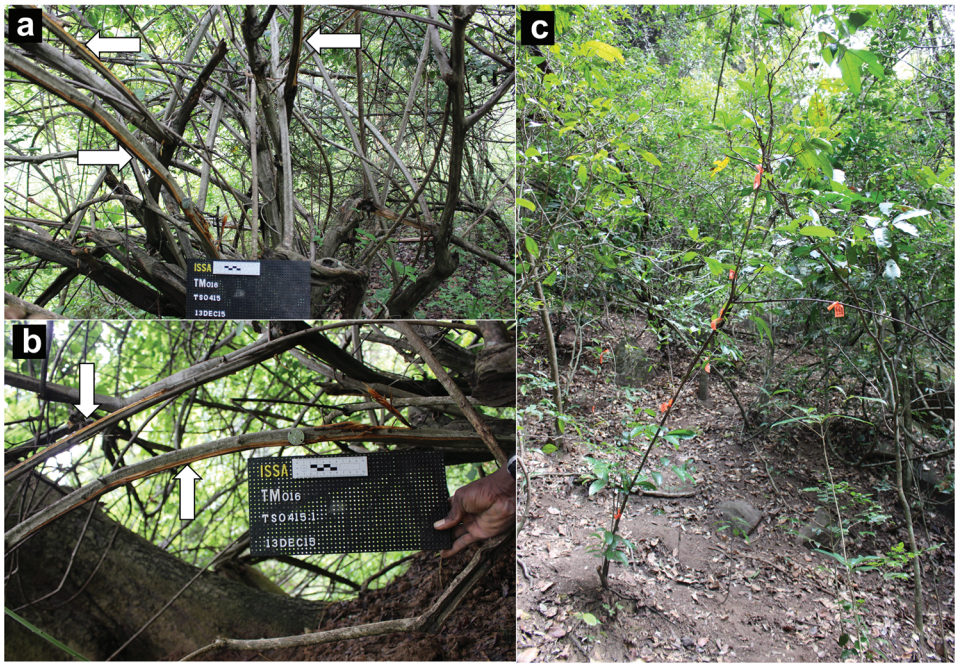


Figure 4. Examples of source plant locations at Issa where chimpanzees removed tool material, indicated by arrows (*a*, *b*) or orange tape (*c*). Photo credit: Katarina Almeida-Warren.

Distance from the mound has a clear negative effect on the number of removals at Issa, while at Gombe and Mahale, this effect shows positive and neutral trends, respectively. Conversely, species abundance has a clear negative effect on the number of removals at Gombe, while there is no evident trend for Issa or Mahale.

Discussion

The breadth and diversity of insectivory by modern nonindustrialized human societies (Allsop and Miller 1996; Berbesque and Marlowe 2009) and wild ape populations (Bogart and Pruetz 2011; Deblauwe 2009; Hicks et al. 2019; Schöning et al. 2008) make it likely that early humans were also exploiting this resource (Backwell and d'Errico 2001; Lesnik 2014; O'Malley and McGrew 2014). Given the prevalence of perishable tools to harvest insects among chimpanzees (McGrew 1992), it seems likely that early humans also used similar technologies (McGrew 2014).

Our previous studies indicate differences across study sites in the material selection and transport of termite-fishing tools (Almeida-Warren et al. 2017; Pascual-Garrido 2018). In this study, we evaluate the extent to which raw material availability and thus the local environment dictate these differences. Our results show that chimpanzees living in a drier and more open habitat with less raw material available nearby exploited sources more intensively, with more parts detached per individual plant, and reused them more frequently. Independent of habitat, Issa and Mahale chimpanzees preferred bark to fish termites, while Gombe chimpanzees used various materials. Unless other environmental differences, such as the efficiency of different raw material types, influence this choice, this discrepancy may be socially driven. Our study shows that, as described for early humans (Braun et al. 2008, 2009; Goldman-Neuman and Hovers 2009, 2012; Harmand 2009) and chimpanzee stone technology (Carvalho et al. 2008; Luncz et al. 2016), raw material plays a major role in the variation of chimpanzee perishable technology. While part of this variation may be due to differences in the ecological context (i.e., raw material abundance), other aspects, such as material selection, could not be attributed to the same ecological reasons and thus, if socially learned and transmitted repeatedly across generations, as suggested by recent findings from Pascual-Garrido and Scheffrahn (2020), may be termed cultural (Koops, Schuppli, and van Schaik 2018; van Schaik et al. 2003; Whiten et al. 1999, 2001).

Raw Material Use and Selection

We would expect that if chimpanzees show no selectivity for the raw materials they use to manufacture tools, the distribution of artifacts would reflect the distribution of available material types around the mounds. However, when we compared the actual tool assemblage with an expected assemblage based on the percentage of raw material available around mounds, there were consistent differences. At all sites, twigs were the most abundant material, followed by bark and, in a much lower proportion, grass and vine (cf. table 2). Despite this, only Gombe chimpanzees employed different materials for tools, while Issa and Mahale chimpanzees used only bark. If chimpanzee technology were positively correlated to the availability of materials, we would expect chimpanzees at Issa and Mahale to also incorporate other materials and, more importantly, for all three communities to favor twigs. This is clearly not the case.

On the basis of the recovery of chimpanzee assemblages, preferences for materials have been described across sites (cf. Stewart and Piel 2014). In some cases, their use is linked to differences in tool functions (probe vs. puncture; Sanz and Morgan 2007). However, this cannot be applied to our studied communities given the presence of termite-fishing probes alone. While the lack of use of grass and vines at Issa may correspond

Table 4. Results from the final reduced model (generalized linear mixed model; lacking the nonsignificant three-way and two-way interactions) investigating potential predictors influencing number of removals

Term	Estimate	SE	Lower CI	Upper CI	χ^2	df	P[c]
Intercept	.258	.244	−.220	.736			NI[d]
SiteIssa[a]	.417	.288	−.148	.982			NI[d]
SiteMahale[a]	−1.208	.435	−2.060	−.356			NI[d]
Distance[b]	.121	.287	−.442	.684			NI[d]
Abundance[b]	−.523	.106	−.732	−.315			NI[d]
SiteIssa × distance	−.740	.295	−1.318	−.162	7.747	2	.021
SiteMahale × distance	−.081	.517	−1.093	.932			
SiteIssa × abundance	.565	.129	.313	.817	2.538	2	<.001
SiteMahale × abundance	.636	.439	−.223	1.496			

Note. CI = confidence interval.

[a] Site was dummy coded, with Gombe as the reference category.

[b] Variables were z transformed to a mean of 0 and SD of 1.

[c] Results from the likelihood ratio test using the drop1 function.

[d] Not indicated (NI) because it has a limited interpretation.

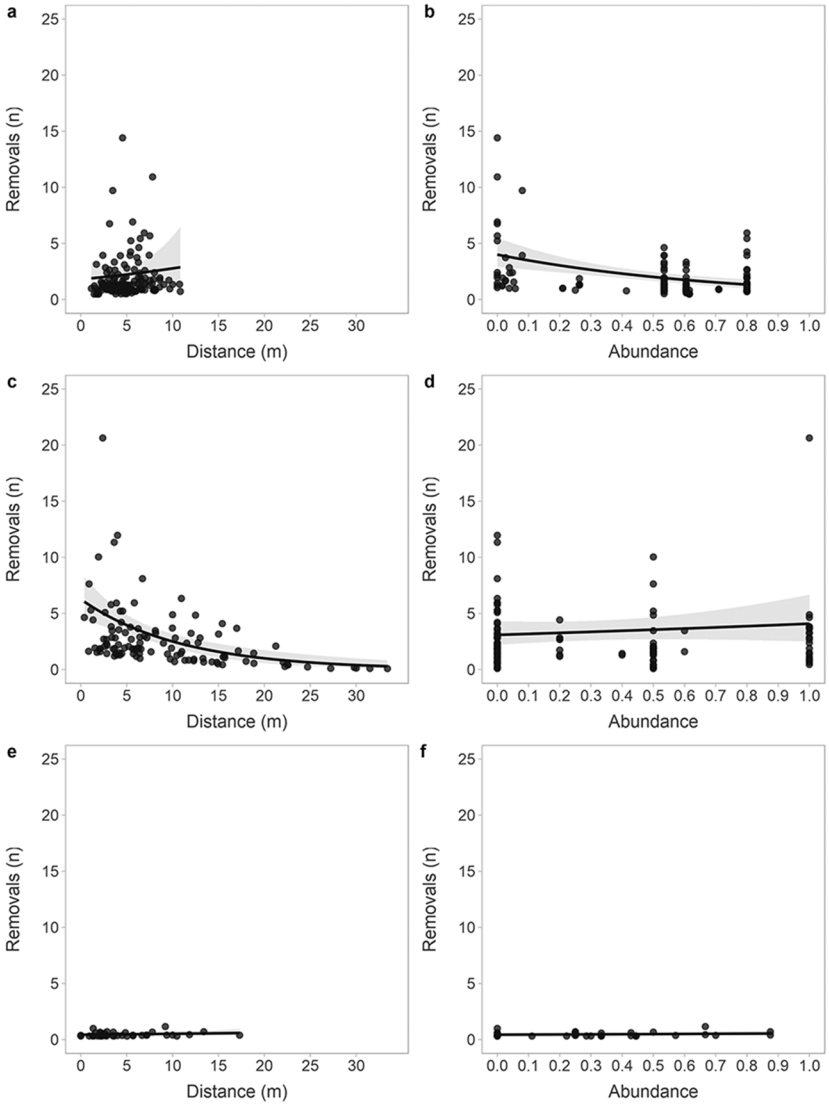


Figure 5. Comparison of the number of removals per sourced plant by study site in response to the distance from the mound (*a*, *c*, *e*) and species abundance (*b*, *d*, *f*). *a*, *b*, Gombe. *c*, *d*, Issa. *e*, *f*, Mahale. The circles represent individual sourced plants recorded at each study site (Gombe: $n = 141$; Issa: $n = 113$; Mahale: $n = 44$). The fitted generalized linear mixed model and confidence intervals are depicted by the line and the gray area, respectively.

to a lower abundance or absence of these materials at mounds, the absence of twigs cannot be explained by the same ecological reasons. That post hoc experiments with twigs showed that this material was also suitable for termite fishing (Almeida-Warren et al. 2017) further supports the lack of an environmental explanation for the absence of twigs in the Issa community. Lack of knowledge or familiarity is also falsified as a possible explanation given the use of other materials by these apes to access underground tubers and fish for *Camponotus* ants (Hernandez-Aguilar, Moore, and Pickering 2007; Wondra et al. 2016). Unless other environmental factors dictate the exclusive employment of bark by Issa chimpanzees (i.e., tool material efficiency, prey behavior), social learning, which plays a fundamental role in the acquisition of termite-fishing skills and is key for the development and maintenance of cultural behaviors and traditions, particularly from mother (and older siblings) to offspring (Koops, Schuppli, and van Schaik 2018; Lonsdorf 2005, 2006; Lonsdorf, Eberly, and Pusey 2004; Musgrave et al. 2016, 2020; Sanz and Morgan 2013; Sanz et al. 2014; Schuppli and van Schaik 2019), may be responsible for this "specialty."

At Mahale, while bark was also predominantly employed in the past, other types of materials were also used decades ago (McGrew and Collins 1985; Nishida and Uehara 1980; Uehara 1982). That only bark implements were recovered during this study (Pascual-Garrido 2017) may correspond to our low sample size ($n = 25$) compared with the total number of tools collected by McGrew and Collins (1985; $n = 290$) and Nishida and Uehara (1980; $n = 133$). A larger sample size is necessary to assess whether chimpanzees from Bilenge at Mahale

have become exclusive bark users in recent decades. Historical data from Gombe (McGrew, Tutin, and Baldwin 1979) also corroborate changes in the proportion of the class of material employed. At that time, almost half (48%) of the artifacts were made from grass, while bark (21%), vine (17%) and twigs (10%), and leaves of oil palms (4%) were less represented. This contrasts with the percentages reported in our study (bark, 48.7%; twig, 44.0%; vine, 6.0%; grass, 1.2%). Changes in the raw material available might explain these differences. For example, at Gombe, grass near mounds may have decreased during the past decades after the ending of annual burning, which allowed the natural regeneration of vegetation (Collins and McGrew 1988; Anthony Collins, personal communication). Alternatively, previous studies might have focused on mounds in areas where grass was more abundant (McGrew, Tutin, and Baldwin 1979). However, without a detailed description of the raw material available near mounds at that time, this is simply not possible to test. It could also be that changes in tool materials by Gombe chimpanzees occurred as a result of behavioral shifts toward greater material efficiency, as recently documented for drinking sponges (leaf vs. moss) manufactured by the Sonso community at the Budongo Forest, Uganda (Hobaiter et al. 2014; Lamon et al. 2018). Future field experiments should aim to explore the potential role of efficiency in tool material selection for termite fishing by chimpanzees.

Source Species

Plant species used for termite fishing have been recorded at various sites, including the current ones (Almeida-Warren et al. 2017; Pascual-Garrido 2018). Previous studies indicate a prevalence of plant species in tool assemblages (Bermejo and Illera 1999; Fay and Carroll 1994; McGrew and Collins 1985; McGrew, Pruetz, and Fulton 2005; Sanz and Morgan 2007; Sugiyama 1985; Suzuki, Kuroda, and Nishihara 1995). However, without a detailed record of the raw material available, these studies could not assess species selection empirically. McBeath and McGrew (1982) were the first to address the influence of plant variety on chimpanzee biodegradable technology. These authors found that chimpanzees at Mount Assirik, Senegal, concentrated their termite fishing at mounds close to abundant *Grewia lasciodiscus*, the species most represented in tool assemblages. Likewise, botanical surveys conducted at Goualougo, Republic of Congo (Sanz, Morgan, and Gulick 2004), and at Issa Valley (Almeida-Warren et al. 2017) indicate selection for plant species to make termite-fishing implements. Our study provides further evidence supporting this but also reveals differences across the study communities.

At Gombe, chimpanzees seemed to be more "generalist," exploiting almost 90% of all suitable species available in the vicinity of mounds—while at Issa and Mahale, apes were more "specialist," using only 12% of the total suitable species accessible (cf. table A4). These differences may likely correspond to the exclusive use of bark by Issa and Mahale chimpanzees, further evidenced by the differential sourcing of materials from the same plant species (i.e., *Uvaria angolensis*, *Grewia* spp., and *Allophylus congolanus*) between the study communities (cf. table 3). Interestingly, *Monanthotaxis poggei*, *U. angolensis*, and *Grewia forbesii*, three species preferentially used by Gombe chimpanzees, also provide termite-fishing material for apes living in West Africa (McBeath and McGrew 1982; McGrew, Pruetz, and Fulton 2005). Perhaps these taxa hold still-unexplored mechanical and physical characteristics that make them ideal for termite fishing.

But what makes a "good" material for termite-fishing tools remains largely unexplored and deserves further investigation. As McGrew, Tutin, and Baldwin (1979) pointed out decades ago, "The nature of the task defines the material to be used" (205). At Goualougo, for example, puncturing sticks are manufactured mostly from branches of *Thomandersia hensii*, a rigid and straight tree, while *Sarcophrynium* spp., a species with sufficiently flexible twigs, is mostly sourced for fishing probes (Sanz and Morgan 2007). The same holds true for chimpanzees at Bai Hokou and the Ndoki Forest, Republic of Congo: tool types are manufactured from plant species that offer specific physical characteristics (Fay and Carroll 1994; Suzuki, Kuroda, and Nishihara 1995). Most of the source species at our studied sites belong to the Annonaceae and Tiliaceae families (Pascual-Garrido 2018). These families may embody physical and mechanical characteristics ideal for termite fishing, although we still do not know what characteristics are being selected by chimpanzees or whether and how the selection criteria are passed on, for example, via tool transfers or peering observation of users (Biro et al. 2003; Musgrave et al. 2016, 2020; Schuppli and van Schaik 2019; Whiten 2019).

Still, within the set of optimal species for tool manufacturing, why should chimpanzees at Gombe use bark and twigs, while those at Issa specialize on bark when twigs are predominant at this site? While still-unexplored local ecological factors may shape preferences for tool material types (e.g., termite nest structure), we suspect that differences in the tool materials used among our study sites are socially influenced and thus reflect socially learned variants (i.e., population-specific socially transmitted behaviors within and across generations; Koops, Schuppli, and van Schaik 2018; Lonsdorf 2006; Musgrave et al. 2020, 2021; Whiten et al. 1999). Cultural differences as a driving factor in primate technology should not be overlooked (Boesch et al. 2020; Koops, Schöning, and Hashimoto 2015; Luncz, Wittig, and Boesch 2015; Möbius et al. 2008; Pascual-Garrido 2019; Schöning et al. 2008; Whiten 2019). In his pioneering studies at Gombe, Teleki (1974) concluded that selection proficiency for tool manufacture is a learned skill. This may be information acquired solely through repetitive individual trial and error but may also be accompanied through social learning via stimulus enhancement, peering behavior, or active facilitation, such as tool transfers (Hobaiter et al. 2014; Lonsdorf 2005; Lonsdorf, Eberly, and Pusey 2004; Musgrave et al. 2016, 2020; Sanz et al. 2014; Sanz and Morgan 2013; Schuppli and van Schaik 2019). Given that material selectivity often improves tool efficiency, it would be

advantageous to retain this information (Lamon et al. 2018; Musgrave et al. 2016, 2020; Sanz et al. 2014).

Reuse of Source Plants: Distance of Transport and Species Abundance

Reuse of stone tools to crack nuts by chimpanzees reduces the energetic costs associated with the procurement and transport of new material (Boesch and Boesch 1984; Carvalho et al. 2008; Luncz et al. 2016). While the lifetime of perishable implements is comparably short, the reuse of organic tools has been documented for types that require specific materials, not always readily available, and several modifications. This is the case for puncturing sticks at the Goualougo Triangle, Republic of Congo, that are cached for later use (Sanz and Morgan 2007). But perhaps because of their more delicate physical characteristics and thus quicker deterioration, carrying and reusing fishing probes by chimpanzees is less frequent and is reduced to only a few hours or, at most, a day (Davidson and McGrew 2005; Sanz and Morgan 2007; Teleki 1974). Likewise, the repetitive use of individual sources might help reduce the time invested in searching for a new source, especially for species that may not be abundant nearby. Such is the case for *Thomandersia* trees, which Goualougo chimpanzees repeatedly exploit for puncturing sticks. This genus of tree, though one of the most common in the study area, is not always located close to the tool use site (Sanz and Morgan 2007). In this study, we provide new evidence that chimpanzees reuse sources of raw material for the manufacture of termite-fishing tools, with differences emerging among sites.

At Issa, not only did the chimpanzees extract, on average, more parts per individual plant, but also the distance from the source to the mound was negatively correlated with the number of parts removed, with fewer parts detached from sources found farther away (cf. table 4; fig. 5). This may reflect a strategy to minimize the costs of transport from source to tool site (Blumenschine et al. 2008; Potts 1994) in an environment where suitable sources are not only less abundant (cf. table A2) but also farther away (Pascual-Garrido 2018). Such a strategy would enable Issa apes to maximize the procurement of tool material with the least investment of energy (Carvalho et al. 2008; Luncz et al. 2016). Abundance did not seem to affect the number of parts removed, perhaps because of the overall rarity of source species in the mound vicinity; Issa chimpanzees target all source species equally.

At Mahale, sources were exploited mostly once, and neither the distance of the source from the targeted mound nor the abundance of the source species seemed to have an effect on the number of parts taken per source. With abundant bark sources available nearby and approximately 80% of the plants around mounds providing suitable bark (cf. table A2), Mahale apes have abundant sources from which to choose, which they do, given that only 12% of all available species are used (cf. table A4). Similar findings have been described among chimpanzees at Mount Assirik, where 90% of all sources were located in close proximity to the targeted mounds (McGrew, Tutin, and Baldwin 1979). At Gombe, where raw material was the most abundant among all study sites (cf. table 1), a slightly different picture emerged: even when apes obtained their material from a relatively close distance and at distances similar to those at Mahale (Pascual-Garrido 2018), a species' abundance showed a negative trend relative to the number of times it was sourced. Rare species were procured more often.

Use and reuse of tool materials provide valuable insights into hominoid technological patterns. Boesch and Boesch (1984) proposed that the transport of stone tools to *Panda* nut-cracking sites by chimpanzees living in the Taï Forest, Cotê d'Ivoire, follows a least-distance strategy, with hammerstone weights decreasing with increasing distances from the nearest location of tool material sources (Luncz et al. 2016). The optimal use of resources with flexible, dynamic, opportunistic, and low-energy strategies to solve problems, which share affinities to the Oldowan, has also been described for nut-cracking chimpanzees in Bossou, Guinea (Carvalho et al. 2008). While perishable implements do not impose a weight constraint similar to that of stones ("A chimpanzee carrying a 3 kg stone walks on three limbs and carries the stone in one arm" [Boesch and Boesch 1984:164]) and so can be carried in the mouth, the distance traveled from a suitable source to the tool site could still demand extra energetic costs, especially for sources that are rare and at a considerable distance (Sanz and Morgan 2007). That chimpanzees at Gombe, Issa, and Mahale selected and transported different materials for termite-fishing tools and reused sources in ways that seemed to be influenced by the abundance of raw material available suggests that, as described for lithic technology (Carvalho et al. 2008), different resource exploitation strategies might also be at play for organic technology. Further investigations, including individual follows, are necessary to corroborate this.

Conclusion

Besides the human lineage, the selection and transport of materials for tool manufacture has been documented across many species. For example, New Caledonian crows (*Corvus moneduloides*) select and carry materials to fish for larvae at tree holes (Bluff et al. 2010; Klump, Cantat, and Rutz 2019; Rutz et al. 2007); woodpecker finches (*Cactospiza pallida*) employ twigs, cactus spines, or leaf petioles to probe for insects inside tree holes, sometimes carrying the tool from branch to branch (Hundley 1963); and orangutans (*Pongo abelii*) prefer certain lining materials, which they may carry for as far as 50 m from the nest site (leaf carrying), to construct their nests (Russon et al. 2007; van Casteren et al. 2012). This suggests that the selection and transport of materials are vital components of tool use or manufacture. However, what probably sets chimpanzees apart from the rest of the nonhuman tool manufacturers, including other apes, is their prolific and flexible use of materials for a diverse range of implements, more akin to

humans than to any other living nonhuman species (McGrew 1992; McGrew et al. 2019; Rolian and Carvalho 2017).

Stone tool use by Plio-Pleistocene hominins involved selectivity and transport behaviors dependent on the raw material available, with patterns of variation reflecting their cultural diversity (Braun et al. 2008, 2009; Goldman-Neuman and Hovers 2009, 2012; Kimura 1999; Stout et al. 2005, 2010). In this study, we provide evidence that part of what archaeologists have reconstructed about the behaviors associated with the Oldowan can be accommodated within the perishable technology used by wild chimpanzees and thus likely was present in the last human-chimpanzee common ancestor (McGrew 2010), before the advent of the Oldowan (Carvalho and Beardmore-Herd 2019; Panger et al. 2002). These commonalities include selection and transport behaviors for tool manufacture (Braun et al. 2008, 2009; Goldman-Neuman and Hovers 2009, 2012; Schick 1987), tool-using strategies dependent on the raw material available (Kimura 1999), and technocultural diversity (Stout et al. 2005, 2010). Our studies continue to support Wynn and McGrew's (1989) and Wynn et al.'s (2011) assertions that everything archaeologists have reconstructed about the behavior of the Oldowan can be accommodated within the "ape adaptive grade" (more recently updated to the "simian adaptive grade"; McGrew et al. 2019), except for two specific behavioral patterns that still remain unknown among modern apes, one of which is relevant here: Oldowan hominins carried raw material and implements farther than any living ape, sometimes for up to tens of kilometers, and they competed with large carnivores for animal prey.

Future Directions

Given the predominance of biodegradable material in chimpanzees' (McGrew 1992) and hunter-gatherers' material culture (González-Ruibal, Hernando, and Politis 2011; Hoffecker and Hoffecker 2018), the prevalence of C_4 grassland since the late Miocene (Faith, Rowan, and Du 2019), and the possible exploitation of termite mounds early in our own lineage (Backwell and d'Errico 2001), it is likely that early humans also made use of this resource with a much richer and more diverse and varied tool kit (and associated technical behaviors) than is currently visible in the archaeological record (Backwell and d'Errico 2001; Carvalho and Almeida-Warren 2019; Dominguez-Rodrigo et al. 2001; Panger et al. 2002; Toth and Schick 2009). It is largely thought in the paleoanthropology community that the advent of flaked stone tool technology marked a qualitative leap in human evolution (Braun et al. 2019; Shea 2016). However, this and other studies, seeking to understand the Oldowan as being on a continuum of a way of life that might have been in place for millions of years, call for the placement of our early ancestors in their appropriate evolutionary context (Carvalho and Beardmore-Herd 2019; Panger et al. 2002; Wynn 1981; Wynn et al. 2011).

The archaeology of the perishable, even at its infancy, is providing a new framework for reconstructing archaeologically invisible aspects of early human behavior and our own technological origins (Almeida-Warren et al. 2017; Hernandez-Aguilar 2009; Hicks et al. 2019; Koops, Schöning, and Hashimoto 2015; Pascual-Garrido 2018; Sanz and Morgan 2007; Sept 1992; Stewart, Piel, and McGrew 2011). Future efforts should concentrate on providing information that will help contextualize the current archaeological record and aid investigations into potential, yet currently unknown, hominin sites (Carvalho and Almeida-Warren 2019). Current research in this direction includes mapping chimpanzee tool use sites to enable comparison with early archaeological sites (Almeida-Warren et al. 2018), using long-term records of chimpanzee perishable technology to model ranging patterns in early hominins (Hernandez-Aguilar 2009; Sept 1992; Stewart, Piel, and McGrew 2011), primate archaeological analysis of chimpanzee artifacts to enable comparisons with implements employed for similar purposes in the archaeological record (Backwell and d'Errico 2001; Heaton and Pickering 2006), and the identification of termite evidence at early human sites (Lesnik et al. 2019). The archaeology of the perishable, even within its limitations, may contribute to a comprehensive understanding of primate technology as a whole, including the origins of human technology. This study also emphasizes the importance of continuing to preserve culturally healthy wild chimpanzee populations, maintaining their ability to access the tool materials on which their traditions depend (Brakes et al. 2019).

Acknowledgments

We are grateful for permission to conduct research in Gombe Stream National Park, Mahale Mountains National Park, and Issa Valley by TANAPA, TAWIRI, and COSTECH; field assistance at Issa from Shedrack Lucas, Patrick Hassan, Godfrey Stephano, Mashaka Kalutwa, Busoti Juma, Mlema Juma, Msigwa Rashid, Sebastian Ramirez-Amaya, and Eden Wondra, at Mahale by Shaka and Singa Kabugonga, and at Gombe by Matendo Msafiri Katoto and Nasibu Zuberi Madumbi; logistical support from the Jane Goodall Institute, Greater Mahale Ecosystem Research and Conservation Project, and Mahale Mountains Chimpanzee Research Project; and plant identifications by Frank Mbago, Department of Botany, University of Dar es Salaam. Special thanks go to Anne Pusey, Anthony Collins, Deus Mjungu, Michio Nakamura, and Alex Piel for aiding logistics in the field; Edward Kohi, Pius Kavana, and Maria Mbogo for the safekeeping of Alejandra Pascual-Garrido's equipment in Kigoma town; and Alex Mielke and Thomas Püschel for assistance with data analysis. We are very grateful to Luis da Silva for providing the illustration of chimpanzees sourcing raw material for termite-fishing tools. William C. McGrew, Volker Sommer, two anonymous reviewers, and the editorial team at *Current Anthropology* provided much constructive critique and greatly improved the article. This research greatly benefited from discussions with Susana Carvalho, Anthony Collins, and William C. McGrew. Alejandra Pascual-Garrido was supported by a Leverhulme Trust Early Career Fellowship and

received further funding for fieldwork from the Boise Trust Fund, University of Oxford. During writing, Alejandra Pascual-Garrido was supported by the John Fell Fund, University of Oxford.

Comments

Susana Carvalho
Primate Models for Behavioural Evolution Lab, School of Anthropology and Museum Ethnography, University of Oxford, 51/53 Banbury Road, Oxford OX2 6PE, United Kingdom, and Primatology and Paleoanthropology, Gorongosa National Park, Sofala, Mozambique (susana.carvalho@anthro.ox.ac.uk). 26 X 20

No Country for Old Archaeology

Along came primate archaeology. At its inception, it targeted lithic technology, debunking myths about the exclusive "hominin country club" that accepted only members of our clade as makers of archaeological records. Because of it, we learned that nonhumans leave behind assemblages that last thousands of years (Falótico et al. 2019; Mercader et al. 2007) and realized that there is intra- and interspecies variability in tools used for the same functions by contemporaneous communities of nonhuman primates (Carvalho et al. 2008; Luncz et al. 2019). We found that unintentional by-products of stone tool use by monkeys can mimic Oldowan morphotypes (Proffitt et al. 2016). Meanwhile, surveys commenced in older deposits, and we discovered that archaeology is older than the Oldowan and that *Homo* is most certainly not the first toolmaker (Harmand et al. 2015; McPherron et al. 2010; but see Carvalho and Beardmore-Herd 2019 for a review).

These discoveries were far-reaching, but the study by Pascual-Garrido and Almeida-Warren reminds us that we have barely scratched the surface of primate archaeology's potential. Moreover, their work highlights how we overlooked what most likely was the majority of the hominin tool kit, thus missing the opportunity to understand behaviors that may depict a more complex scenario of our technological evolution. Perishable materials usually do not endure for as long as lithics do (but see Pante et al. 2020; Wadley et al. 2020). After all, we cannot find the older than the Oldowan until we survey deposits older than 2.6 Ma, and to find organic tools, we must search for them—both in the present and in the past.

The authors' "archaeology of the perishable" shows that three communities (Mahale, Issa, Gombe) of the same subspecies of *Pan troglodytes* ranging in different ecological settings transport and reuse selected organic raw materials, exploiting resources near the tool use sites, albeit with differences at the most open site, Issa. Even more interesting are the plant removals at the source sites, which scarify and remain detectable. And the farther you move away from the site, the fewer plant removals found. So the number of removals could be used as an indicator of the distance from the tool source to the tool site. In reality, termite mounds can fossilize (Darlington 2005), and so could some of the more robust woody vegetal sources from which these removals occur. Hence, if removal patterns are carefully recorded and the neo-taphonomy understood, it may be possible to identify this sourcing and transport in the fossil record.

Meanwhile, as the authors' work reveals, there are important insights about behavioral evolution and technology—as well as some cautionary tales—from observing our closest living relatives using perishable tools to fish for insects. For example, the work presented reaffirms the importance of considering the ecology of culture (per Koops, Visalberghi, and van Schaik 2014). At Issa, the most open of the three sites, the lower density of resources may be altering the cost-benefit balance of this type of tool use and hence influencing how far and how often tools get transported. Why carry raw materials long distances if they are widely available? How do we truly know hominin tool transport distances if we are in the dark about nonlithic technology and assume that transport occurred in a single journey instead of in numerous short bouts? This piece prompts us to think of the importance of not using "one size fits all" when considering transport distances to infer species' cognitive skills or complexity, especially if we are inferring skills from the absence of evidence.

Consider the example of the Bossou chimpanzees that use more than 20 different tool types, with only one being a lithic tool use (Matsuzawa 2011). At a forest location where stone tool use is customary, 1,200 hours of footage were collected over 30 years: they contain an individual average of 7.8% stone tool use time (Max Bain, Arsha Nagrani, Daniel Schofield, Sophie Berdugo, Joana Bessa, Jake Owen, Kimberley J. Hockings, et al., unpublished). Now imagine carrying out an archaeological excavation of Bossou that recovered only lithic records and thus having less than 7.8% of the species' technological activity budget to consider when reconstructing the group lifeways. You would never know about the pestle pound, ant dip, algae scoop, and so on or about the optimization of resource use, which might include transporting one stone 100 times over several years. What could this say about technological complexity, foresight, and strategies for the exploitation of resources? One cannot assume a species' ability from studying one mode of tool use, or, better said, one cannot compare skill on the basis of comparing hominin lithics versus nonhominin lithics. Only a holistic understanding of the overall optimal foraging strategies can unveil such evolutionary pathways.

This piece carves a path that deserves further work. In the absence of early perishable archaeological records, deeper archaeological knowledge of the technological elements of modern species' repertoires is fundamental. If we are to find earlier organic records, we must know first how to identify them, how such sites form, and what features may last and develop the analytical methods that will take us further than what we are classically trained to do. There are reasons for hope with the archaeology of the perishable. Just as with termite fishing, other chimpanzee behaviors, for example, tortoise smashing (Pika et al. 2019), crab processing (Koops et al. 2019), tree drumming (Babiszewska et al. 2015), accumulative stone throwing (Kühl

et al. 2016), or bark peeling (Lapuente et al. 2020), hold potential for expanding investigations.

Notably, in an era in which analyzing mega–data sets at the computer is commended, this piece speaks to the importance of carrying out systematic, robust fieldwork. The comparison of the three chimpanzee communities entailed remarkable efforts—and would not be possible to attain using only camera traps! We need more empirical studies that bring back natural history. It is urgent to look at technological and cultural evolution in broader taxonomic and ecological contexts, especially in highly endangered species and populations. Finally, to investigate technological evolution, we need to make use of . . . evolution. Not linear, not deterministic, but evolution in a mosaic fashion. The work by these archaeologists of the perishable is helping us to step away from the lithic mania and allowing the mosaic to take shape.

Wei Chu
Institute of Prehistoric Archeology, University of Cologne, Weyertal 125, 50923 Cologne, Germany (wchu@uni-koeln.de). 23 X 20

This thought-provoking paper aims to provide insights into ephemeral technologies by using archaeological methods to compare termite mound fishing among different chimpanzee communities. The collected data show that the differences in tool selection, procurement, and management obtained from discarded tools may be partially explained by local environmental considerations but may also reflect socially transmitted behavior, in other words, ecology and culture. The authors suggest that understanding these patterns will help to contextualize the archaeological record and, in turn, provide insight into early human behavior.

Interdisciplinary collaboration between primatology and archaeology, astonishingly, is still quite novel despite being long identified as a need (Mason 1990). The authors respond to this need with an elegant, thoughtful, empirical approach for which they must be thoroughly congratulated. By using archaeological methods to study chimpanzee tool use, the paper shows the potential for future collaborative research and highlights how far we still are from true synthesis. I would like to comment on some of the archaeological aspects of this study, focusing on (1) the methodology, (2) the extent to which the data support the interpretations, and (3) issues surrounding the potential future applications of the methodology.

The authors use archaeological field techniques to analyze chimpanzee tool use patterns. This approach is one of the more difficult methods to apply to primate behavior—as opposed to more readily translatable analytical methods that may be used to understand perishable technology, such as *chaîne opératoire* or microwear (Carvalho et al. 2008; Marreiros et al. 2020). Some may bristle that the archaeological record is a reduced, biased, and static data set that is difficult to compare with the analyzed data here. Indeed, palimpsests and taphonomic alterations are the rule for archaeological sites, but they are always a question of scale, and many of the same issues are at stake when comparing archaeological sites (Bertran et al. 2019). By reducing archaeological field methods down to their simplest and focusing efforts on understanding behavioral patterns, this paper circumvents many complications. I imagine that, following this example, researchers may integrate other more targeted archaeological techniques to frame their work to strengthen their conclusions (Friesem 2016).

The role of seasonality was wisely minimized in this study. Given that chimpanzees have a range of physiological and behavioral responses to annual cycles suggests, however, that they may be an important factor in their tool provisioning as well. A range of different landscapes may also be similarly pertinent (van Leeuwen, Hill, and Korstjens 2020). Seasonal rhythms are an important factor in the archaeological interpretations, ones that may even be observable in the extant lithic record (Hosfield 2020; Richter et al. 2012). Understanding perennially controlled patterns of chimpanzee tool use may be one useful avenue to further synthesize the fields of primatology and archaeology in a meaningful way.

For ethical reasons, the chimpanzees' tool manufacture and use could not be recorded by live observation, though I wonder whether visual recordings could at some point alleviate this. A strength of primatology, ethnoarchaeology, and ethology more broadly is that they can incorporate aspects of intangible knowledge that archaeologists are unlikely to detect into research and material practices (Cazzella 2016). Given the complex social structure of chimpanzees, it would be valuable, for example, to integrate in the research even such simple categories as gender and age, which could be situated into the wider behavioral ecology and cultural transmission debates, which are currently anthropocentric. Such an approach would also give us a fuller understanding of the proximate and ultimate explanations of primate tool use and provide more robust context to the archaeological record (Tinbergen 1963).

The authors suggest that chimpanzee fishing patterns can be used to help explain ranging behavior among early hominins. I have no doubt that extant behaviors can reasonably be used to phylogenetically triangulate a point of origin. However, the extent to which entomophagy played a main role in the diet and evolution of hominoids is still unclear (Scott 2019), and suggesting an analogy between chimpanzees and early hominoids with regard to this form of subsistence may still be speculative, something for which future studies may provide further insight. We are reminded that the use of relational analogies, even within species, to infer past behavior has long stirred debate and undoubtably will continue to do so (Cunningham and McGeough 2018; Gosselain 2016; Lyons and David 2019), a complication only further compounded by comparing behavior among genera that diverged long before major changes in locomotion and diet were in place.

The article promotes the application of the archaeology of the perishable to improve our models of early hominin ranging patterns, identify unknown sites, and augment our understanding of Paleolithic implements. These are important,

ambitious goals and ones for which expectations must surely be tempered: the fact that primate conspecific behavior is so variable only highlights the difficulties in understanding past hominoid actions, about which so little is known. The archaeological record provides little in terms of a solid framework, as time, climate change, and geological events have rendered landscapes and archaeological sites, particularly from the early African Plio-Pleistocene, difficult for direct comparison at comparable scales (Villaseñor, Bobe, and Behrensmeyer 2020). Similar efforts to apply primate archaeology to explain early hominin dwelling behavior have underscored the difficulties in such approaches, and the lack of substantial progress since then should at least be a sobering reminder that real advances, at least on the part of archaeology, are slow going (Chu 2009; Sept 1992, 1998; Stewart, Piel, and McGrew 2011).

Still, this study and primate archaeology at large aim to augment our understanding of early human evolution and provide compelling evidence that interdisciplinary approaches can only add to the sparse archaeological record. Archaeology often plays a dominant role in explaining human evolution and, by integrating a range of different disciplinary branches, provides, at the very least, a cross-check to prevalent models of early hominin evolution.

Francesco d'Errico and Lucinda R. Backwell
Préhistoire à l'Actuel: Culture, Environnement et Anthropologie, Unité Mixte de Recherche 5199, Centre National de la Recherche Scientifique, Université de Bordeaux, Bâtiment B2, Allée Geoffroy Saint Hilaire, CS 50023 F, 33615 Pessac CEDEX, France, and Centre for Early Sapiens Behaviour, Department of Archaeology, History, Cultural Studies and Religion, University of Bergen, Øysteinsgate 3, 5020 Bergen, Norway (francesco.derrico@u-bordeaux.fr)/Evolutionary Studies Institute, University of the Witwatersrand, 1 Jan Smuts Avenue, Braamfontein 2001, Johannesburg, South Africa, and Instituto Superior de Estudios Sociales, Consejo Nacional de Investigaciones Científicas y Técnicas, San Lorenzo 429, San Miguel de Tucumán, CP4000, Tucumán, Argentina (lucinda.backwell@wits.ac.za). 1 X 20

The contribution of Pascual-Garrido and Almeida-Warren is paradigmatic of how a comparative analysis of plant tools manufactured and used by different chimpanzee groups can distinguish, if conducted with the intellectual and methodological acuity demonstrated by the authors, factors related to cultural preferences learned socially from those dependent on environmental constraints. A more problematic endeavor, however, is verifying to what extent the model that emerges from these results is relevant to understanding the cultural adaptations of the first hominins. Ideally, the model would require establishing parallels between comparable tasks in terms of neuromotor, cognitive, and learning constraints, localization, and the type of resources exploited. Without a pertinent frame of reference, the danger is that the chimpanzee model remains just a model or that we compare apples and oranges. Knapped lithics do not lend themselves well to such a comparison because they are overly dependent on the presence of suitable rocks for knapping in the geological environment, which may have involved longer transport distances than those required for the subsistence activities of today's chimpanzees. Lithics are also ill suited for comparison because knapping requires training and ensuing long-term selection that must continue for hundreds of generations, activities in which chimpanzees have not engaged in their evolutionary history. Stone is also unsuitable for comparison because the tasks in which the knapped tools were involved were either multiple or devoted to the exploitation of large animal carcasses, behaviors absent in chimpanzees. The same problem is posed by the rare knapped bone tools discovered at Olduvai Gorge in Tanzania (Backwell and d'Errico 2003; Leakey 1971). A comparison based on percussion tools would be best (Arroyo and de la Torre 2016, 2018; Arroyo et al. 2016; Mora and de la Torre 2005), but it is hampered by the fact that an intersite approach, such as that followed by Pascual-Garrido and Almeida-Warren, is made difficult by the fact that such tools are found at only one site, Olduvai, sporadically at more recent sites, or too far away from this key site (Goren-Inbar et al. 2002) to make meaningful comparisons.

The bone tools used by hominins in southern Africa (Brain and Shipman 1993; Robinson 1959) are much better suited to test the relevance of the chimpanzee model but have not been used to any great extent to date. Many ethologists working on chimpanzee cultures have limited their reading of our paper on termite foraging by early hominins (Backwell and d'Errico 2001) by not examining in detail the data that accompanied that paper and those that followed (Backwell and d'Errico 2003, 2004, 2008, 2009; Caruana, d'Errico, and Backwell 2013; d'Errico and Backwell 2003, 2009; d'Errico, Backwell, and Berger 2001; Hanon 2019; Stammers, Caruana, and Herries 2018) or the potential of this material for intersite comparisons. The advantage of these tools is that they were certainly used as digging sticks in termite mounds and perhaps other environments. They therefore reflect, like the activities described by Pascual-Garrido and Almeida-Warren, the practice of a repetitive task carried out locally by distinct groups, learned mostly by observation, and not requiring, like knapped lithics, the long-term implementation of specialized neuromotor skills. These bone tools are now known from five geographically close sites: Swartkrans, Sterkfontein, Drimolen, Kromdraai, and Cooper's, which shared comparable paleoenvironmental conditions (de Ruiter, Sponheimer, and Lee-Thorp 2008; Peterson et al. 2018; Reynolds and Kibii 2011). Like Pascual-Garrido and Almeida-Warren, we have endeavored to document different aspects of the *chaîne opératoire*, in particular those related to the choice of bone used as tools in comparison with the taxonomic composition, size, and thickness of the bones making up the faunal assemblages stratigraphically associated with them. In addition to elements common to all sites, such as the use of elongated, highly weathered fragments of the diaphysis of large animals, we have been able to highlight behaviors that are found only at certain sites, such as the rare use at Swartkrans of fresh bone or horn-cores sharpened by abrasion to compensate for the rapid wear of the tool tip due to the less robust nature of this bone type. The number of tools found at some sites is too small to

reach statistically valid conclusions when comparing sites, but many tools found in recent excavations are still waiting for detailed analysis. The possibility of verifying, in a relevant way, to what extent the cultural behaviors of the first hominins or of some of them correspond to those brilliantly documented by Pascual-Garrido and Almeida-Warren is therefore open, all the more so since the methods to make these objects speak are in place.

Thurston Cleveland Hicks
Faculty of "Artes Liberales," University of Warsaw, Pałac Zamoyskich, Ulicy Nowy Świat 69, 200 m od Kampusu Głównego UW, Poland (clevehicks@hotmail.com). 18 X 20

This important and well-crafted study expands our understanding not only of the behavior of our extant panin cousins but also of the vanished vegetal technologies we presume our own hominin ancestors must have used. Those ancient wands, probes, and clubs are, unlike stone tools, invisible in the hominin fossil record before about 300,000 years ago. Studying the behavior of nonhuman great apes offers us insight into what those lost tool traditions might have been like. In this paper, the authors make effective use of archaeological evidence from three chimpanzee communities inhabiting nearby Tanzanian forests and woodlands that all happen to use vegetal tools to fish for termites (this is fortuitous, as a number of chimpanzee populations ignore this nutritious resource even where it is abundant, such as in my study region in northern Democratic Republic of the Congo [DRC]; Hicks et al. 2019). In our efforts to understand the full diversity of chimpanzee behavior across Africa under a range of habitats and circumstances, we are faced with the limitation that only a tiny proportion of communities have been habituated for observation. The authors' work significantly advances the methodology for reconstructing and comparing nonhuman great ape behaviors on the basis of indirect evidence.

Only recently have enough populations of African great apes been studied to give us a hint of their behavioral diversity, some of which likely reflects culture or socially transmitted population-specific behaviors. Hobaiter et al. (2017) demonstrated that neighboring chimpanzee communities in the Budongo Forest favor different prey species despite comparable prey abundance, and Samuni, Wegdell, and Surbeck (2020) revealed similar dietary diversity among neighboring bonobo communities (for another example involving chimpanzee plant foods, see Nishida et al. 1983). Gorillas, which, like bonobos, have little to show in terms of material culture, nevertheless display a number of potential cultural variants across their range (Robbins et al. 2016). Where direct observation of behavior is impossible, which is the case for the majority of nonhuman great ape populations, indirect remains of material culture as well as camera trap data are now being used to investigate potentially divergent traditions (Hicks et al. 2020; Luncz, Wittig, and Boesch 2015).

A frequent bugbear of such efforts to claim cultural differences is the fact that ecological factors (reviewed in McGrew 1992) and possibly even genetic ones (Langergraber et al. 2011) also impact great ape behavior. By focusing exclusively on Tanzanian chimpanzees, Pascual-Garrido and Almeida-Warren have minimized the potential influence of any major genetic differences among the populations. The authors carefully compared termite-fishing sites at three localities, recording the materials used in tool construction as well as plant availability for tool making. They discovered that, although all of the chimpanzees used and reused sources both close to and farther away from the termite mounds, the more open country Issa chimpanzees used more parts of each plant and focused more on plant sources closer to the mounds. This is likely due to increased transportation costs in a more open habitat (might the danger of encountering a predator with increasing distance traveled also play a part?).

Another of the key findings of this study is that two of the three chimpanzee communities (Issa and Mahale) used only bark to make their tools, whereas at Gombe, the apes used a diverse mix of materials, including twigs as often as bark. Because of the authors' careful attention to detail and context, we can be certain that the preference of Issa and Mahale chimpanzees for bark as a tool material is not due to differences in the availability of bark or twigs. This makes it much more plausible that these group differences might be cultural (we are duly cautioned, however, about the authors' small sample size for tool sites at Mahale). In addition, they are even able to point to possible changes in tool source preference over time: at Mahale approximately 40 years ago, the chimpanzees used a variety of source types, not just bark. Similarly, the Gombe chimpanzees once used more grass to fashion their tools than they do today. It would be interesting to know how such changes might come about: a transfer in of traditions from neighboring communities? In the case of Gombe, the authors speculate that (among other theories) the reduction in the use of grass to make tools may be related to ecological change due to human activities, in this case, the cessation of annual burning, which has allowed forests to regenerate and replace grass. Here we see an excellent possible example of the tight intertwining of ecology and culture.

Ever since William McGrew and Caroline Tutin left Gombe to visit Mahale and, through their observations and conversations with Junichiro Itani, realized that Gombe and Mahale chimpanzees had developed different grooming traditions (McGrew 2004; McGrew and Tutin 1978), a realization has been forming that humans are not alone in our propensity for the socially transmitted diversification of traditions among populations. As the years have passed, primatologists have developed an increasingly sophisticated approach to handling the difficult task of disentangling cultural explanations from those based on ecology or genetics (made even more difficult by the likelihood that these three factors are entangled). With this paper, Pascual-Garrido and Almeida-Warren have advanced the comparative approach further with their careful attention to

the ecological context in which similar tools are used for the same type of food at three nearby sites. This study will serve as a model for future efforts to understand the context in which great ape tool traditions have evolved in areas such as the vast and interconnected chimpanzee "behavioral realm" I study in northern DRC.

One thing that I appreciate about this paper is that the results are not the end of it. In the lengthy and insightful discussion, the authors are unafraid to speculate and explore the bigger picture, always careful to delineate between what is known and what remains uncertain. This approach is essential for designing new studies to fill the vexing gaps in our knowledge and for inspiring more researchers to add their findings to our steadily increasing data set on behavioral diversity in our nonhuman great ape cousins.

William C. McGrew
School of Psychology and Neuroscience, University of St Andrews, Fife KY16 9JP, Scotland, and Evolutionary Primatology, University of Cambridge, Cambridge, United Kingdom (wcm2@st-andrews.ac.uk, wcm21@cam.ac.uk). 22 X 20

Modeling Past Technological Evolution with Ethoarchaeology

Most of the biodegradable material culture of our long gone evolutionary predecessors is absent, along with their behavior. The challenge presented by these missing organic materials has been tackled ingeniously and assiduously by paleoarchaeologists, but, lacking behavior and artifacts, their conclusions are limited to inferences. Even when precious organic remnants of prehistoric material culture survive and are recovered, interpretation of their function remains inferential (e.g., Hardy et al. 2020). Even more tenuous is the intuitive attribution of unobservable cognitive processes underlying the "missing majority" of artifacts (Hurcombe 2008). So, what to do?

On the basis of organic remnants or their mineralized counterparts, archaeologists turn to actualistic studies, which usually entail experimental replications. Vanhaeren et al. (2013) used modern snail shells to stand in for Middle Stone Age equivalents in experiments on use wear. Seeking to learn how these "beads" had been strung, they put the modern shells to laboratory wear with different stringing patterns. They found matches that indicated the functional patterns of the missing strings, with changes in style over time. Wadley (2005) noted evidence that flaked stone tools from the Middle Stone Age had been hafted by some adhesive mixed with ocher. The adhesive component turned out to be *Acacia* gum, but the combination worked only if heated precisely in terms of time and temperature.

Primatologists *can* observe the behavior of our nearest living relations and study their artifacts, organic and inorganic, in action as the next best approximation for modeling what is missing in prehistory. The luxury of having access to the apes' actions allows the full *chaîne opératoire* to be recorded and analyzed (Carvalho et al. 2008). Even if behavioral observations are incomplete or absent (for unhabituated or only partly habituated subjects) or are constrained (by the limits of camera trapping), they provide fragments that can be knitted together. For example, partly habituated chimpanzees (*Pan troglodytes schweinfurthii*) at Semliki, Uganda, dig holes in sandy riverbeds to access drinking water in the dry season; even before the apes were seen to use these wells, their extractive ("sponge") tools and evidence of the sequence of their production were available (see fig. 6).

Organic raw material, especially nonwoody vegetation, can be fragile and ephemeral. Wood can last for hundreds of thousands of years in certain (usually anoxic) conditions (Goren-Inbar, Werker, and Feibel 2002). Resins mixed with ocher last tens of thousands of years, still adhering to stone tools. Other residues persisting as by-products on inorganic tools, such as cashew nuts cracked by capuchin monkeys, can last for tens of years (Falótico et al. 2019). Most chimpanzee tools made of vegetation endure for much less time; the longest known so far are still-living twigs and branches in chimpanzee nests, which last for a few years (Stewart, Piel, and McGrew 2011). Artifacts such as termite-fishing tools may last only a few days or weeks but still are available to be reused and so may contribute to a palimpsest assemblage to be unraveled.

Pascual-Garrido and Almeida-Warren have taken the analytic process further than any other study of primate nonlithic technology, especially in tackling the early, more difficult stages of the *chaîne*, such as sourcing the origins of the raw materials. It is easy to collect tools abandoned at a termite mound but harder to learn where they came from! They also have led the way by indirectly but empirically tackling the distances traveled as raw materials were transported to the mound; previous studies dealt only with nearby sources a few meters away. Most importantly, they have pursued the puzzle of the types of raw materials used, in which some populations use only a single type but others a wide variety. These findings tend to concentrate at the beginning and end of the *chaîne*, but there is much more to be done following archaeological precedents.

Waiting to be studied are debitage, especially if it can be refitted; what to make of unused tools; the characteristics of abandoned tools; the enigma of some probes being used at both ends but others only at one end; the limits of various raw material types, for example, whether their cross-sectional shape reflects the "attachability" of termite prey; the physical characteristics of plant materials, presuming some optimality between too rigid and too floppy; aspects of wear at the inserted end of a tool; possible seasonal differences in the raw materials, for example, seasonal shoots, chosen on the basis of their vegetational state; which woody plants, for example, those with robust bast, make good sources of bark; and so on. Many of these questions can be tackled systematically via actualistic attempts by the researchers to replicate what the apes are doing.

All the above and much more can be tested against the observational data from watching chimpanzees in action, that is,



Figure 6. Tools used by chimpanzees to extract drinking water from wells dug in sand, Semliki, Uganda. *Top*, three leaves taken from a source plant but left unused beside a well. *Middle*, processed leaves, with softer portions between the leaf veins removed. *Bottom*, "sponges" made from combined processed portions, still wet from use (McGrew, Marchant, and Hunt 2007).

by applying the etho- part of ethoarchaeology (McGrew et al. 2003). For example, by retrieving the artifacts of known individuals left behind after a fishing session, the observers can start to tackle the perennial problem of who contributes to the palimpsest. Furthermore, they can see whether practices from the start to the finish of the *chaîne* show individual differences; for example, do maternal kin show more similarities in technique than others?

Finally, ethnographic scrutiny of the technology of living foraging societies may yield key differences and similarities in termite acquisition. Isoptera, especially the fungus-growing, mound-building Macrotermitinae favored by chimpanzees, commonly figure in human entomophagy. Pioneering work by Wendell Oswalt (1976) still provides a systematic methodology for studying the techniques and tools of the elementary technology of termitivory. There is so much more to do, and the authors seem set to be the ones to do it!

Stephanie Musgrave and Crickette Sanz
Department of Anthropology, University of Miami, PO Box 248106, Coral Gables, Florida 33124-2005, USA (smusgrave@miami.edu)/ Department of Anthropology, Washington University, 1 Brookings Drive, St. Louis, Missouri 63130, USA, and Congo Program, Wildlife Conservation Society, Brazzaville, Republic of Congo. 30 X 20

Examining tool raw material procurement is fundamental to our attempts to reconstruct the technologies of early hominins. The authors bring unique expertise on tool variation within *Pan* to this endeavor, and they have pioneered interdisciplinary approaches that incorporate archaeological methods into the study of chimpanzee perishable tool behaviors. These advances have significantly enriched our understanding of primate technology and intraspecific behavioral variation. We commend their extension of this approach in the present study, as applying standardized methods across study sites affords fascinating insights into the ecological correlates of tool-assisted foraging. However, there are also myriad opportunities to link such archaeological data with long-term records and behavioral observations from these field sites. Such an integrated approach would foster a more comprehensive understanding of nonhuman primate material culture and improve our ability to reconstruct the invisible aspects of hominin technologies.

As the authors recognize, the ecological context of tool material procurement can elucidate both the cognitive underpinnings of tool behavior and broader landscape-scale patterns of technology. Among the most striking findings of this study are the population differences in raw material sourcing, specifically that only bark tools were recovered from Mahale and Issa, while variable material sourcing was documented for Gombe chimpanzees. Given that *Macrotermes* exhibits substantial inter- and intraspecific variation in response to both biotic and abiotic factors (Korb 2013), it will be illuminating to investigate whether prey species or termite mound characteristics influence the choice of tool materials (e.g., Sanz et al. 2014). Analyzing the mechanical and textural properties of raw

material types will also help to clarify to what extent chimpanzees select for particular characteristics that crosscut material categories. In addition, populations might use different postures or techniques (Boesch et al. 2020) that could make a particular plant material or species more effective. Differences in prey behavior (e.g., for army ants, Schöning et al. 2008) may also influence what strategies are energetically profitable.

Assessing the energetic requirements of termite gathering, including procurement, could also illuminate how patterns of raw material selection relate to foraging efficiency more broadly, as has been documented for lithic tool use in nonhuman primates (e.g., Luncz et al. 2016, 2018; Sirianni, Mundry, and Boesch 2015; Visalberghi et al. 2015) and suggested for hominin tool users (e.g., Blumenschine et al. 2008). Specifically, integrating data on the spatial distribution of termite nests and individual source plants, as well as chimpanzee home ranges, population density, and community boundaries, could further elucidate the ecological and social dynamics contributing to landscape-scale patterns of material sourcing and tool use. This information could also reveal whether communities spatially overlap at termite nests, which could facilitate information exchange between communities.

Ecological influences are compatible with a significant role for social learning in generating intraspecific behavioral variation (Byrne 2007; Koops, Visalberghi, and van Schaik 2014), and we agree with the authors that social learning likely influences tool raw material selection. In comparing the tool transfer behavior of chimpanzees of the Goualougo Triangle, Republic of Congo, with that of the Kasakela community at Gombe, we found that infants at both sites reuse discarded tools and are allowed to take tools from others, though mothers at Goualougo transfer tools to offspring more frequently and more actively (Musgrave et al. 2020). At Gombe, female compared with male offspring watch their mothers more and are more similar to their mothers with respect to the length of the tools inserted into termite nests (Lonsdorf, Eberly, and Pusey 2004). Together, these observations indicate that multiple social learning mechanisms occur in this context. It is also possible that abundant suitable raw material near termite mounds, as documented at Gombe, rewards frequent individual experimentation with diverse materials. This could promote more variable sourcing of plants by Gombe chimpanzees, even while termite fishing is maintained over generations by social learning.

Linking the plant sourcing and tool data to individual chimpanzees via direct observations will help to illuminate what contributes to variation in raw material sourcing within and between populations, for example, whether individuals or groups specialize in particular tool materials (e.g., Fujii, Ralls, and Tinker 2017) and whether preferences are transmitted within matrilines (e.g., Lamon et al. 2017) or adopted by immigrants (e.g., Luncz, Wittig, and Boesch 2015). This will also clarify whether population variation in social interactions in these contexts (e.g., in the quality or quantity of tool transfers) mediates the fidelity of intergenerational transmission. Further, individual follows could reveal whether population differences in how youngsters procure tools are associated with different patterns of raw material sourcing and discard.

The present work should also inspire further investigation of the cognitive underpinnings of tool behavior, particularly regarding the planning and memory capacities (Krause and Sanz 2019) that chimpanzees rely on for efficient foraging (Rosati 2017) yet that remain understudied in wild populations (Janmaat 2019). For example, integrating spatial data (on termite nests, source plants, and home ranges) with direct observations of tool use and of visitation to other food sources (e.g., fruiting trees) could provide novel insights into the factors governing when and where to gather termites and with what raw materials and the time depth over which chimpanzees plan these activities. Individual follows will also help to illuminate how tool complexity relates to the acquisition of mental templates of tool form (Jelbert et al. 2018) and the social scaffolding of tool skills (Musgrave et al. 2020). For example, at Gombe, infants learn to make fishing probes before or at the same time that they learn to use them (Lonsdorf 2005). At Goualougo, where chimpanzees manufacture probes predominantly from just one or two herb species of the Marantaceae family (Sanz and Morgan 2007) and modify these herb probes into a more efficient brush-tipped design (Sanz, Call, and Morgan 2009), youngsters learn to termite fish significantly earlier than they learn to make brush-tipped probes (Musgrave et al. 2021).

While the many important contributions of the current work are to be recognized, we do hope that they inspire further research to integrate the authors' findings with long-term data from these sites. Such a holistic approach would enhance comparative studies of primate technology and strengthen models of hominin behavior and cognition.

Michio Nakamura
Graduate School of Science, Kyoto University, Kitashirakawa Oiwake-cho, Sakyo, Kyoto 606-8502, Japan (nakamura@jinrui.zool.kyoto-u.ac.jp). 22 X 20

In this study, Pascual-Garrido and Almeida-Warren investigated the "availability" of different types of raw material (viz. bark, twig, vine, and grass) for termite-fishing tools used by chimpanzees. The strong point of this study was that they made direct comparisons among three different sites in Tanzania. Although this paper is about more than just availability, I would like to focus my comments on this issue. This is because the novel and fundamental data presented here were on this availability, whereas other data used in further analyses were applied from already published papers.

To measure availability, Pascual-Garrido and Almeida-Warren set "a 5-m circle" (I am not sure whether this 5 m means radius, diameter, or circumference) around a target termite mound and counted the number of "living plants" (perhaps individual plants) in one-fourth of the circle (a quadrant).

The decimals shown in the columns of material types in table 1 appear to be proportions. Although they did not explain the way in which they did the calculation, I understood the figures to be referring to simple divisions of the numbers of plants (e.g., ".486" in the Gombe Bark cell means that there were 222 plants that could potentially produce bark tools, and thus $222/457 = 0.486$). If this is correct, then I wonder whether such numbers alone are good proxies of the availability of raw material types.

For instance, the sizes of plants as a source of tools also seem to matter because a large plant individual can provide more tools than a small one. For simplicity, in an extreme case, only one individual plant might inhabit the quadrant. If this is a large plant, say, a large tree, chimpanzees could make many tools from it. Thus, the raw material required is sufficiently available for them. On the other hand, if this is a small grass, only one tool could be procured from the quadrant, and thus raw material availability would be very low. Therefore, even when the number of individual plants (and thus the proportion) is equal, the availability of raw materials may be different.

Equally important is how plants (both individuals and species) are distributed in the quadrants. For example, if there are some individual plants very close to the mound that could provide a lot of tools, chimpanzees may not dare to search for tools in the outer quadrant area. Thus, in such a case, the weights of the number of plants in the center and at the periphery of each quadrant may be different.

The density of plants that are not suitable for making tools may also matter. When we see mean numbers of 65.3 in Gombe and 33 in Issa in table 1, we are tempted to think that raw materials are more easily obtained in Gombe. However, things are not that simple. Suppose that there are 1,000 and 33 individual plants (including nonmaterial plants) in the Gombe and Issa quadrants, respectively. Then Gombe chimpanzees must find 65.3 plants of 1,000 plants, whereas Issa chimpanzees can choose whichever plants to make a tool. In that scenario, despite the larger mean number of raw material plants, Gombe chimpanzees must expend more effort finding suitable material for tools. As such, the obtainability of tools is measured not only by the absolute number of suitable plants. In other words, in denser vegetation, chimpanzees may have more difficulty finding certain plants than in sparser vegetation.

In the discussion, Pascual-Garrido and Almeida-Warren argued that social learning may be responsible for the selection of tools because of "the lack of an environmental explanation for the absence of twigs in the Issa community." Although I agree that we need to think of cultural variants, I wonder whether they really scrutinized every environmental explanation before concluding what was lacking. For example, assume that plant species whose twigs are suitable as tools are often distributed in the center of quadrants in Gombe, whereas they are distributed at the periphery of quadrants in Issa (such a skewed distribution of plants is possible across different vegetation types). Then, although the absolute numbers of twig plants in the quadrants do not differ, Gombe chimpanzees may use more twig tools than their Issa counterparts (only because twigs can easily be obtained closer to the mound). Similarly, if there is a conspicuous species suitable for bark tools (such as a large tree) within a quadrant in Issa (this is possible if the plant species is the dominant one there), Issa chimpanzees may frequently obtain bark tools from this conspicuous tree (just because it is easy to find that tree). Therefore, before concluding "the lack of an environmental explanation," we may need further descriptions of the prevailing environmental conditions. I think so because Pascual-Garrido and Almeida-Warren have been working on material evidence in the environment rather than observing chimpanzee tool behavior itself. As written above, the distribution of plants in the quadrant and perhaps information about plant sizes could be used to evaluate whether such ecological explanations can be ruled out, as the authors have currently concluded. The fact that only a limited number of plant species are used for bark tools at Issa and Mahale may also be explained by the specific distributions and sizes of such plant species.

Finally, I offer two other miscellaneous comments. First, I was slightly confused because the result on the "reuse of source plants" seemed to have become muddled with the discussion of the "reuse of tools." The former refers to the multiple scars left on plants (these scars may be made at one time), and the latter is about the use of the same stone or stick tool again on a different day. These seem to be slightly different issues. Second, although Pascual-Garrido and Almeida-Warren state that competition with large carnivores for animal prey remains unknown for apes, some observations have suggested that such competition exists (Nakamura et al. 2019). However, the latter is not related to the use of tools.

Fiona A. Stewart
Department of Biological and Environmental Sciences, Liverpool John Moores University, Parsons Building, Byrom Street, Liverpool L3 3AF, United Kingdom, and Department of Anthropology, University College London, London, United Kingdom (f.a.stewart@ljmu.ac.uk). 22 X 20

In 2009, primate archaeology catapulted itself into a new domain as a means of understanding the unseen (Haslam et al. 2009). And whereas revealing work in the archaeological record of extant primates remains an active domain, for obvious reasons, much work has focused on the lithic record (reviewed in Carvalho and Almeida-Warren 2019). Application of archaeological techniques to the study of primate stone tool use has reshaped our view of the Plio-Pleistocene, suggesting that material culture was produced by a number of species across the landscape, and will ultimately help to identify the evolutionary origins of hominin tool use (Carvalho and Almeida-Warren 2019). More recently, Pascual-Garrido, Almeida-Warren, and colleagues have forged their own branch of research with the burgeoning subdiscipline of "the archaeology of the perishable"; they have applied archaeological techniques

to the study of chimpanzee termite fishing, a behavior that does not fossilize but was likely part of several hominin species' behavioral repertoire.

In the current study, Pascual-Garrido and Almeida-Warren build on their previous research to demonstrate that our reconstructed understanding of tool use behavior in the Oldowan is reflected in chimpanzee termite-fishing behavior, including selectivity and the reuse of tool sources that vary depending on raw material availability but also as a reflection of cultural diversity. Only by such comprehensive and careful identification of tool sources and the availability of suitable sources have they been able to identify these features across multiple communities of chimpanzees in Tanzania.

Cultural variation across chimpanzee communities is well documented (McGrew 2004; Whiten et al. 1999), and termite fishing was one of the first cultural behaviors recorded and studied. In fact, a 2020 study that analyzed behavioral observations from camera traps across 10 termite-fishing chimpanzee communities revealed exceptional cultural diversity—or termite-fishing "etiquette" (Boesch et al. 2020). Behaviors unconstrained by environmental conditions were investigated as culture. Pascual-Garrido and Almeida-Warren's study not only describes likely cultural variation in tool selection among communities by controlling for available material but also raises the possibility of cultural change within communities over time. Availability alone, though, does not explain tool material selection across these populations, and future work could further incorporate the interplay between environmental and social influences in shaping termite-fishing culture (sensu Koops, Visalberghi, and van Schaik 2014). Combining these archaeological techniques with direct behavioral observations of the ontogeny of tool use and individual follows is a necessary next step and a powerful method to tease apart the environmental and social influences on the development of tool use patterns across populations. Likewise, investigating the environmental influences on termite fishing within these populations is informative. Is there a difference in mound structure among these populations that makes flexible bark—used exclusively in the Issa community—more efficient tool material? Or does termite behavior differ in drier, more open miombo woodland habitats, where twigs could lack the flexibility needed to access deeply enough into the mound at certain times of the fishing season?

Issa is a comparatively dry and open habitat compared with other chimpanzee habitats and emerges as an outlier in this comparison of tool source reuse intensity in relation to availability and proximity to the mounds. Pascual-Garrido and Almeida-Warren's findings that Issa chimpanzees used sources more intensely closer to mounds while Gombe chimpanzees targeted rare species suggest different strategies influenced by culture, environment, and the availability of resources. Chimpanzees in dry habitats like Issa have been proposed as models for understanding how similar environments may have shaped the behavior of early hominins (Moore 1996). At Issa, suitable material availability is almost half of that at Mahale and Gombe, which, in combination with selectivity for bark, could explain greater tool source use intensity. But whether the extra energetic costs of sourcing tools farther away shape the observed pattern deserves further scrutiny. Physiological measures of the energy balance of chimpanzees in West Africa suggest that forest-dwelling chimpanzees can experience periods of energy imbalance more than savanna woodland populations (Wessling et al. 2018). Similar physiological data on energy expenditure and intake across multiple populations are needed to better understand whether a need for energy conservation could influence tool-sourcing patterns. Pascual-Garrido and Almeida-Warren also suggest that tools may be sourced en route to the mounds with forward planning for fishing. It is equally possible that opportunistic tool sourcing as individuals approach a mound would result in more tools sourced in sight of the mound to influence use intensity. With Issa chimpanzees now habituated, there is scope for comparisons of individual follows of termite fishers between Gombe and Issa to further elucidate the mechanisms creating the pattern of perishable archaeology.

Issa chimpanzees also reuse nesting spots within trees that show similar scarring from prior nest-building events (Stewart, Piel, and McGrew 2011). I proposed that this might occur if nest building itself creates a suitable location for building again in the future through the shaping of branches continuing to grow in their new position and a coppicing effect on the trees sprouting new growth where branches were broken. A fruitful next step would be to explore a similar effect in tool sourcing and its potential influence on tool availability. The opposite effect could also result, with tool sources gradually being depleted over time, leading to individuals searching farther afield as closer resources are exhausted.

Irrespective of the mechanisms by which the pattern of tool source reuse occurs across these chimpanzee communities, there is a clear relationship between the availability of material and tool sourcing intensity that resembles that described in the archaeological record. Future work linking the (extant) archaeological signatures with direct behavioral observations and additional environmental and social influences can further elucidate the patterns observed in early archaeological sites and archaeologically invisible behaviors. As the archaeology of the perishable expands together with primate archaeology, such tools will continue to reveal more about our hominin ancestors and the evolution of technology.

Reply

We thank the commentators for the constructive and supportive responses to our paper. We are encouraged by the positivity with which our work was received by leading scholars in the fields of primate archaeology, primatology, and archaeology. Even in the infancy of primate archaeology and with the

limitations of working with ephemeral records, it is gratifying to see that there is a promising future for the archaeology of the perishable. Various suggestions made for future avenues of research match those that we are currently undertaking, which is encouraging.

As one of the main founders of the field of primate archaeology, Carvalho brings the bigger picture to our study. She reminds us that at the beginning of the twenty-first century, we possessed an archaeological record for one single lineage: our own. Now, only two decades later, we can add apes, Old World monkeys, and New World monkeys into what was previously an exclusively human "lithics" club. Like Carvalho, we hope that our work will help researchers realize that it is time to step away from lithic fixation and push the boundaries of the field further. Our study focused on one of many chimpanzee behaviors that could leave an archaeological signature. Carvalho goes further and suggests expanding this work to other chimpanzee behaviors that may also leave recognizable signatures, as not to do so will continue to offer partial and biased perspectives on technological evolution. We are particularly excited about the archaeological potential of tree drumming (Babiszewska et al. 2015) and bark peeling (Lapuente et al. 2020) as extensions of our methods to other chimpanzee behaviors. We agree with Carvalho that without knowing what features or traces to look for in the archaeological record, we will continue to be blinkered by the lithic bias. After all, plant-based technology is the most common, diverse, and complex form of nonhuman primate tool use, as well as the only form involving manufacture. Carvalho's ingenious example provides a cautionary analogy of how much would be missed if we reconstructed the tool repertoire of Bossou chimpanzees from archaeological excavations that recovered only their lithic tools: lithics constitute just one of the 22 different tool types that they are known to use (Matsuzawa 2011). Plant-based technologies likely dominated the hominin technological repertoire, but they will remain eclipsed unless we develop novel analytical methods to enable their identification in archaeological records (Hardy 2018).

Chu questions the relevance of termite-fishing chimpanzees as models for the practice of entomophagy in early hominins given that the extent to which this type of subsistence influenced the hominin diet is still unclear (Scott 2019). The role of invertebrates has been largely understudied in the evolution of the human diet (McGrew 2014). Only recently has the paleoanthropology community started to pay attention to the role that insects might have had in hominin diets, in particular after the discovery of bone artifacts that might have been used to dig up termite mounds by *Paranthropus* (cf. McGrew 2021 for an alternative view of the use of these tools). This, together with isotopic evidence of significant amounts of C_4 resources in the *Paranthropus* diet, suggests insects, in particular grass-eating termites, as a possible source of the hominin's C_4 signature (Lesnik 2014). Furthermore, insects and insect resources probably have been exploited by the order Primates since its origins; all living primates are probably to some degree insectivorous. Insects are relatively high in energy, fat, and high-quality protein and may contain vitamins and minerals that are limited in common plants and fruits (O'Malley and McGrew 2014). Among long-term study populations of chimpanzees, invertebrates make up a larger proportion of the diet than vertebrate prey (Pruetz 2006). Furthermore, worldwide, insects (and some insect products, such as honey) are avidly consumed by many human societies (Bodenheimer 1951). Therefore, it is likely that early humans also made use of this resource and probably used a much richer and more diverse tool kit, including perishable tools, than is seen in the archaeological record (Lesnik 2018). Of course, we do not propose chimpanzees as living fossils of early humans, but they are our closest living relatives. Linking their behavior and artifacts to hominins, when done carefully, can be useful for identifying the common characteristics that were likely present after the divergence of the two clades (Rolian and Carvalho 2017).

Backwell and d'Errico suggest that bone tools may have been used for termite foraging by hominins in South Africa (Backwell and d'Errico 2001, 2008). Like Chu, Backwell and d'Errico question the use of termite-fishing chimpanzees as hominin models as a point of comparison for early hominin stone tool technology in this instance. Instead, Backwell and d'Errico encourage ethologists working on chimpanzee cultures to consider bone tools as the hominin technological evidence for which modern chimpanzees could be suitable models. We welcome Backwell and d'Errico's suggestion to consider bone tool technologies when modeling hominin behavior in the future, but their model has limitations: First, chimpanzees have yet to be seen using bone tools either in captivity or in the wild. Second, chimpanzees do not dig up termite mounds, although some populations may use perforating and puncturing tools to gain access to termites in their earthen nests. Third, *Trinervitermes*, the termite genus chosen by d'Errico, Backwell, and Berger (2001) for their experimental digging into termite mounds, has not been reported to be consumed by any population of chimpanzees either with or without the use of tools (McGrew 2021). Like Backwell and d'Errico, we aim to help address similarities and differences between modern chimpanzee behavior and that inferred from early hominin artifacts.

Hicks reaffirms the importance of considering the ecology of culture (per Koops, Visalberghi, and van Schaik 2014) when studying great ape traditions. This focus requires a level of detail not attainable using camera traps but only through natural history studies. Hicks describes the time when William McGrew and Caroline Tutin left Gombe to visit Mahale and discovered, through their observations and conversations with Junichiro Itani, that Gombe and Mahale chimpanzees had developed different grooming traditions. His description resonates with Carvalho's previous advice of not using "one size fits all" to infer species' cognitive skills or complexity, especially if we are making inferences from the absence of evidence. Tool use variation across groups within the same population may result from different environmental affordances (e.g., Uehara 1982) or different cultural knowledge (O'Malley et al. 2012). Variation across

individuals within a population may result from differing experiences in ontogeny, in particular from mother (and older siblings) to offspring (Lonsdorf 2006; Musgrave et al. 2020). Disentangling how much each of these factors contributes to the patterns of tool use variation seen in chimpanzee populations across Africa is perhaps one of the biggest challenges that remains ahead.

McGrew provides examples of archaeologists using actualistic studies, which usually require experimental replication, for the study of organic or mineralized materials. We agree with him in that implementing a similar approach with the study of chimpanzee perishable tools, that is, by the researchers replicating what apes are doing, will help to pinpoint the questions that remain to be investigated. For example, do certain physical properties of the tools (e.g., cross-sectional shape) increase termite-fishing efficiency, and is this in turn influenced by the physical characteristics of the termite prey? Studies mimicking the use of tools by chimpanzees at army ant nests have provided insights not only into the cognitive abilities of the tool users but also into the behavior of the insect prey and their influence on tool design (Möbius et al. 2008). Comparable studies for termite fishing are still lacking.

Also worthy of further investigation are wear patterns on tool ends, which, in the absence of direct behavioral observation, can help to clarify the diagnostic features of a tool and help to distinguish materials that have been used as tools from those that have not (Carvalho and Almeida-Warren 2019). McGrew (and Chu, Musgrave and Sanz, and Stewart) emphasizes the urgent need to pursue the etho- part of ethoarchaeology, in which indirect data can be tested by observation of the chimpanzees in action. We agree with McGrew that retrieving the artifacts left by known individuals after a fishing session offers the observers the unique opportunity to study the creation of palimpsests in real time—an opportunity that archaeologists will never have.

Musgrave and Sanz highlight that integrating behavioral observations helps to elucidate what contributes to variation within and between populations, whether from individual or group preferences for tool material types, matrilines, or immigrants. We endorse Chu's proposal that such inquiries should include variables such as gender and age. These foci are particularly relevant for tools used for foraging, where sex differences exist and in which technical skills are acquired at a certain age (Boesch and Boesch 1984; de A. Moura and Lee 2010; Falótico and Ottoni 2014; Fox et al. 2004; Gumert, Hoong, and Malaivijitnond 2011; Lonsdorf 2005; Musgrave et al. 2021). This could be straightforwardly done in the habituated communities of Gombe or Issa. For nonhabituated subjects, such as the Bilenge apes of Mahale, the use of camera traps could assist (Lapuente, Hicks, and Linsenmair 2017). But even when behavioral observations are incomplete, they provide fragments that can be tied together, as McGrew exemplifies with a photograph showing the sequence of production and use of sponge tools by partly habituated chimpanzees (*Pan troglodytes schweinfurthii*) at Semliki, Uganda.

Assessing the energetic requirements of termite gathering by integrating data on the spatial distribution of termite nests and the individual source plants, as proposed by Musgrave and Sanz, is another crucial step in developing this research further and will help us fully understand how the different patterns of raw material selection relate to forage efficiency more broadly. Given that empirical data on the adaptive significance of tool use are surprisingly scarce (Biro, Haslam, and Rutz 2013), these investigations should be accompanied by studies that analyze the energetic payoffs of tool use behaviors. Even among the long-studied chimpanzee populations of Gombe and Mahale in Tanzania and Bossou in Guinea, which have yielded studies of the energetic and nutritional yields of insectivory (O'Malley and Power 2014), it is surprising that only one study has investigated the link between tool-assisted extractive foraging and fitness (Mackworth-Young and McGrew 2014) and none have investigated the potential variation in dietary payoffs among chimpanzee communities with different tool use behaviors (Musgrave et al. 2021). Such research would help answer questions such as: Do certain types of materials and techniques used offer better fitness returns than others? We agree with Musgrave and Sanz on the need to expand studies to a landscape scale (which we are undertaking) by including a spatial analysis of termite mounds, source plants, and other food sources. We particularly need to investigate the ecological and social drivers of the selection, reuse, and abandonment of tool use sites. Such studies will allow the identification of chimpanzee-like patterns of landscape use and provide a model that may enable us to answer one of the longest-standing questions in the archaeology of human origins: How did our earliest technological ancestors interact with their environment?

We welcome Nakamura's thoughtful critique of the methods we have employed, particularly the traditional method used to measure the availability of raw material for termite-fishing tools, which consists of counting the number of suitable plants near mounds (Almeida-Warren et al. 2017; Koops, McGrew, and Matsuzawa 2013; McBeath and McGrew 1982; McGrew et al. 2007). Nakamura suggests that the size of the plant also matters, simply because a large plant can provide more tools than a small one. We have collected these data, including the source plants' height and the number of branches available per source plant, but it will require further studies of the physical and mechanical characteristics of the source plants for us to examine these relationships. Furthermore, it seems likely that there is a variation in the vegetative parts of each source plant, and so not all plant elements will constitute good sources for tools: branches of specific diameters located at certain heights are used by chimpanzees (Almeida-Warren et al. 2017; Pascual-Garrido 2017). Nakamura's comment on the spatial distributions and sizes of bark- versus twig-providing plants may explain the exclusive use of bark tools by Issa chimpanzees, as this may constitute one of the "other ecological factors," together with tool material efficiency and prey behavior. Raw material studies of termite-fishing tools are limited, as they are normally conducted within 5 m of the termite mound (Almeida-Warren

et al. 2017; Koops, McGrew, and Matsuzawa 2013; McBeath and McGrew 1982; McGrew et al. 2007). Chimpanzees sometimes get their raw materials from farther away (Pascual-Garrido 2018). Thus, it may be time to reexamine and expand on these long-established methods to better address the more nuanced and complex questions arising in this field.

Stewart's proposal motivates us to test a "scaffolding effect" for the reuse of raw material sources similar to that described for the reuse of chimpanzee nests, where nest building itself creates a suitable root location for future rebuilding (Stewart, Piel, and McGrew 2011). Future studies should also investigate whether scars left on source plants as a result of chimpanzees removing material for tools (Pascual-Garrido 2018) are used as an associative (learning) cue for identifying suitable raw material. When sourcing raw material for hooked stick tool manufacture, New Caledonian crows (*Corvus moneduloides*) identify their source material by its stem and possibly also by its leaves (Klump, Cantat, and Rutz 2019). We still do not know what features help chimpanzees identify their raw materials, but we hope that future experiments will investigate this. Stewart's suggestion of the opposite effect is also possible; that is, if closer tool sources are gradually being depleted, this may lead to individuals using sources located farther away. In Gashaka-Gumti National Park in Nigeria, Pascual-Garrido et al. (2012) found that the sourcing of raw material for tools used to harvest ants and bee products by chimpanzees follows such a depletion effect. We also take on board Stewart's suggestion of conducting a thorough investigation of the structure of termite mounds and the behavior of the termite prey. These foci should reveal whether prey species or termite mound characteristics influence chimpanzee termite-fishing cultures across populations (Sanz et al. 2014), as has been described for chimpanzee army ant dipping (Schöning et al. 2008).

We must express our gratitude to the chimpanzees for continuing to offer us clues about our origins and ourselves. In the Anthropocene, it is up to us to ensure the survival of our closest living relatives and the traditions on which their well-being and survival depend.

—Alejandra Pascual-Garrido and Katarina Almeida-Warren

References Cited

Allsop, Karen A., and Jennie B. Miller. 1996. Honey revisited: a reappraisal of honey in pre-industrial diets. *British Journal of Nutrition* 75(4):513–520.

Almeida-Warren, Katarina, David R. Braun, Tetsuro Matsuzawa, and Susana Carvalho. 2018. Mapping primate archaeology: new tools for standardizing spatial data collection across the primate order. Poster presented at the XXVII International Primatological Society Congress, Nairobi, August 19–25.

Almeida-Warren, Katarina, Volker Sommer, Alexander K. Piel, and Alejandra Pascual-Garrido. 2017. Raw material procurement for termite fishing tools by wild chimpanzees in the Issa Valley, western Tanzania. *American Journal of Physical Anthropology* 164(2):292–304, https://doi.org/10.1002/ajpa.23269.

Andrefsky, William. 1994. Raw-material availability and the organization of technology. *American Antiquity* 59(1):21–34.

Arroyo, Adrián, and Ignacio de la Torre. 2016. Assessing the function of pounding tools in the Early Stone Age: a microscopic approach to the analysis of percussive artefacts from Beds I and II, Olduvai Gorge (Tanzania). *Journal of Archaeological Science* 74:23–34. [Fd'E/LRB]

———. 2018. Pounding tools in HWK EE and EF-HR (Olduvai Gorge, Tanzania): percussive activities in the Oldowan-Acheulean transition. *Journal of Human Evolution* 120:402–421. [Fd'E/LRB]

Arroyo, Adrián, Satoshi Hirata, Tetsuro Matsuzawa, and Ignacio de la Torre. 2016. Nut cracking tools used by captive chimpanzees (*Pan troglodytes*) and their comparison with Early Stone Age percussive artefacts from Olduvai Gorge. *PLoS ONE* 11(11):e0166788. [Fd'E/LRB]

Babiszewska, Magdalena, Anne Marijke Schel, Claudia Wilke, and Katie E. Slocombe. 2015. Social, contextual, and individual factors affecting the occurrence and acoustic structure of drumming bouts in wild chimpanzees (*Pan troglodytes*). *American Journal of Physical Anthropology* 156(1):125–134.

Backwell, Lucinda R., and Francesco d'Errico. 2001. Evidence of termite foraging by Swartkrans early hominids. *Proceedings of the National Academy of Sciences of the USA* 98(4):1358–1363.

———. 2003. Additional evidence on the early hominid bone tools from Swartkrans with reference to spatial distribution of lithic and organic artefacts: research articles: human origins research in South Africa. *South African Journal of Science* 99(5/6):259–267. [Fd'E/LRB]

———. 2004. New bone tools from Swartkrans. In *Swartkrans: a cave's chronicle of early man*. Charles K. Brain, ed. Pp. 279–295. Pretoria: Transvaal Museum Monographs. [Fd'E/LRB]

———. 2008. Early hominid bone tools from Drimolen, South Africa. *Journal of Archaeological Science* 35(11):2880–2894, https://doi.org/10.1016/j.jas.2008.05.017.

———. 2009. Additional evidence of early hominid bone tools from South Africa: first attempt at exploring inter-site variability. *Palaeontologia Africana* 44:91–94. [Fd'E/LRB]

Berbesque, Julia Colette, and Frank W. Marlowe. 2009. Sex differences in food preferences of Hadza hunter-gatherers. *Evolutionary Psychology* 7(4):601–616.

Bermejo, Magdalena, and German Illera. 1999. Tool-set for termite-fishing and honey extraction by wild chimpanzees in the Lossi Forest, Congo. *Primates* 40(4):619–627.

Bertran, Pascal, Dominique Todisco, Jean-Guillaume Bordes, Emmanuel Discamps, and Luc Vallin. 2019. Perturbation assessment in archaeological sites as part of the taphonomic study: a review of methods used to document the impact of natural processes on site formation and archaeological interpretations. *PALEO: Revue d'Archéologie Préhistorique* 30(1):52–75, https://doi.org/10.4000/paleo.4378. [WC]

Biro, Dora, Michael Haslam, and Christian Rutz. 2013. Tool use as adaptation. *Philosophical Transactions of the Royal Society of London: Series B, Biological Sciences* 368(1630):20120408, https://doi.org/10.1098/rstb.2012.0408.

Biro, Dora, Noriko Inoue-Nakamura, Rikako Tonooka, Gen Yamakoshi, Claudia Sousa, and Tetsuro Matsuzawa. 2003. Cultural innovation and transmission of tool use in wild chimpanzees: evidence from field experiments. *Animal Cognition* 6(4):213–223.

Bluff, Lucas A., Jolyon Troscianko, Alex A. S. Weir, Alex Kacelnik, and Christian Rutz. 2010. Tool use by wild New Caledonian crows *Corvus moneduloides* at natural foraging sites. *Proceedings of the Royal Society B: Biological Sciences* 277(1686):1377–1385.

Blumenschine, Robert J., Fidelis T. Masao, Joanne C. Tactikos, and James I. Ebert. 2008. Effects of distance from stone source on landscape-scale variation in Oldowan artefact assemblages in the Paleo-Olduvai Basin, Tanzania. *Journal of Archaeological Science* 35(1):76–86.

Bodenheimer, Friedrich S. 1951. *Insects as human food: a chapter of the ecology of man*. London: W. Junk.

Boesch, Cristophe, and Hedwige Boesch. 1984. Mental map in wild chimpanzees: an analysis of hammer transports for nut cracking. *Primates* 25(2):160–170.

Boesch, Christophe, Ammie K. Kalan, Roger Mundry, Mimi Arandjelovic, Simone Pika, Paula Dieguez, Emmanuel Ayuk Ayimisin, et al. 2020. Chimpanzee ethnography reveals unexpected cultural diversity. *Nature Human Behaviour* 4(9):910–916, https://doi.org/10.1038/s41562-020-0890-1.

Bogart, Stephanie L., and Jill D. Pruetz. 2011. Insectivory of savanna chimpanzees (*Pan troglodytes verus*) at Fongoli, Senegal. *American Journal of Physical Anthropology* 145(1):11–20.

Brain, Charles K., and Pat Shipman. 1993. The Swartkrans bone tools. In *Swartkrans: a cave's chronicle of early man*. Charles K. Brain, ed. Pp. 195–215. Cape Town: C. T. P. Book Printers. [Fd'E/LRB]

Brakes, Philippa, Sasha R. X. Dall, Lucy M. Aplin, Stuart Bearhop, Emma L. Carroll, Paolo Ciucci, Vicki Fishlock, et al. 2019. Animal cultures matter for conservation. *Science* 363(6431):1032–1034, https://doi.org/10.1126/science.aaw3557.

Braun, David R., Vera Aldeias, Will Archer, J. Ramon Arrowsmith, Niguss Baraki, Christopher J. Campisano, Alan L. Deino, et al. 2019. Earliest known

Oldowan artifacts at >2.58 ma from Ledi-Geraru, Ethiopia, highlight early technological diversity. *Proceedings of the National Academy of Sciences of the USA* 116(24):11712–11717, https://doi.org/10.1073/pnas.1820177116.

Braun, David R., Thomas Plummer, Peter Ditchfield, Joseph V. Ferraro, David Maina, Laura C. Bishop, and Richard Potts. 2008. Oldowan behavior and raw material transport: perspectives from the Kanjera Formation. *Journal of Archaeological Science* 35(8):2329–2345.

Braun, David R., Thomas Plummer, Joseph V. Ferraro, Peter Ditchfield, and Laura C. Bishop. 2009. Raw material quality and Oldowan hominin toolstone preferences: evidence from Kanjera South, Kenya. *Journal of Archaeological Science* 36(7):1605–1614.

Byrne, Richard. 2007. Culture in great apes: using intricate complexity in feeding skills to trace the evolutionary origin of human technical prowess. *Philosophical Transactions of the Royal Society of London: Series B, Biological Sciences* 362(1480):577–585. [SM/CS]

Caruana, Matthew V., Francesco d'Errico, and Lucinda R. Backwell. 2013. Early hominin social learning strategies underlying the use and production of bone and stone tools. In *Tool use in animals: cognition and ecology*. Crickette M. Sanz, Josep Call, and Christophe Boesch, eds. Pp. 242–285. Cambridge: Cambridge University Press. [Fd'E/LRB]

Carvalho, Susana, and Katarina Almeida-Warren. 2019. Primate archaeology. In *Encyclopedia of animal behavior*. 2nd edition. Jae Chun Choe, ed. Pp. 397–407. London: Elsevier.

Carvalho, Susana, and Megan Beardmore-Herd. 2019. Technological origins: primate perspectives and early hominin tool use in Africa. In *Oxford research encyclopedia of African history*. Thomas Spear, ed. Oxford: Oxford University Press.

Carvalho, Susana, Eugénia Cunha, Cláudia Sousa, and Tetsuro Matsuzawa. 2008. *Chaînes opératoires* and resource-exploitation strategies in chimpanzee (*Pan troglodytes*) nut cracking. *Journal of Human Evolution* 55(1):148–163.

Cazzella, Alberto. 2016. Ethnoarchaeology of the intangible culture: a trajectory towards paleoethnology as a global discipline? In *The intangible elements of culture in ethnoarchaeological research*. Stefano Biagetti and Francesca Lugli, eds. Pp. 37–46. Cham, Switzerland: Springer, https://doi.org/10.1007/978-3-319-23153-2_2. [WC]

Chu, Wei. 2009. A functional approach to Paleolithic open-air habitation structures. *World Archaeology* 41:348–362. [WC]

Collins, D. Anthony, and William C. McGrew. 1987. Termite fauna related to differences in tool-use between groups of chimpanzees (*Pan troglodytes*). *Primates* 28(4):457–471, https://doi.org/10.1007/BF02380861.

———. 1988. Habitats of three groups of chimpanzees (*Pan troglodytes*) in western Tanzania compared. *Journal of Human Evolution* 17(66):553–574.

Conard, Nicholas J., Jordi Serangeli, Utz Böhner, Britt M. Starkovich, Christopher E. Miller, Brigitte Urban, and Thijs Van Kolfschoten. 2015. Excavations at Schöningen and paradigm shifts in human evolution. *Journal of Human Evolution* 89:1–17.

Cunningham, Jerimy J., and Kevin M. McGeough. 2018. The perils of ethnographic analogy: parallel logics in ethnoarchaeology and Victorian Bible customs books. *Archaeological Dialogues* 25(2):161–189, https://doi.org/10.1017/S1380203818000181. [WC]

Darlington, Jo P. E. C. 2005. Distinctive fossilised termite nests at Laetoli, Tanzania. *Insectes Sociaux* 52(4):408–409.

Davidson, Iain, and William C. McGrew. 2005. Stone tools and the uniqueness of human culture. *Journal of the Royal Anthropological Institute* 11(4):793–817.

de A. Moura, Antonio, and Phyllis Lee. 2010. Wild capuchins show male-biased feeding tool use. *International Journal of Primatology* 31(3):457–470, https://doi.org/10.1007/s10764-010-9406-6.

Deblauwe, Isra. 2009. Temporal variation in insect-eating by chimpanzees and gorillas in southeast Cameroon: extension of niche differentiation. *International Journal of Primatology* 30(2):229–252.

Delagnes, Anne, and Hélène Roche. 2005. Late Pliocene hominid knapping skills: the case of Lokalalei 2C, West Turkana, Kenya. *Journal of Human Evolution* 48(5):435–472.

de la Torre, Ignacio, Rafael Mora, Manuel Dominguez-Rodrigo, Luis de Luque, and Luis Alcala. 2003. The Oldowan industry of Peninj and its bearing on the reconstruction of the technological skills of Lower Pleistocene hominids. *Journal of Human Evolution* 44(2):203–224.

d'Errico, Francesco, and Lucinda R. Backwell. 2003. Possible evidence of bone tool shaping from the early hominid site of Swartkrans, South Africa. *Journal of Archaeological Science* 30:1559–1576. [Fd'E/LRB]

———. 2009. Assessing the function of early hominin bone tools. *Journal of Archaeological Science* 36(8):1764–1773. [Fd'E/LRB]

d'Errico, Francesco, Lucinda R. Backwell, and Lee R. Berger. 2001. Bone tool use in termite foraging by early hominids and its impact on our understanding of early hominid behaviour. *South African Journal of Science* 97(3/4):71–75.

de Ruiter, Darryl J., Matt Sponheimer, and Julia A. Lee-Thorp. 2008. Indications of habitat association of *Australopithecus robustus* in the Bloubank Valley, South Africa. *Journal of Human Evolution* 55(6):1015–1030. [Fd'E/LRB]

Dobson, Annette J. 2002. *An introduction to generalized linear models*. New York: Chapman & Hall.

Dominguez-Rodrigo, Manuel, Jordi Serralonga, Jordi Juan-Tresserras, Luis Alcala, and Luis Luque. 2001. Woodworking activities by early humans: a plant residue analysis on Acheulian stone tools from Peninj (Tanzania). *Journal of Human Evolution* 40(4):289–299.

Faith, Tyler, John Rowan, and Andrew Du. 2019. Early hominins evolved within non-analog ecosystems. *Proceedings of the National Academy of Sciences of the USA* 116(43):21478–21483.

Falótico, Tiago, and Eduardo B. Ottoni. 2014. Sexual bias in probe tool manufacture and use by wild bearded capuchin monkeys. *Behavioural Processes* 108:117–122, https://doi.org/10.1016/j.beproc.2014.09.036.

Falótico, Tiago, Tomos Proffitt, Eduardo B. Ottoni, Richard A. Staff, and Michael Haslam. 2019. Three thousand years of wild capuchin stone tool use. *Nature Ecology and Evolution* 3(7):1034–1038, https://doi.org/10.1038/s41559-019-0904-4. [SC, WCM]

Fay, Michael C., and Richard W. Carroll. 1994. Chimpanzee tool use for honey and termite extraction in Central Africa. *American Journal of Primatology* 34(4):309–317.

Fox, Elizabeth A., Carel P. van Schaik, Arnold Sitompul, and Donielle N. Wright. 2004. Intra- and interpopulational differences in orangutan (*Pongo pygmaeus*) activity and diet: implications for the invention of tool use. *American Journal of Physical Anthropology* 125(2):162–174, https://doi.org/10.1002/ajpa.10386.

Fox, Jon, and Sanford Weisberg. 2011. *An R companion to applied regression*. 2nd edition. New York: Sage.

Friesem, David E. 2016. Geo-ethnoarchaeology in action. *Journal of Archaeological Science* 70:145–157, https://doi.org/10.1016/j.jas.2016.05.004. [WC]

Fujii, Jessica A., Katherine Ralls, and M. Tim Tinker. 2017. Food abundance, prey morphology, and diet specialization influence individual sea otter tool use. *Behavioral Ecology* 28(5):1206–1216. [SM/CS]

Goldman-Neuman, Talia, and Erella Hovers. 2009. Methodological considerations in the study of Oldowan raw material selectivity: insights from A. L. 894 (Hadar, Ethiopia). In *Interdisciplinary approaches to the Oldowan*. Erella Hovers and David R. Braun, eds. Pp. 71–84. Dordrecht, Germany: Springer.

———. 2012. Raw material selectivity in Late Pliocene Oldowan sites in the Makaamitalu Basin, Hadar, Ethiopia. *Journal of Human Evolution* 62(3):353–366.

González-Ruibal, Alfredo, Almudena Hernando, and Gustavo Politis. 2011. Ontology of the self and material culture: arrow-making among the Awá hunter-gatherers (Brazil). *Journal of Anthropological Archaeology* 30(1):1–16.

Goodall, Jane. 1964. Tool-using and aimed throwing in a community of free-living chimpanzees. *Nature* 201:1264–1266.

———. 1986. *The chimpanzees of Gombe: patterns of behaviour*. Cambridge, MA: Harvard University Press.

Goren-Inbar, Naama, Gonen Sharon, Yoel Melamed, and Mordechai Kislev. 2002. Nuts, nut cracking, and pitted stones at Gesher Benot Ya'aqov, Israel. *Proceedings of the National Academy of Sciences of the USA* 99(4):2455–2460.

Goren-Inbar, Naama, Ella Werker, and Craig Feibel. 2002. *The Acheulian site of Gesher Benot Ya'aqov, Israel: the wood assemblage*. Oxford: Oxbow. [WCM]

Gosselain, Olivier P. 2016. To hell with ethnoarchaeology! *Archaeological Dialogues* 23(2):215–228, https://doi.org/10.1017/S1380203816000234. [WC]

Gruber, Thibaud, Kevin B. Potts, Christopher Krupenye, Maisie Rose Byrne, Constance Mackworth-Young, William C. McGrew, Vernon Reynolds, and Klaus Zuberbühler. 2012. The influence of ecology on chimpanzee (*Pan troglodytes*) cultural behavior: a case study of five Ugandan chimpanzee communities. *Journal of Comparative Psychology* 126(4):446–457.

Gumert, Michael D., Low Kuan Hoong, and Suchinda Malaivijitnond. 2011. Sex differences in the stone tool-use behavior of a wild population of Burmese long-tailed macaques (*Macaca fascicularis aurea*). *American Journal of Primatology* 73(12):1239–1249, https://doi.org/10.1002/ajp.20996.

Hanon, Raphael. 2019. Les comportements de subsistance des hominines du Pléistocène inférieur d'Afrique du Sud: étude zooarchéologique du site de Cooper's D (Bloubank Valley). PhD thesis, National History Museum, Paris. [Fd'E/LRB]

Hardy, Bruce L., M.-H. Moncel, Celine Kerfant, Matthieu Lebon, Ludovic Bellot-Gurlet, and Nicolas Melard. 2020. Direct evidence of Neanderthal fibre technology and its cognitive and behavioural implications. *Scientific Reports* 10:4889. [WCM]

Hardy, Karen. 2018. Plant use in the Lower and Middle Palaeolithic: food, medicine and raw materials. *Quaternary Science Reviews* 191:393–405, https://doi.org/10.1016/j.quascirev.2018.04.028.

Harmand, Sonia. 2009. Variability in raw material selection at the Late Pliocene sites of Lokalalei, West Turkana, Kenya. In *Interdisciplinary approaches to the Oldowan*. Erella Hovers and David R. Braun, eds. Pp. 85–99. Dordrecht, Germany: Springer.

Harmand, Sonia, Jason E. Lewis, Craig S. Feibel, Christopher J. Lepre, Sandrine Prat, Arnaud Lenoble, Xavier Boes, et al. 2015. 3.3-million-year-old stone tools from Lomekwi 3, West Turkana, Kenya. *Nature* 521(7552):310–315. [SC]

Harrison, Xavier A. 2014. Using observation-level random effects to model overdispersion in count data in ecology and evolution. *PeerJ* 2:e616, https://peerj.com/articles/616.

Haslam, Michael, Adriana Hernandez-Aguilar, Victoria Ling, Susana Carvalho, Ignacio de la Torre, April Destefano, Andrew Du, et al. 2009. Primate archaeology. *Nature* 460(7253):339–344.

Haslam, Michael, Adriana Hernandez-Aguilar, Tomos Proffitt, Adrian Arroyo, Tiago Falótico, Dorothy Fragaszy, Michael Gumert, et al. 2017. Primate archaeology evolves. *Nature Ecology and Evolution* 1:1431–1437.

Heaton, Jason L., and Travis R. Pickering. 2006. Archaeological analysis does not support intentionality in the production of brushed ends on chimpanzee termiting tools. *International Journal of Primatology* 27(6):1619–1633.

Hernandez-Aguilar, R. Adriana. 2009. Chimpanzee nest distribution and site reuse in a dry habitat: implications for early hominin ranging. *Journal of Human Evolution* 57(4):350–364.

Hernandez-Aguilar, R. Adriana, Jim Moore, and Travis R. Pickering. 2007. Savanna chimpanzees use tools to harvest the underground storage organs of plants. *Proceedings of the National Academy of Sciences of the USA* 104(49): 19210–19213.

Hicks, Thurston C., Hjalmar S. Kühl, Christophe Boesch, Paula Dieguez, Ayuk Emmanuel Ayimisin, Rumen Martin Fernandez, Donatienne Barubiyo Zungawa, et al. 2019. Bili-Uére: a chimpanzee behavioural realm in northern Democratic Republic of Congo. *Folia Primatologica* 90(1):3–64.

Hicks, Thurston C., Hjalmar S. Kühl, Christophe Boesch, Steph B. J. Menken, John Hart, Peter Roessingh, Corneille Ewango, and Roger Mundry. 2020. The relationship between tool use and prey availability in chimpanzees (*Pan troglodytes schweinfurthii*) of northern Democratic Republic of Congo. *International Journal of Primatology* 41:936–959. [TCH]

Hobaiter, Catherine, Timothée Poisot, Klaus Zuberbühler, William Hoppitt, and Thibaud Gruber. 2014. Social network analysis shows direct evidence for social transmission of tool use in wild chimpanzees. *PLoS Biology* 12(9): e1001960, https://dx.plos.org/10.1371/journal.pbio.1001960.

Hobaiter, Catherine, Liran Samuni, Caroline Mullins, Walter John Akankwasa, and Klaus Zuberbühler. 2017. Variation in hunting behaviour in neighbouring chimpanzee communities in the Budongo Forest, Uganda. *PLoS ONE* 12(6):e0178065. [TCH]

Hoffecker, John F., and Ian T. Hoffecker. 2018. The structural and functional complexity of hunter-gatherer technology. *Journal of Archaeological Method and Theory* 25:202–225.

Hosfield, Robert. 2020. *The earliest Europeans: a year in the life: survival strategies in the lower Palaeolithic*. Oxford: Oxbow. [WC]

Humle, Tatyana, Charles T. Snowdon, and Tetsuro Matsuzawa. 2009. Social influences on ant-dipping acquisition in the wild chimpanzees (*Pan troglodytes verus*) of Bossou, Guinea, West Africa. *Animal Cognition* 12(suppl. 1):S37–S48.

Hundley, Margaret H. 1963. Notes on methods of feeding and the use of tools in the Geospizinae. *The Auk* 80(2):372–373.

Hurcombe, Linda. 2008. Organics from inorganics: using experimental archaeology as a research tool for studying perishable material culture. *World Archaeology* 40(1):83–115. [WCM]

Inoue, Eiji, Yasuko Tashiro, Hideshi Ogawa, Miho Inoue-Murayama, Toshisada Nishida, and Osamu Takenaka. 2013. Gene flow and genetic diversity of chimpanzees in Tanzanian habitats. *Primate Conservation* 26(1):67–74.

Janmaat, Karline R. L. 2019. What animals do not do or fail to find: a novel observational approach for studying cognition in the wild. *Evolutionary Anthropology: Issues, News, and Reviews* 28(6):303–320. [SM/CS]

Jelbert, Sarah A., Roger J. Hosking, Adrian H. Taylor, and Russell D. Gray. 2018. Mental template matching is a potential cultural transmission mechanism for New Caledonian crow tool manufacturing traditions. *Scientific Reports* 8(1):1–8. [SM/CS]

Jones, Clyde, and Jorge Sabater Pi. 1969. Sticks used by chimpanzees in Rio Muni, West Africa. *Nature* 223:100–101.

Kimura, Yuki. 1999. Tool-using strategies by early hominids at Bed II, Olduvai Gorge, Tanzania. *Journal of Human Evolution* 36(6):807–831.

Klump, Barbara, Mathieu Cantat, and Christian Rutz. 2019. Raw material selectivity in hook-tool-crafting New Caledonian crows. *Biology Letters* 15(2): 20180836, https://royalsocietypublishing.org/doi/10.1098/rsbl.2018.0836.

Koops, Kathelijne, William C. McGrew, and Tetsuro Matsuzawa. 2013. Ecology of culture: do environmental factors influence foraging tool use in wild chimpanzees, *Pan troglodytes verus*? *Animal Behaviour* 85(1):175–185, https://doi.org/10.1016/j.anbehav.2012.10.022.

Koops, Kathelijne, Caspar Schöning, and Chie Hashimoto. 2015. Cultural differences in ant-dipping tool length between neighbouring chimpanzee communities at Kalinzu, Uganda. *Scientific Reports* 5:12456, http://www.nature.com/articles/srep12456.

Koops, Kathelijne, Caroline Schuppli, and Carel P. van Schaik. 2018. Cultural primatology. In *The international encyclopedia of biological anthropology*. Wenda Trevathan, Matt Cartmill, Darna L. Dufour, Cark Spencer Larsen, Dennis H. O'Rourke, Karen Rosenberg, and Karen B. Strier, eds. Hoboken, NJ: Wiley & Sons.

Koops, Kathelijne, Elisabetta Visalberghi, and Carel P. van Schaik. 2014. The ecology of primate material culture. *Biology Letters* 10(11):20140508, https://doi.org/10.1098/rsbl.2014.0508.

Koops, Kathelijne, Richard W. Wrangham, Neil Cumberlidge, Maegan A. Fitzgerald, Kelly L. van Leeuwen, Jessica M. Rothman, and Tetsuro Matsuzawa. 2019. Crab-fishing by chimpanzees in the Nimba Mountains, Guinea. *Journal of Human Evolution* 133:230–241. [SC]

Korb, Judith. 2013. Termite mound architecture, from function to construction. In *Biology of termites: a modern synthesis*. David Edward Bignell, Yves Roisin, and Nathan Lo, eds. Pp. 349–373. Dordrecht, Germany: Springer. [SM/CS]

Krause, Mark A., and Crickette M. Sanz. 2019. The evolution of learning and memory in humans: comparative perspectives on testing adaptive hypotheses. In *Handbook of cognitive archaeology*. Tracy B. Henley, Matt J. Rossano, and Edward P. Kardas, eds. Pp. 174–195. New York: Routledge. [SM/CS]

Kühl, Hjalmar S., Ammie K. Kalan, Mimi Arandjelovic, Floris Aubert, Lucy D'Auvergne, Annemarie Goedmakers, Sorrel Jones, et al. 2016. Chimpanzee accumulative stone throwing. *Scientific Reports* 6:22219. [SC]

Lamon, Noemie, Christof Neumann, Jennifer Gier, Klaus Zuberbühler, and Thibaud Gruber. 2018. Wild chimpanzees select tool material based on efficiency and knowledge. *Proceedings of the Royal Society B: Biological Sciences* 285(1888):20181715, https://royalsocietypublishing.org/doi/10.1098/rspb.2018.1715.

Lamon, Noemie, Christof Neumann, Thibaud Gruber, and Klaus Zuberbühler. 2017. Kin-based cultural transmission of tool use in wild chimpanzees. *Science Advances* 3(4):e1602750. [SM/CS]

Langergraber, Kevin E., Christophe Boesch, Eiji Inoue, Miho Inoue-Murayama, John C. Mitani, Toshisada Nishida, Anne Pusey, et al. 2011. Genetic and "cultural" similarity in wild chimpanzees. *Proceedings of the Royal Society B: Biological Sciences* 278(1704):408–416. [TCH]

Langergraber, Kevin E., Kay Prüfer, Caroline Rowney, Christophe Boesch, Catherine Crockford, Katie Fawcett, Eiji Inoue, et al. 2012. Generation times in wild chimpanzees and gorillas suggest earlier divergence times in great ape and human evolution. *Proceedings of the National Academy of Sciences of the USA* 109(39):15716–15721.

Lapuente, Juan, Mimi Arandjelovic, Hjalmar Kühl, Paula Dieguez, Christophe Boesch, and K. Eduard Linsenmair. 2020. Sustainable peeling of Kapok Tree (*Ceiba pentandra*) bark by the chimpanzees (*Pan troglodytes verus*) of Comoé National Park, Ivory Coast. *International Journal of Primatology* 41:962–988. [SC]

Lapuente, Juan, Thurston C. Hicks, and K. Eduard Linsenmair. 2017. Fluid dipping technology of chimpanzees in Comoé National Park, Ivory Coast. *American Journal of Primatology* 79(5):e22628, https://doi.org/10.1002/ajp.22628.

Leakey, M. D. 1971. *Excavations in beds I and II, 1960–1963*, vol. 3 of *Olduvai Gorge*. Cambridge: Cambridge University Press. [Fd'E/LRB]

Leakey, M. D., and R. L. Hay. 1979. Pliocene footprints in the Laetolil beds at Laetoli, northern Tanzania. *Nature* 278:317–323.

Leakey, M. D., R. L. Hay, G. H. Curtis, R. E. Drake, M. K. Jackes, and T. D. White. 1976. Fossil hominids from Laetolil beds. *Nature* 262:460–466.

Lesnik, Julie J. 2011. Bone tool texture analysis and the role of termites in the diet of South African hominids. *PaleoAnthropology* 2011:268–281, https://doi.org/10.4207/PA.2011.ART57.

———. 2014. Termites in the hominin diet: a meta-analysis of termite genera, species and caste as a dietary supplement for South African robust australopithecines. *Journal of Human Evolution* 71:94–104, https://doi.org/10.1016/j.jhevol.2013.07.015.

———. 2018. *Edible insects and human evolution*. Gainesville: University Press of Florida.

Lesnik, Julie J., Robert O'Malley, Audax Mabulla, Enrique Baquedano, Manuel Dominguez-Rodrigo, and Clayton Magill. 2019. Evidence of *Macrotermes* termites within the *Zinjanthropus* horizon at Olduvai Gorge, Tanzania. Paper presented at the 88th Annual Meeting of the American Association of Physical Anthropologists, Cleveland, OH, March 27–30.

Lonsdorf, Elizabeth V. 2005. Sex differences in the development of termite-fishing skills in the wild chimpanzees, *Pan troglodytes schweinfurthii*, of Gombe National Park, Tanzania. *Animal Behaviour* 70(3):673–683, https://doi.org/10.1016/j.anbehav.2004.12.014.

———. 2006. What is the role of mothers in the acquisition of termite-fishing behaviors in wild chimpanzees (*Pan troglodytes schweinfurthii*)? *Animal Cognition* 9(1):36–46, https://doi.org/10.1007/s10071-005-0002-7.

Lonsdorf, Elizabeth V., Lynn E. Eberly, and Anne E. Pusey. 2004. Sex differences in learning in chimpanzees. *Nature* 428(6984):715–716.

Luncz, Lydia V., Mike Gill, Tomos Proffitt, Magdalena S. Svensson, Lars Kulik, and Suchinda Malaivijitnond. 2019. Group-specific archaeological signatures of stone tool use in wild macaques. *eLife* 8:e46961. [SC]

Luncz, Lydia V., Roger Mundry, and Christophe Boesch. 2012. Evidence for cultural differences between neighboring chimpanzee communities. *Current Biology* 22(10):922–926.

Luncz, Lydia V., Tomos Proffitt, Lars Kulik, Michael Haslam, and Roman M. Wittig. 2016. Distance-decay effect in stone tool transport by wild chimpanzees. *Proceedings of the Royal Society B: Biological Sciences* 283(1845):20161607, https://royalsocietypublishing.org/doi/10.1098/rspb.2016.1607.

Luncz, Lydia V., Gilia Sirianni, Roger Mundry, and Christophe Boesch. 2018. Costly culture: differences in nut-cracking efficiency between wild chimpanzee groups. *Animal Behaviour* 137:63–73. [SM/CS]

Luncz, Lydia V., Roman M. Wittig, and Christophe Boesch. 2015. Primate archaeology reveals cultural transmission in wild chimpanzees (*Pan troglodytes verus*). *Philosophical Transactions of the Royal Society B: Biological Sciences* 370(1682):20140348, https://royalsocietypublishing.org/doi/10.1098/rstb.2014.0348.

Lyons, Diane, and Nicholas David. 2019. To hell with ethnoarchaeology . . . and back! *Ethnoarchaeology* 11(2):99–133, https://doi.org/10.1080/19442890.2019.1642557. [WC]

Mackworth-Young, Constance, and William C. McGrew. 2014. Elementary technology correlates with lifetime reproductive success in wild chimpanzees, but why? *Pan Africa News* 21(2):12–15.

Marreiros, João, Ivan Calandra, Walter Gneisinger, Eduardo Paixão, Antonella Pedergnana, and Lisa Schunk. 2020. Rethinking use-wear analysis and experimentation as applied to the study of past hominin tool use. *Journal of Paleolithic Archaeology* 3:475–502, https://doi.org/10.1007/s41982-020-00058-1. [WC]

Mason, William A. 1990. Premises, promises, and problems of primatology. *American Journal of Primatology* 22(2):123–138, https://doi.org/10.1002/ajp.1350220206. [WC]

Matsuzawa, Tetsuro. 2011. Field experiments of tool use. In *The chimpanzees of Bossou and Nimba*. Tetsuro Matsuzawa, Tatyana Humle, and Yukimaru Sugiyama, eds. Pp. 157–164. Tokyo: Springer.

McBeath, Norman M., and William C. McGrew. 1982. Tools used by wild chimpanzees to obtain termites at Mt Assirik, Senegal: the influence of habitat. *Journal of Human Evolution* 11(1):65–72, https://doi.org/10.1016/S0047-2484(82)80032-8.

McGrew, William C. 1992. *Chimpanzee material culture: implications for human evolution*. Cambridge: Cambridge University Press.

———. 2004. *The cultured chimpanzee: reflection on cultural primatology*. Cambridge: Cambridge University Press.

———. 2010. In search of the last common ancestor: new findings on wild chimpanzees. *Philosophical Transactions of the Royal Society B: Biological Sciences* 365(1556):3267–3276.

———. 2014. The "other faunivory" revisited: insectivory in human and non-human primates and the evolution of human diet. *Journal of Human Evolution* 71:4–11, https://doi.org/10.1016/j.jhevol.2013.07.016.

———. 2021. Chimpanzees digging up termites: a problematic but persisting issue. *Pan Africa News*.

McGrew, William C., Pamela J. Baldwin, Linda F. Marchant, Jill D. Pruetz, Sarah Scott, and Caroline E. G. Tutin. 2003. Ethoarchaeology and elementary technology of unhabituated wild chimpanzees at Assirik, Senegal, West Africa. *PaleoAnthropology* 2003:1–20. [WCM]

McGrew, William C., and D. Anthony Collins. 1985. Tool use by wild chimpanzees (*Pan troglodytes*) to obtain termites (*Macrotermes herus*) in the Mahale Mountains, Tanzania. *American Journal of Primatology* 9(1):47–62.

McGrew, William C., Tiago Falótico, Michael D. Gumert, and Eduardo B. Ottoni. 2019. A simian view of the Oldowan. In *Squeezing minds from stones*. Karenleigh A. Overmann and Frederick L. Coolidge, eds. Pp. 13–41. Oxford: Oxford University Press.

McGrew, William C., Linda Marchant, Melanie Beuerlein, Deirdre Vrancken, Barbara Fruth, and Gottfried Hohmann. 2007. Prospects for bonobo insectivory: Lui Kotal, Democratic Republic of Congo. *International Journal of Primatology* 28(6):1237–1252, https://doi.org/10.1007/s10764-007-9215-8.

McGrew, William C., Linda F. Marchant, and Kevin D. Hunt. 2007. Ethoarchaeology of manual laterality: well-digging by wild chimpanzees. *Folia Primatologica* 78(4):240–244. [WCM]

McGrew, William C., Jill D. Pruetz, and S. J. Fulton. 2005. Chimpanzees use tools to harvest social insects at Fongoli, Senegal. *Folia Primatologica* 76(4):222–226.

McGrew, William C., and Caroline E. G. Tutin. 1978. Evidence for a social custom in wild chimpanzees? *Man* 13(2):234–251. [TCH]

McGrew, William C., Caroline E. G. Tutin, and Pamela J. Baldwin. 1979. Chimpanzees, tools and termites: cross-cultural comparisons of Senegal, Tanzania, and Rio Muni. *Man*, n.s., 14(2):185–214.

McPherron, Shannon P., Zeresenay Alemseged, Curtis W. Marean, Jonathan G. Wynn, Denné Reed, Denis Geraads, René Bobe, and Hamdallah A. Béarat. 2010. Evidence for stone-tool-assisted consumption of animal tissues before 3.39 million years ago at Dikika, Ethiopia. *Nature* 466(7308):857–860. [SC]

Mercader, Julio, Huw Barton, Jason Gillespie, Jack Harris, Steven Kuhn, Robert Tyler, and Christophe Boesch. 2007. 4,300-year-old chimpanzee sites and the origins of percussive stone technology. *Proceedings of the National Academy of Sciences of the USA* 104(9):3043–3048.

Mercader, Julio, Melissa A. Panger, and Christophe Boesch. 2002. Excavation of a chimpanzee stone tool site in the African rainforest. *Science* 296(5572):1452–1455.

Möbius, Yasmin, Christophe Boesch, Kathelijne Koops, Tetsuro Matsuzawa, and Tatyana Humle. 2008. Cultural differences in army ant predation by West African chimpanzees? a comparative study of microecological variables. *Animal Behaviour* 76(1):37–45, https://doi.org/10.1016/j.anbehav.2008.01.008.

Moore, Jim. 1996. Savanna chimpanzees, referential models and the last common ancestor. In *Great ape societies*. William C. McGrew, Linda F. Marchant, and Toshisada Nishida, eds. Pp. 275–292. Cambridge: Cambridge University Press. [FAS]

Mora, Rafael, and Ignacio de la Torre. 2005. Percussion tools in Olduvai Beds I and II (Tanzania): implications for early human activities. *Journal of Anthropological Archaeology* 24(2):179–192. [Fd'E/LRB]

Musgrave, Stephanie, Elizabeth Lonsdorf, David Morgan, Madison Prestipino, Laura Bernstein-Kurtycz, Roger Mundry, and Crickette M. Sanz. 2020. Teaching varies with task complexity in wild chimpanzees. *Proceedings of the National Academy of Sciences of the USA* 117(2):969–976.

Musgrave, Stephanie, Elizabeth Lonsdorf, David Morgan, and Crickette M. Sanz. 2021. The ontogeny of termite gathering among chimpanzees in the Goualougo Triangle, Republic of Congo. *American Journal of Physical Anthropology* 174(2):187–200, https://doi.org/10.1002/ajpa.24125.

Musgrave, Stephanie, David Morgan, Elizabeth Lonsdorf, Roger Mundry, and Crickette M. Sanz. 2016. Tool transfers are a form of teaching among chimpanzees. *Scientific Reports* 6:34783, http://www.nature.com/articles/srep34783.

Nakamura, Michio, Nadia Corp, Mariko Fujimoto, Shiho Fujita, Shunkichi Hanamura, Hitoshige Hayaki, Kazuhiko Hosaka, et al. 2013. Ranging behavior of Mahale chimpanzees: a 16-year study. *Primates* 54(2):171–182.

Nakamura, Michio, Kazuhiko Hosaka, Noriko Itoh, Takuya Matsumoto, Takahisa Matsusaka, Nobuko Nakazawa, Hitonaru Nishie, et al. 2019. Wild chimpanzees deprived a leopard of its kill: implications for the origin of hominin confrontational scavenging. *Journal of Human Evolution* 131:129–138. [MN]

Nishida, Toshisada, and Shigeo Uehara. 1980. Chimpanzees, tools and termites: another example from Tanzania. *Current Anthropology* 21(5):671–672.

Nishida, Toshisada, Richard W. Wrangham, Jane Goodall, and Shigeo Uehara. 1983. Local differences in plant-feeding habits of chimpanzees between the

Mahale Mountains and Gombe National Park, Tanzania. *Journal of Human Evolution* 12(5):467–480. [TCH]

Nishie, Hitonaru. 2011. Natural history of *Camponotus* ant-fishing by the M group chimpanzees at the Mahale Mountains National Park, Tanzania. *Primates* 52:329–342.

Nonaka, Kenichi. 1996. Ethnoentomology of the Central Kalahari San. *African Study Monographs* 22(suppl.):S29–S46.

O'Malley, Robert C., and William C. McGrew. 2014. Primates, insects and insect resources. *Journal of Human Evolution* 71:1–3, https://doi.org/10.1016/j.jhevol.2014.02.010.

O'Malley, Robert C., and Michael L. Power. 2014. The energetic and nutritional yields from insectivory for Kasekela chimpanzees. *Journal of Human Evolution* 71:46–58, https://doi.org/10.1016/j.jhevol.2013.09.014.

O'Malley, Robert C., William Wallauer, Carson M. Murray, and Jane Goodall. 2012. The appearance and spread of ant fishing among the Kasekela chimpanzees of Gombe: a possible case of intercommunity cultural transmission. *Current Anthropology* 53(5):650–663, https://doi.org/10.1086/666943.

Oswalt, Wendell H. 1976. *An anthropological analysis of food-getting technology*. London: John Wiley & Sons. [WCM]

Panger, Melissa A., Alison S. Brooks, Brian G. Richmond, and Bernard Wood. 2002. Older than the Oldowan? rethinking the emergence of hominin tool use. *Evolutionary Anthropology* 11(6):235–245.

Pante, Michael, Ignacio de la Torre, Francesco d'Errico, Jackson Njau, and Robert Blumenschine. 2020. Bone tools from Beds II–IV, Olduvai Gorge, Tanzania, and implications for the origins and evolution of bone technology. *Journal of Human Evolution* 148:102885. [SC]

Pascual-Garrido, Alejandra. 2017. Termite fishing by Mahale chimpanzees: revisited, decades later. *Pan Africa News* 24(2):15–19, https://doi.org/10.5134/228897.

———. 2018. Scars on plants sourced for termite fishing tools by chimpanzees: towards an archaeology of the perishable. *American Journal of Primatology* 80(9):e22921. http://doi.wiley.com/10.1002/ajp.22921.

———. 2019. Cultural variation between neighbouring communities of chimpanzees at Gombe, Tanzania. *Scientific Reports* 9:8260, http://www.nature.com/articles/s41598-019-44703-4.

Pascual-Garrido, Alejandra, and Rudolf H. Scheffrahn. 2020. Cultural dietary stasis? four decades on, Mahale chimpanzees still favour *Macrotermes*. *Pan Africa News* 27(1):6–9.

Pascual-Garrido, Alejandra, Buba Umaru, Oliver Allon, and Volker Sommer. 2013. Apes finding ants: predator-prey dynamics in a chimpanzee habitat in Nigeria. *American Journal of Primatology* 75(12):1231–1244.

Pascual-Garrido, Alejandra, Buba Umaru, George Nodza, and Volker Sommer. 2012. Obtaining raw material: plants as tool sources for Nigerian chimpanzees. *Folia Primatologica* 83(1):24–44, https://doi.org/10.1159/000338898.

Peterson, Alexandria, Elicia F. Abella, Frederick E. Grine, Mark F. Teaford, and Peter S. Ungar. 2018. Microwear textures of *Australopithecus africanus* and *Paranthropus robustus* molars in relation to paleoenvironment and diet. *Journal of Human Evolution* 119:42–63. [Fd'E/LRB]

Piel, Alexander K., Fiona A. Stewart, Lilian Pintea, Yingying Li, Miguel A. Ramirez, Dorothy E. Loy, Patricia A. Crystal, et al. 2013. The Malagarasi River does not form an absolute barrier to chimpanzee movement in western Tanzania. *PLoS ONE* 8(3):e58965, https://dx.plos.org/10.1371/journal.pone.0058965.

Pika, Simone, Harmonie Klein, Sarah Bunel, Pauline Baas, Erwan Théleste, and Tobias Deschner. 2019. Wild chimpanzees (*Pan troglodytes troglodytes*) exploit tortoises (*Kinixys erosa*) via percussive technology. *Scientific Reports* 9(1):7661. [SC]

Potts, Richard. 1994. Variables versus models of early Pleistocene hominid land use. *Journal of Human Evolution* 27(1/3):7–24.

Proffit, Tomos, Lydia V. Luncz, Tiago Falótico, Eduardo B. Ottoni, Ignacio de la Torre, and Michael Haslam. 2016. Wild monkeys flake stone tools. *Nature* 539:85–88.

Pruetz, Jill D. 2006. Feeding ecology of savanna chimpanzees (*Pan troglodytes verus*) at Fongoli, Senegal. In *Feeding ecology in apes and other primates: ecological, physical and behavioral aspects*. Gottfried Hohmann, Martha M. Robbins, and Christophe Boesch, eds. Pp. 161–182. Cambridge: Cambridge University Press.

R Core Team. 2017. R: a language and environment for statistical computing. Vienna: R Foundation for Statistical Computing.

Reynolds, Sally, and Job M. Kibii. 2011. Sterkfontein at 75: review of paleoenvironments, fauna, dating and archaeology from the hominin site of Sterkfontein (Gauteng Province, South Africa). *Palaeontologia Africana* 46:59–88. [Fd'E/LRB]

Richter, Daniel, and Matthias Krbetschek. 2015. The age of the Lower Paleolithic occupation. *Journal of Human Evolution* 89:46–56.

Richter, Jürgen, Thomas Hauck, Ralf Vogelsang, Thomas Widlok, Jean-Marie Le Tensorer, and Peter Schmid. 2012. "Contextual areas" of early *Homo sapiens* and their significance for human dispersal from Africa into Eurasia between 200 Ka and 70 Ka. In *Temporal and spatial corridors of* Homo sapiens sapiens *population dynamics during the Late Pleistocene and Early Holocene*. Special issue, *Quaternary International* 274:5–24, https://doi.org/10.1016/j.quaint.2012.04.017. [WC]

Robbins, Martha M., Chieko Ando, Katherine A. Fawcett, Cyril C. Grueter, Daniela Hedwig, Yuji Iwata, Jessica L. Lodwick, et al. 2016. Behavioral variation in gorillas: evidence of potential cultural traits. *PLoS ONE* 11(9):p.e0160483. [TCH]

Robinson, John T. 1959. A bone implement from Sterkfontein. *Nature* 184:583–585. [Fd'E/LRB]

Rolian, Campbell, and Susana Carvalho. 2017. Tool use and manufacture in the last common ancestor of *Pan* and *Homo*. In *Chimpanzees and human evolution*. Martin Muller, Richard Wrangham, and David Pilbeam, eds. Pp. 602–644. Cambridge, MA: Harvard University Press.

Rosati, Alexandra G. 2017. Foraging cognition: reviving the ecological intelligence hypothesis. *Trends in Cognitive Sciences* 21(9):691–702. [SM/CS]

Russon, Anne E., Dwi Putri Handayani, Purwo Kuncoro, and Agnes Ferisa. 2007. Orangutan leaf-carrying for nest building: toward unravelling cultural processes. *Animal Cognition* 10(2):189–202.

Rutz, Christian, Lucas A. Bluff, Alex A. S. Weir, and Alex Kacelnik. 2007. Video cameras on wild birds. *Science* 318(5851):765, http://www.sciencemag.org/cgi/doi/10.1126/science.1146788.

Samuni, Liran, Franziska Wegdell, and Martin Surbeck. 2020. Behavioural diversity of bonobo preference as a potential cultural trait. *eLife* 9:e59191. [TCH]

Sanz, Crickette M., Josep Call, and David B. Morgan. 2009. Design complexity in termite-fishing tools of chimpanzees (*Pan troglodytes*). *Biology Letters* 5(3):293–296. [SM/CS]

Sanz, Crickette M., Isra Deblauwe, Nikki Tagg, and David B. Morgan. 2014. Insect prey characteristics affecting regional variation in chimpanzee tool use. *Journal of Human Evolution* 71:28–37, https://doi.org/10.1016/j.jhevol.2013.07.017.

Sanz, Crickette M., and David B. Morgan. 2007. Chimpanzee tool technology in the Goualougo Triangle, Republic of Congo. *Journal of Human Evolution* 52(4):420–433, https://doi.org/10.1016/j.jhevol.2006.11.001.

———. 2013. Ecological and social correlates of chimpanzee tool use. *Philosophical Transactions of the Royal Society B: Biological Sciences* 368(1630):20120416, https://royalsocietypublishing.org/doi/10.1098/rstb.2012.0416.

Sanz, Crickette M., David B. Morgan, and Steve Gulick. 2004. New insights into chimpanzees, tools, and termites from the Congo Basin. *American Naturalist* 164(5):567–581.

Schick, Kathy D. 1987. Modelling the formation of Early Stone Age artefact concentrations. *Journal of Human Evolution* 16(7/8):789–807.

Schielzeth, Holger, and Wolfgang Forstmeier. 2009. Conclusions beyond support: overconfident estimates in mixed models. *Behavioral Ecology* 20(2):416–420.

Schöning, Caspar, Tatyana Humle, Yasmin Möbius, and William C. McGrew. 2008. The nature of culture: technological variation in chimpanzee predation on army ants revisited. *Journal of Human Evolution* 55(1):48–59, https://doi.org/10.1016/j.jhevol.2007.12.002.

Schuppli, Caroline, and Carel P. van Schaik. 2019. Animal cultures: how we've only seen the tip of the iceberg. *Evolutionary Human Sciences* 1:E2, https://doi.org/10.1017/ehs.2019.1.

Scott, Jeremiah E. 2019. Macroevolutionary effects on primate trophic evolution and their implications for reconstructing primate origins. *Journal of Human Evolution* 133:1–12, https://doi.org/10.1016/j.jhevol.2019.05.001. [WC]

Sept, Jeanne M. 1992. Was there no place like home? a new perspective on early hominid archaeological sites from the mapping of chimpanzee nests. *Current Anthropology* 33(2):187–207.

———. 1998. Shadows on a changing landscape: comparing nesting patterns of hominids and chimpanzees since their last common ancestor. *American Journal of Primatology* 46(1):85–101. [WC]

Shea, John J. 2016. *Stone tools in human evolution: behavioral differences among technological primates*. New York: Cambridge University Press.

Sirianni, Giulia, Roger Mundry, and Christophe Boesch. 2015. When to choose which tool: multidimensional and conditional selection of nut-cracking hammers in wild chimpanzees. *Animal Behaviour* 100:152–165. [SM/CS]

Stammers, Rhiannon C., Matthew V. Caruana, and Andy I. Herries. 2018. The first bone tools from Kromdraai and stone tools from Drimolen, and the

place of bone tools in the South African Earlier Stone Age. *Quaternary International* 495:87–101. [Fd'E/LRB]

Stewart, Fiona A., and Alexander K. Piel. 2014. Termite fishing by wild chimpanzees: new data from Ugalla, western Tanzania. *Primates* 55:35–40.

Stewart, Fiona A., Alexander K. Piel, and William C. McGrew. 2011. Living archaeology: artefacts of specific nest site fidelity in chimpanzees. *Journal of Human Evolution* 61(4):388–395.

Stout, Dietrich, Jay Quade, Sileshi Semaw, Michael J. Rogers, and Naomi E. Levin. 2005. Raw material selectivity of the early stone toolmakers at Gona, Afar, Ethiopia. *Journal of Human Evolution* 48(4):365–380.

Stout, Dietrich, Michael J. Rogers, Adrian V. Jaeggi, and Sileshi Semaw. 2019. Archaeology and the origins of human cumulative culture. *Current Anthropology* 60(3):309–340.

Stout, Dietrich, Sileshi Semaw, Michael J. Rogers, and Dominique Cauche. 2010. Technological variation in the earliest Oldowan from Gona, Afar, Ethiopia. *Journal of Human Evolution* 58(6):474–491.

Sugiyama, Yukimaru. 1985. The brush-stick of chimpanzees found in southwest Cameroon and their cultural characteristics. *Primates* 26:361–374.

Suzuki, Akira. 1966. On the insect eating habits among wild chimpanzees living in the savanna woodland of western Tanzania. *Primates* 7:481–487.

Suzuki, Shigeru, Suehisa Kuroda, and Tomoaki Nishihara. 1995. Tool-set for termite fishing by chimpanzees in the Ndoki Forest, Congo. *Behaviour* 132(3): 219–235.

Teleki, Geza. 1974. Chimpanzee subsistence technology: materials and skills. *Journal of Human Evolution* 3(6):575–594.

Thieme, Hartmut. 1997. Lower Palaeolithic hunting spears from Germany. *Nature* 385:807–809.

Tinbergen, N. 1963. On aims and methods of ethology. *Zeitschrift für Tierpsychologie* 20(4):410–433, https://doi.org/10.1111/j.1439-0310.1963.tb01161.x. [WC]

Toth, Nicholas, and Kathy Schick. 2009. The Oldowan: the tool making of early hominins and chimpanzees compared. *Annual Review of Anthropology* 38:289–305.

Uehara, Shigeo. 1982. Seasonal changes in the techniques employed by wild chimpanzees in the Mahale Mountains, Tanzania, to feed on termites (*Pseudacanthotermes spiniger*). *Folia Primatologica* 37(1/2):44–76, https://doi.org/10.1159/000156020.

van Casteren, Adam, William I. Sellers, Susannah K. S. Thorpe, Sam Coward, Robin H. Crompton, Julia P. Myatt, and A. Roland Ennos. 2012. Nest-building orangutans demonstrate engineering know-how to produce safe, comfortable beds. *Proceedings of the National Academy of Sciences of the USA* 109(18):6873–6877.

Vanhaeren, Marian, Francesco d'Errico, Karen van Niekerk, Christopher Henshilwood, and Rudolph Erasmus. 2013. Thinking strings: additional evidence for personal ornament use in the Middle Stone Age at Blombos Cave, South Africa. *Journal of Human Evolution* 64(6):500–517. [WCM]

van Leeuwen, Kelly L., Ross A. Hill, and Amanda H. Korstjens. 2020. Classifying chimpanzee (*Pan troglodytes*) landscapes across large-scale environmental gradients in Africa. *International Journal of Primatology* 41:800–821, https://doi.org/10.1007/s10764-020-00164-5. [WC]

van Schaik, Carel P., Marc Ancrenaz, Gwendolyn Borgen, Birute Galdikas, Cheryl D. Knott, Ian Singleton, Akira Suzuki, Sri Suci Utami, and Michelle Merrill. 2003. Orangutan cultures and the evolution of material culture. *Science* 299(5603):102–105.

Villaseñor, Amelia, René Bobe, and Anna K. Behrensmeyer. 2020. Middle Pliocene hominin distribution patterns in eastern Africa. *Journal of Human Evolution* 147:102856, https://doi.org/10.1016/j.jhevol.2020.102856. [WC]

Visalberghi, Elisabetta, Giulia Sirianni, Dorothy Fragaszy, and Christophe Boesch. 2015. Percussive tool use by Taï Western chimpanzees and Fazenda Boa Vista bearded capuchin monkeys: a comparison. *Philosophical Transactions of the Royal Society B: Biological Sciences* 370(1682):20140351. [SM/CS]

Wadley, Lyn. 2005. Putting ochre to the test: replication studies and adhesives that may have been used for hafting tools in the Middle Stone Age. *Journal of Human Evolution* 49(5):587–601. [WCM]

Wadley, Lyn, Irene Esteban, Paloma de la Peña, Marine Wojcieszak, Dominic Stratford, Sandra Lennox, Francesco d'Errico, et al. 2020. Fire and grass-bedding construction 200 thousand years ago at Border Cave, South Africa. *Science* 369(6505):863. [SC]

Wessling, E. G., Tobias Deschner, Roger Mundry, Jill D. Pruetz, Roman M. Wittig, and Hjalmar S. Kühl. 2018. Seasonal variation in physiology challenges the notion of chimpanzees (*Pan troglodytes verus*) as a forest-adapted species. *Frontiers in Ecology and Evolution* 6:60. [FAS]

Whiten, Andrew. 2019. Social learning: peering deeper into ape culture. *Current Biology* 29(17):829–850.

Whiten, Andrew, Jane Goodall, William C. McGrew, Toshisada Nishida, Vernon Reynolds, Yukimaru Sugiyama, Caroline E. G. Tutin, Richard W. Wrangham, and Christophe Boesch. 1999. Cultures in chimpanzees. *Nature* 399:682–685.

———. 2001. Charting cultural variation in chimpanzees. *Behaviour* 138(11/12): 1481–1516.

Wondra, Eden M., Adam van Casteren, Alejandra Pascual-Garrido, Fiona A. Stewart, and Alexander K. Piel. 2016. A new report of chimpanzee ant-fishing from the Issa Valley, Tanzania. *African Primates* 11:1–18.

Wynn, Thomas. 1981. The intelligence of Oldowan hominids. *Journal of Human Evolution* 10(7):529–541.

Wynn, Thomas, Adriana Hernandez-Aguilar, Linda F. Marchant, and William C. McGrew. 2011. "An ape's view of the Oldowan" revisited. *Evolutionary Anthropology* 20(5):181–197.

Wynn, Thomas, and William C. McGrew. 1989. An ape's view of the Oldowan. *Man* 24(3):383–398.

Zuur, Alain F., Elena N. Ieno, Neil J. Walker, Anatoly A. Saveliev, and Graham M. Smith. 2009. GLMM and GAMM. In *Mixed effects models and extensions in ecology with R*. Pp. 323–341. New York: Springer.

Check for updates

Received: 6 October 2021 | Revised: 22 November 2021 | Accepted: 30 November 2021

DOI: 10.1111/conl.12860

Conservation Letters
A journal of the Society for Conservation Biology
Open Access
WILEY

PERSPECTIVE

Using nonhuman culture in conservation requires careful and concerted action

Susana Carvalho[1,2,3] | **Erin G. Wessling**[4] | **Ekwoge E. Abwe**[5,6] | **Katarina Almeida-Warren**[1,3] | **Mimi Arandjelovic**[7] | **Christophe Boesch**[7,8] | **Emmanuel Danquah**[9] | **Mamadou Saliou Diallo**[10] | **Catherine Hobaiter**[11] | **Kimberley Hockings**[12] | **Tatyana Humle**[13] | **Rachel Ashegbofe Ikemeh**[14] | **Ammie K. Kalan**[15] | **Lydia Luncz**[16] | **Gaku Ohashi**[17] | **Alejandra Pascual-Garrido**[1,18] | **Alex Piel**[19] | **Liran Samuni**[4] | **Serge Soiret**[20,21] | **Crickette Sanz**[22,23] | **Kathelijne Koops**[24,25]

[1] Primate Models for Behavioural Evolution Lab, Institute of Human Sciences, University of Oxford, Oxford, UK

[2] Gorongosa National Park, Sofala, Mozambique

[3] Interdisciplinary Center for Archaeology and Evolution of Human Behaviour, Universidade do Algarve, Faro, Portugal

[4] Department of Human Evolutionary Biology, Harvard University, Cambridge, Massachusetts

[5] San Diego Zoo Wildlife Alliance, San Diego, California

[6] Ebo Forest Research Project, Douala, Cameroon

[7] Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany

[8] Wild Chimpanzee Foundation, Cologny, Switzerland

[9] Faculty of Renewable Natural Resources, Department of Wildlife and Range Management, Kwame Nkrumah University of Science and Technology, Kumasi, Ghana

[10] Guinée Ecologie, Conakry, Guinea

[11] School of Psychology and Neuroscience, University of St Andrews, St Andrews, UK

[12] Centre for Ecology and Conservation, University of Exeter, Penryn, UK

[13] Division of Human and Social Science, School of Anthropology and Conservation, Durrell Institute of Conservation and Ecology, University of Kent, Canterbury, UK

[14] SW/Niger Delta Forest Project, Garki, Abuja, Nigeria

[15] Department of Anthropology, University of Victoria, Victoria, Canada

[16] Technological Primates Research Group, Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany

[17] Chubu University, Kasugai, Aichi, Japan

[18] Department of Anthropology, Durham University, Durham, UK

[19] Department of Anthropology, University College London, London, UK

[20] Laboratoire de Zoologie et de Biologie Animale, Université Félix Houphouët-Boigny, Abidjan, Côte d'Ivoire

[21] Centre Suisse de Recherches Scientifiques en Côte d'Ivoire (CSRS), Abidjan, Côte d'Ivoire

[22] Department of Anthropology, Washington University in Saint Louis, Saint Louis, Missouri

[23] Wildlife Conservation Society, Congo Program, Brazzaville, Republic of Congo

[24] Ape Behaviour & Ecology Group, Department of Anthropology, University of Zurich, Zürich, Switzerland

[25] Department of Archaeology, University of Cambridge, Cambridge, UK

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.
© 2022 The Authors. Conservation Letters published by Wiley Periodicals LLC

Correspondence
Susana Carvalho, Primate Models for Behavioural Evolution Lab, Institute of Human Sciences, University of Oxford, Oxford, UK.
Email: susana.carvalho@anthro.ox.ac.uk
Erin G. Wessling, Department of Human Evolutionary Biology, Harvard University, Cambridge, MA.
Email: ewessling@fas.harvard.edu
Crickette Sanz, Department of Anthropology, Washington University in Saint Louis, MO 63130.
Email: csanz@wustl.edu
Kathelijne Koops, Ape Behaviour & Ecology Group, Department of Anthropology, University of Zurich, Zürich, Switzerland.
Email: kathelijne.koops@uzh.ch

Susana Carvalho, Erin G. Wessling, Crickette Sanz, and Kathelijne Koops contributed equally.

Abstract

Discussions of how animal culture can aid the conservation crisis are burgeoning. As scientists and conservationists working to protect endangered species, we call for reflection on how the culture concept may be applied in practice. Here, we discuss both the potential benefits and potential shortcomings of applying the animal culture concept, and propose a set of achievable milestones that will help guide and ensure its effective integration existing conservation frameworks, such as Adaptive Management cycles or Open Standards.

KEYWORDS
Adaptive Management, animal culture, conservation policy, Open Standards, target definition

1 | INTRODUCTION

Culture was long thought to be unique to humans, but has since been identified in a growing number of taxa (Whiten, 2021). Nonhuman culture continues to stimulate novel research and extensive debate. The most recent examples of its relevance and research scope concern the importance of documenting and preserving nonhuman cultural heritage for future generations (Kühl et al., 2019), as well as the potential role of animal culture in biodiversity conservation such as considering social learning and culture as conservation units (Brakes et al., 2019, 2021). More specifically, the integration of animal culture into conservation applications has been proposed as a means to maximize the survival prospects and reproductive outputs of individuals, social groups, and populations. One example is the argument that certain individuals within a social group may require targeted protection as important repositories of knowledge (e.g., elephant matriarchs; Brakes et al., 2019, 2021). Moreover, a focus on culture may help attract public interest (i.e., culture as a trait that connects humans to nonhuman species) and may promote funding for and focus on flagship species. But, the proposed use of nonhuman culture as a conservation tool leads to the critical question of: how can an animal culture approach be practically applied to enhance species conservation? More importantly, how can we ensure that empirical data on behavioral variation are fully integrated into applied, cost-efficient, and sustainable, conservation practices?

Currently, conservation prioritization practices focus on the most vulnerable species and populations, and on areas with high biodiversity. The current wave of "culture for conservation" arguments call for a more holistic assessment of individual, population, and species viability, which goes beyond population statistics to include the specific behavioral and ecological contexts crucial for population maintenance and survival. While "culture for conservation" can aid in bridging this gap, we suggest it should not be used as a stand-alone conservation tool. Rather, the culture concept must be integrated within existing conservation strategies, using an approach that is rigorous and evidence-based while also being attainable and efficient to implement. The culture for conservation concept should both complement and enhance current conservation standards (Junker et al., 2020). Given the urgent need for actionable and tractable responses to the alarming biodiversity decline, we call for caution in how the concept of culture is applied in conservation practice, and suggest milestones to develop a monitorable and effective approach to the use of animal culture as a conservation tool that accounts for (and balances) its risks and benefits.

2 | FROM THEORY TO PRACTICE

For many, the notion of using animal culture in conservation still remains abstract and a practical pathway is needed to ensure the culture concept is effectively applied. To advance the discussion of how animal culture can be used in conservation, we propose that specific milestones be met before further action in a particular species or population is undertaken (Figure 1). Most of these

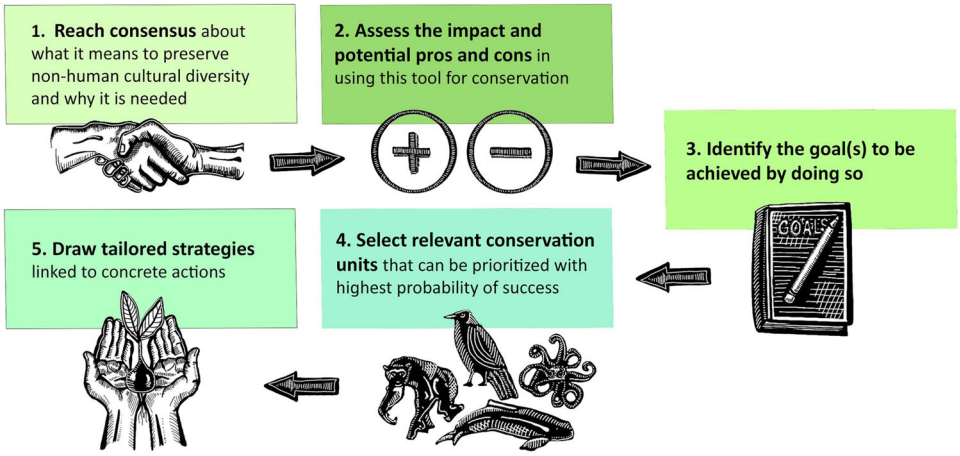


FIGURE 1 Milestones for an effective incorporation of nonhuman cultures into conservation planning. Specific actions and outputs for the different milestones could include stakeholder workshops to generate guidelines on preserving cultural diversity, impact assessments based on pilot projects and studies, integrating goals into action plans, a priority list of conservation units, and planning research and conservation projects

milestones mirror common conservation practices such as the Open Standards approach (CMP, 2020), in that they aim to establish tangible goals and facilitate comprehensive solutions to a holistic perspective of threats to conservation targets. For an effective process, the definition of these milestones should be guided by a diverse and representative group of stakeholders, for example, experts, conservationists, governmental officials, local communities, and NGOs. Due to structural similarities to these approaches, the proposed process can be incorporated into existing conservation frameworks, such as Adaptive Management (McCarthy & Possingham, 2007) or Open Standards (CMP, 2020).

First, conservationists and scientists would benefit from reaching an operational consensus on fundamental concepts and criteria for what constitutes animal culture in the wild, what it means to preserve it, and why culture preservation is needed. This exercise (see Point 1, Figure 1) must be realistic and should not hinder conservation efforts, but is necessary to determine which conservation units or practices are best suited to apply this new tool. Operationalizing the concepts of culture and behavioral diversity will help determine (1) whether all species that exhibit social learning should be primary "conservation through culture" targets and/or (2) whether efforts should prioritize species with an established cultural repertoire, that is, a set of group-specific, socially transmitted behaviors (e.g., orangutans, *Pongo* spp.; or killer whales, *Orcinus orca*).

Second, once we have reached consensus on the need for invoking the culture concept and an operational definition of culture as it relates to conservation is formalized, assessments based on pilot projects and ongoing field research can be used to better understand the potential impacts (positive and negative) of using culture as a tool for conservation (see Point 2, Figure 1).

Next, we need to identify the goals to be achieved by using culture in conservation (see Point 3, Figure 1), develop prioritization of these targets (if multiple), and agree on actionable processes. Such an approach is similar to the definition of goal formation (i.e., conservation target and vision definition) during processes like Open Standards (CMP, 2020). After goals are defined, the identification of requisite information for effective practice will necessarily follow and become clear. For example, conservationists may need to adopt strategies to accommodate understudied species or populations where knowledge of their behavioral and cultural repertoire is currently unknown or incomplete, but this can only be achieved once a shared understanding of what constitutes culture is established.

As a next milestone, we can proceed to select relevant conservation units that adhere to the definition of our conservation goals and can be prioritized with the highest probability of success (see Point 4, Figure 1). A practical example would be the need to decide whether species that have large-scale, socially learned, migratory routes, such as right whales (*Eubalaena australis*) should fall under the same "culture for conservation" strategy as species that have limited (albeit trans-national) ranging patterns but display diverse behavioral and cultural repertoires, such as chimpanzees (*Pan troglodytes*), or New Caledonian crows (*Corvus moneduloides*).

Finally, it is necessary to draw tailored, context-specific strategies linked to concrete actions (see Point 5, Figure 1) in order to fully move from theory to conservation practice. These actions will involve monitoring of effectiveness

of proposed action to conserving the selected conservation units.

While the proposed milestones provide a practical means to adapt culture theory into conservation practice, there are some additional concerns that practitioners must consider. For example, social structure and pathways of social information transfer are important for assessing cultural attributes, but are also interconnected with well-established conservation metrics such as population size, viability, and demography. Given the use of concepts such as flagship, umbrella, or keystone species when advocating for conservation of various species, can cultural attributes of a nonhuman species aid in promoting a species' status, or would these be redundant to already existing arguments for conservation? There is potential value in using nonhuman culture to attract public interest and elicit empathy toward species of concern, but this requires sensitive and tailored messaging for different audiences and contexts. Abuse of this approach could lead to allocation of limited conservation resources based on a unidimensional metric, for example, culture.

3 | FILLING GAPS AND AVOIDING PITFALLS

To highlight some important gaps in the current discussions of "culture for conservation," we refer to the well-studied and often-cited example of nut cracking by wild chimpanzees (Brakes et al., 2019, 2021). Nut cracking is proposed as a single behavior of key conservation concern due to a suggested link to vital rates, such as reproduction and survival (Brakes et al., 2021). However, it could be argued that populations with high behavioral diversity may be more resilient to environmental change (Kalan et al., 2020; Whitehead & Rendell, 2015). Before applying the concept of culture to conservation practice, practitioners must reach a consensus about the conservation value of single behaviors (e.g., nut cracking) compared to overall behavioral diversity in species conservation.

For chimpanzees, how do non-nut cracking, but behaviorally diverse populations fit into conservation-through-culture schemes? The answer depends on how conservation policy makers prioritize the intrinsic value and cultural indicators of populations, independent of their influence on vital rates. We argue that cultural behavior need not necessarily be linked to vital rates, as previously proposed (Brakes et al., 2021) in order to be prioritized. Moreover, it is unclear whether cultural foraging behaviors like nut cracking are comparatively more important for the maintenance of vital rates than hygiene, comfort, or self-medication cultural behaviors. A sole focus on vital rates raises difficulties for practitioners regarding how to incorporate cultural variation in social behaviors or communication (e.g., the grooming hand-clasp or group dialects in chimpanzees), into conservation responses. In these cases, the link from culture to survival and reproductive rates may be indirect at best, although these behaviors may play a significant role in social cohesion and grouping patterns. Even for a behavior like nut cracking, which is often proposed to be a response to food scarcity and thus may be more intuitively linked to vital rates than nonforaging behaviors (e.g., Yamakoshi, 1998), the proposed relationship with food scarcity remains empirically inconsistent (Koops et al., 2014). Despite being one of the most studied tool-use behaviors of one of the most intensively studied animals, a clear answer as to the influences of nut cracking on reproduction and survival is still lacking.

Arguments for conservation, therefore, cannot be contingent on meeting (impractically) high empirical standards, such as a link to vital rates (Brakes et al., 2019, 2021). Specifically, behaviors like nut cracking serve as a demonstration of why the long-term research needed to establish these connections is incompatible with the urgent timeframe for which we must act. Consequently, adding cultural uniqueness as a criterion for conservation efforts might lead to delay in taking conservation action if these links must first be demonstrated. Importantly, it may be impossible for a nonhuman animal (in practice) to meet the largely academic cultural benchmarks set by recent proposals (Brakes et al., 2019, 2021). Proposed benchmarks such as "understanding linkages between culture and vital rates, cultural evolution, and adaption to rapid global change" or "understand[ing] the circumstances under which social learning and culture are likely to impact population viability through phenotypic variation" (Brakes et al., 2021, P. 8) are practically challenging, and are unlikely to translate into effective conservation practices in a short time frame. We therefore caution that advancing weak evidence and proposing unclear benchmarks has the potential to undermine both the uptake, as well as the utility, of culture as a criterion for conservation effort altogether.

It follows that a focus on such benchmarks could reduce credibility of the culture concept to local stakeholders who play a critical role in ensuring sustainable conservation on the ground. For example, a lack of clear definitions about what constitutes animal culture or sufficient evidence for self-defined necessary benchmarks (e.g., social transmission; Brakes et al., 2019, 2021) may lead to ineffective communication with policy makers, government officials, and conservation NGOs. To advance conservation initiatives for endangered species, immediate messaging of how such a framework can be applied is needed because species often listed as key examples of cultural species are in free-fall. The nut cracking western chimpanzees (*P. t.*

verus) are critically endangered and have declined by 80% over the last two decades (Kühl et al., 2017). Whooping cranes (*Grus americana*), which are observed to have social learning, are down to a relictual population in the wild (Mueller et al., 2013). Given the severity of losses in the face of growing anthropogenic threats, scholars and practitioners alike need to be aware of the consequences of proposed but insufficiently defined solutions that risk delaying effective action, and should seek to mitigate those consequences as best as possible.

4 | TOWARD CAREFUL AND CONCERTED ACTION

Scientists and conservationists must be aware of the pitfall of prioritizing the monitoring of extinction crises rather than taking steps toward mitigating them (Lindenmayer et al., 2013; Nichols & Williams, 2006). Whereas data gathering may provide insights into the direct benefits of cultural behaviors to conservation, or help identify new cultural traits across populations, encouraging further efforts to fill remaining knowledge gaps may be misguided when conservation needs are immediate and financial support is limited. Adoption of culture as a conservation tool could potentially help garner broader support for conservation efforts, but it could also imply a trade-off, where a finite amount of effort is distributed among a larger number of populations. There is a risk that the number of populations considered conservation priorities increases significantly if criteria for prioritization are not clearly defined and rapidly measurable. Discoveries of new cultural traits could be boundless and may continuously grow with each new studied population (Boesch et al., 2020). Large-scale cultural surveying necessitates immense effort, funding, and crucially, time, which may detract from direct conservation actions. Importantly, the discovery of new cultural traits will not provide further justification for the argument that cultural heritage of nonhuman species must be preserved in species where it is already established. To develop effective conservation strategies, researchers studying animal cultures and conservation practitioners need to remain in close communication to ensure efforts in both disciplines are neither wasted nor duplicated, and remain focused toward tangible, well-defined goals.

We must also consider how the ability for a given species or population to meet the benchmarks to be classified as a "cultural species" may impart cascading biases on how conservation need is identified and how action is subsequently prioritized. Knowledge of the social-learning mechanisms of behavioral traits are already biased toward well-studied populations of well-known species (Besanson & McNamara, 2019). Such populations are most likely to be the first groups for which benchmarks, such as culture-dependent viability, can be reached, while also already being among the best protected (Besanson & McNamara, 2019). Additionally, this bias extends to how detectable or identifiable traces of cultural behaviors may be. While some behaviors, like tool use, are more easily quantifiable and can be recorded based on indirect evidence, other behaviors, like communicative signals, require years of direct observation to thoroughly understand. In that sense, the observable behavioral diversity across populations is functionally biased toward material cultures. Hence, we need to tailor our approach both to the species/populations and to the types of cultural behaviors recorded.

5 | CONCLUSION

While a goal of conservation action is often to conserve particular species, it can also be about maintaining, restoring, and enhancing ecosystem function and services, and protecting biological diversity as a whole—irrespective of a species' status as cultural or not. To address this, connections between animal cultures and habitat protection need to be clarified. The core aim of future efforts should be to directly contribute to conservation, which may involve initiatives like formalized action planning (IUCN, 2020), awareness raising, community-based conservation, and local human development. Moreover, conserving nonhuman cultural heritage for future generations should also include documentation, curation, and preservation of material (and nonmaterial) records. Advocacy for incorporation of nonhuman culture into conservation must ultimately complement, and not compete with, existing activities and tools. Following the proposition of formal, and clear milestones (Figure 1), we can best contribute to the shared goals of conservation by developing a multilevel approach that transcends both scale and actor, and includes leadership by local communities, connects with local human development projects, considers a landscape approach to conservation, and promotes global awareness.

ACKNOWLEDGMENTS

This manuscript was improved by feedback from several anonymous reviewers. We thank Elodie Freymann and João Coelho for assistance with graphics.

AUTHOR CONTRIBUTIONS

SC, EW, CS, and KK conceptualized and drafted the manuscript. All authors conceptualized and revised the manuscript, and agreed to be held accountable for the content therein.

DATA ACCESSIBILITY STATEMENT

This manuscript presents no primary data.

CONFLICT OF INTEREST

The authors declare no conflicts of interest.

ORCID

Erin G. Wessling https://orcid.org/0000-0001-9661-4354
Katarina Almeida-Warren https://orcid.org/0000-0002-7634-9466
Catherine Hobaiter https://orcid.org/0000-0002-3893-0524
Serge Soiret https://orcid.org/0000-0001-6773-500X
Kathelijne Koops https://orcid.org/0000-0001-7097-2698

REFERENCES

Bezanson, M., & McNamara, A. (2019). The what and where of primate field research may be failing primate conservation. *Evolutionary Anthropology: Issues, News, and Reviews*, *28*, 166–178.

Boesch, C., Kalan, A. K., Mundry, R., Arandjelovic, M., Pika, S., Dieguez, P., Ayimisin, E. A., Barciela, A., Coupland, C., Egbe, V. E., Eno-Nku, M., Fay, J. M., Fine, D., Hernandez-Aguilar, R. A., Hermans, V., Kadam, P., Kambi, M., Llana, M., Maretti, G.,… Kühl, H. S. (2020). Chimpanzee ethnography reveals unexpected cultural diversity. *Nature Human Behaviour*, *4*, 910–916.

Brakes, P., Dall, S. R. X., Aplin, L. M., Bearhop, S., Carroll, E. L., Ciucci, P., Fishlock, V., Ford, J. K. B., Garland, E. C., Keith, S. A., McGregor, P. K., Mesnick, S. L., Noad, M. J., di Sciara, G. N., Robbins, M. M., Simmonds, M. P., Spina, F., Thornton, A., Wade, P. R.,… Rutz, C. (2019). Animal cultures matter for conservation. *Science*, *363*(6431), 1032–1034. https://doi.org/10.1126/science.aaw3557.

Brakes, P., Carroll, E. L., Dall, S. R. X., Keith, S. A., McGregor, P. K., Mesnick, S. L., Noad M. J., Rendell L., Robbins M. M., Rutz C., Thornton A., Whiten A., Whiting M. J., Aplin, L. M., Bearhop S., Ciucci P., Fishlock V., Ford J. K. B., Notarbartolo di Sciara G,… Garland, E. C. (2021). A deepening understanding of animal culture suggests lessons for conservation. *Proceedings of the Royal Society B: Biological Sciences*, *288*, rspb.2020.2718.

Conservation Measures Partnership (CMP). (2020). *Open standards for the practice of conservation. Version 4.0*.

IUCN. (2020). Regional action plan for the conservation of western chimpanzees (Pan troglodytes verus) 2020–2030. Regional action plan for the conservation of western chimpanzees (Pan troglodytes verus) 2020–2030. IUCN, International Union for Conservation of Nature. https://doi.org/10.2305/IUCN.CH.2020.SSC-RAP.2.en

Junker, J., Petrovan, S. O., Arroyo-RodrÍguez, V., Boonratana, R., Byler, D., Chapman, C. A., & Kühl, H. S. (2020). A severe lack of evidence limits effective conservation of the world's primates. *Bioscience*, *70*, 794–803.

Kalan, A. K., Kulik, L., Arandjelovic, M., Boesch, C., Haas, F., Dieguez, P., Barratt, C. D., Abwe, E. E., Agbor, A., Angedakin, S., Aubert, F., Ayimisin E. A., Bailey, E., Bessone, M., Brazzola, G., Buh, V. E., Chancellor, R., Cohen, H., Coupland, C.,… Kühl, H. S. (2020). Environmental variability supports chimpanzee behavioural diversity. *Nature Communications*, *11*, 4451.

Koops, K., Visalberghi, E., & van Schaik, C. P. (2014). The ecology of primate material culture. *Biology Letters*, *10*, 20140508.

Kühl, H. S., Boesch, C., Kulik, L., Haas, F., Arandjelovic, M., Dieguez, P., Bocksberger, G., Agbor, A., Angedakin, S., Ayimisin, E. A., Bessone, M., Brazzola, G., Chancellor, R., Cohen, H., Coupland, C., Danquah, E., Deschner, T., Dowd, D., Goedmakers, A.,… Kalan, A. K. (June 14, 2019). Inclusive chimpanzee conservation response. *Science*. American Association for the Advancement of Science.

Kühl, H. S., Sop, T., Williamson, E. A., Mundry, R., Brugière, D., Campbell, G., Cohen, H., Danquah, E., Ginn, L., Herbinger, I., Jones, S., Junker, J., Kormos, R., Kouakou, C. Y., N'Goran, P. K., Normand, E., Shutt-Phillips, K., Tickle, A., Vendras, E.,… Boesch, C. (2017). The critically endangered western chimpanzee declines by 80%. *American Journal of Primatology*, *79*, e22681.

Lindenmayer, D. B., Piggott, M. P., & Wintle, B. A. (2013). Counting the books while the library burns: Why conservation monitoring programs need a plan for action. *Frontiers in Ecology and the Environment*, *11*, 549–555.

McCarthy, M. A., & Possingham, H. P. (2007). Active adaptive management for conservation. *Conservation Biology*, *21*, 956–963.

Mueller, T., O'Hara, R. B., Converse, S. J., Urbanek, R. P., & Fagan, W. F. (2013). Social learning of migratory performance. *Science*, *341*, 999–1002.

Nichols, J. D., & Williams, B. K. (2006). Monitoring for conservation. *Trends in Ecology & Evolution*, *21*, 668–673.

Whitehead, H., & Rendell, L. (2015). *The cultural lives of whales and dolphins*. Chicago.

Whiten, A. (2021). The burgeoning reach of animal culture. *Science*, *372*, eabe6514.

Yamakoshi, G. (1998). Dietary responses to fruit scarcity of wild chimpanzees at Bossou, Guinea: Possible implications for ecological importance of tool use. *American Journal of Physical Anthropology*, *106*, 283–295.

How to cite this article: Carvalho S., Wessling E. G., Abwe E. E., e al., Using nonhuman culture in conservation requires careful and concerted action. *Conservation Letters*. 2022;e12860. https://doi.org/10.1111/conl.12860