The ontogeny of chimpanzee technology: a longitudinal study of stone tool use in Bossou



Sophie Rose Berdugo

Institute of Human Sciences
School of Anthropology and Museum Ethnography
University of Oxford

A thesis submitted for the degree of
Doctor of Philosophy
Hilary Term 2024

ACKNOWLEDGEMENTS

The COVID-19 pandemic hit six months into this project, and my Mum was diagnosed with acute myeloid leukaemia at the start of my third year. I could not have completed the project without the people who supported me through not only the DPhil process, but also through such an intense and prolonged period of emotional distress.

First, the research would not have been possible without Dr David Taussig (Consultant Haematologist), Dr Emma Nicolson (Director of Stem Cell Transplantation and Consultant Haematologist), Dr Sandra Easdale (Consultant in Haematology and Bone Marrow Transplantation), Dr Radovan Saso (Associate Specialist in Haematology), Kim Davis (Haemato-Oncology Research Sister), and Fiona Fearn (Post Transplant Clinical Nurse Specialist), as well as the countless members of the nursing team and hospital support staff in the Bud Flanagan Wards at The Royal Marden Hospital in Sutton. You worked tirelessly to save my Mum's life, which meant I was eventually able to continue carrying out my research. No words can express my gratitude.

I am incredibly lucky to have had such caring and supportive friends and family with me every step of the way. Thank you to my biggest cheerleader and wonderful partner, Tom, who has been by my side through it all. We have shared all the highs and lows, and even the same desk. I am grateful for it all—none of this could have happened without you. Thank you to my parents who, despite everything that has happened over the past few years, have maintained their unwavering encouragement. You pushed me to always follow my interests and humoured me when I said that interest was chimpanzees. I am so appreciative of all your support, emotional and financial. Huge thanks to my sister, for every phone call and encouraging word, and to my brother, Agnete, and Sam for always cheering me on and making me laugh. Thank you to John and Emily, for welcoming me into your home when we couldn't afford to live in Oxford anymore, and for all the love and laughter. Thank you to Tata and Miles, whose generosity allowed us to write up our DPhils closer to my parents. Every encouraging chat in the entrance way (and hot crossed bun) has been greatly appreciated. I am especially thankful of my therapist, Jackie, who created a space for me to clear my head and who has got me through this journey in one piece. And thank you to all of my friends, old and new, who have stuck with me through thick and thin.

Next, I would like to thank my supervisors, Professor Emma Cohen and Professor Susana Carvalho. I am so fortunate to have not only had such fantastic scientists guiding me, but

also such kind, thoughtful, and encouraging people. Thank you, Emma, for taking a risk and agreeing to supervise a project on chimpanzees—you have been integral to the project, and it would not look like it does today without your invaluable inputs and insights. Your academic rigour has made me a far better researcher, and your compassion and wit made the process easier when it felt like too much. Thank you, Susana, for giving so much care and attention alongside being so generous with your time and expertise. You went above and beyond for me and my research and taught me so much along the way. Your intellectual and emotional support carried me through. And thank you both for helping me fight for extra funding, and for giving me teaching and research opportunities to help with financially supporting myself when I struggled to get adequate funding extensions.

I would also like to thank my lab mates in the Social Body Lab and the Primate Models for Behavioural Evolution Lab for their guidance and friendship. Each and every one of them—Katarina Almeida-Warren, Daniel Schofield, Lucy Baehren, Philippa (Fig) Hammond, João Coelho, Jana Muschinski, Megan Beardmore-Herd, Elodie Freymann, Jacinto Mathe, Rachel Hurwitz, Arran Davis, Josh Bamford, Gabri Paone, and Jon Gorrie—took time to talk about, and support, my research, and ultimately made this time far more enjoyable. So much of this project would not have been possible without Daniel Schofield—thank you for teaching me who each chimpanzee was and for always letting me send screenshots when I couldn't identify someone. Special thanks to Arran Davis for the countless hours of statistical support, which you somehow made fun. Thank you to Katarina Almeida-Warren and Matthew Bluteau for your insights, friendship, and care. And thank you to Elodie Freymann for being such a wonderful friend and companion.

Finally, *Balika Balika* (Manon for thank you) to the chimpanzees of Bossou. It has not been easy, but it has been a privilege to watch you over the past four and a half years. It was heart-breaking to hear that Fanle went missing in February 2024, less than two months before the end of my project. Fanle was the first chimpanzee I could reliably identify, and I watched her throughout her whole life, from being a newborn to raising infants of her own. Her disappearance marked the fifth loss to the Bossou community over the course of my DPhil.

~

This thesis is dedicated to the anonymous Dutch man who donated his stem cells to give my Mum a second chance at life, and to Tom, whose love and support got me through it all.

AUTHORSHIP STATEMENT

This thesis follows the integrated thesis format. All empirical chapters (Chapters 5–7) are either submitted or in preparation for submission to peer-reviewed journals. These chapters involved collaborations with my supervisors (Professor Emma Cohen and Professor Susana Carvalho) who supported their development in an advisory capacity, and other researchers who provided resources, as well as analytical and computational support. I am responsible for the majority contribution of the work, including intellectual development, practical implementation, and writing up.

This research was financially supported by the Boise Fund Trust, Department of Zoology, University of Oxford, and the Clarendon Scholarship, University of Oxford.

ABSTRACT

To unpack the complexities of primate behaviour, it is essential to study individuals over the course of their lifetime. Long-term field studies of wild primates are enabling key evolutionary questions to be addressed for the first time. Critical among these are ontogenetic questions, especially those pertaining to complex traits with prolonged learning periods (such as using stone tools) given the potential for variation between individuals to develop. Such individual differences, whether in the efficiency of producing the behaviour or in the learning process itself, can have far reaching repercussions, including for life history adaptations, cultural and technological evolution, and the fitness of individuals and populations. Answers to these ontogenetic questions can also provide an insight into the social and cognitive processes that supported the acquisition of early lithic technologies in the hominin lineage.

This thesis centres on the ontogeny of technology in the wild chimpanzee population in Bossou, Guinea. In Chapter 1, I provide a brief context for the research and present the research questions and aims. In Chapters 2 and 3, I review the theoretical and empirical literature forming the basis of the research in this thesis. In Chapter 4, I introduce the Bossou field site and chimpanzees, and outline the methods employed to systematically collect data from a long-term video archive. In Chapter 5, I show that the individual Bossou chimpanzees vary in their technological efficiency, and present four measures which are stable and reliable indicators of individual differences in nut-cracking efficiency. In Chapter 6, I demonstrate the developmental origins of this individual variation. In Chapter 7, I present evidence of social learning strategies being employed by the wild chimpanzees when learning from individuals other than their mother, specifically an increased likelihood of non-kin models being peered at even when kin are available. In Chapter 8, I discuss the contributions of these findings, as well as the limitations and directions for future research.

By establishing the presence, and tracking the development, of individual variation in stone tool efficiency in the wild chimpanzees over a 25-year period, this research makes substantial methodological, empirical, and theoretical contributions to the fields of primate behaviour, learning, and conservation. Overall, this thesis provides a critical longitudinal perspective to ongoing debates and open questions in primatology and cognitive and evolutionary anthropology.

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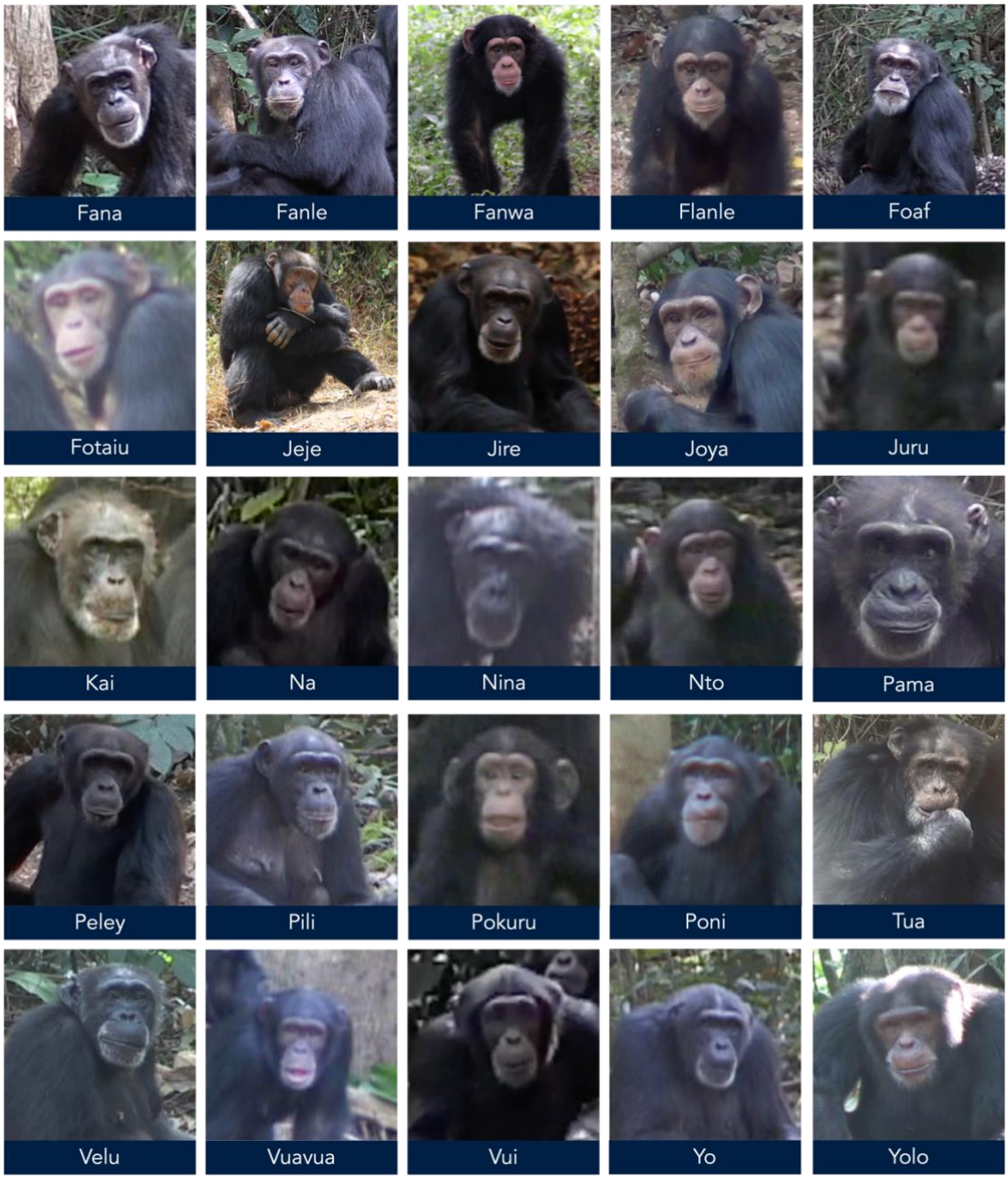


Image credits: Katarina Almeida-Warren (for the photographs of Fanwa and Jeje), and Tetsuro Matsuzawa (for images of everyone else).

1

INTRODUCTION

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> Individual differences… observed in the individuals of the same species inhabiting the same confined locality… are highly important to us, as they afford materials for natural selection to accumulate…
>
> **Darwin (1859, p. 45)**

1.1 BRIEF BACKGROUND

Individual variation is one of the central tenets of evolution by natural selection (Darwin, 1859). Individuals who possess the more contextually advantageous variants of traits are more likely to survive and reproduce, with their descendants inheriting these fitness advantages. This process is not constrained to biological evolution. Social learning—that is, learning from another individual or their products (Heyes, 1994)—acts as a 'second inheritance system' in cultural evolution (Whiten, 2005, p. 52). For example, individual differences in tool use behaviour, and the social transmission of variants, allows for technological and cultural evolution.

Individual differences in the efficiency with which behaviours are performed are especially important given the relevance of efficiency to both genetic and cultural fitness (Gruber et al., 2021; Mesoudi & Thornton, 2018). Gruber et al., (2021) defined efficiency as a measure of the relative benefits of producing a behaviour compared to the costs of learning and producing it. Genetic fitness is improved when there is efficiency at the level of the organism, such as through a reduction in the amount of time taken to access the reward, or an increase in the number of resources obtained by performing the behaviour. Individuals who engage in more efficient traits may have increased reproductive success and be more likely to survive (Gruber et al., 2021; Mesoudi & Thornton, 2018). Efficiency also increases the reproductive fitness of the cultural trait itself, with more efficient behaviours being more learnable, and so are transmitted to the next generation with greater ease or fidelity (Gruber et al., 2021). As such, there are selective pressures acting on behavioural efficiency.

Tool use has played a key role in human evolution, with the development of hominin technology initiating a major adaptive shift (Berdugo, 2019; Carvalho & Beardmore-Herd, 2019). The transition from arboreality to terrestriality in hominins supported the intensification of, and added reliance on, tool use (Meulman et al., 2012; Young et al., 2015), which in turn necessitated protracted periods dedicated to learning to make and use increasingly complex tools (Kaplan et al., 2000; Richerson & Boyd, 2020).

This life history adaptation—shared, albeit to a lesser extent, with extant great apes (Jones, 2011; Kraft et al., 2021)—made hominins more dependent on knowledge transmission from expert conspecifics, accelerating the shift to increased sociality in the lineage (Kaplan et al., 2000). Indeed, hunter-gatherer social networks are organised to support the efficient transmission of information, such as cultural traits (Migliano et al., 2017). This would have placed a selection pressure on group-level cooperation and efficient social learning strategies (Silk & House, 2016). Likewise, social learning became fundamental to the survival of young and new group members, and resulted in increased variation both within and between populations in technological behaviour (Whiten, 2017; Whiten & van de Waal, 2018). Such between-group differences may be cultural, with culture being defined as 'group-typical behaviour patterns shared by members of a community that rely on socially learned and transmitted information' (Laland & Hoppitt, 2003, p. 151). McGrew (2003) synthesised this definition of culture into a short phrase: 'the way we do things' (p. 433).

Although archaeologists and palaeoanthropologists have discovered many remnants of the technological suite of our early human ancestors (outlined in section 2.1), the record is inevitably biased toward stone techno-complexes due to the perishability of non-lithic material (McGrew, 1992a). Moreover, the record remains incomplete as behaviour does not fossilise. Findings from a phylogenetic morphometric analysis suggest that the *Pan*-hominin last common ancestor (LCA; currently dated to ≥ 8 million years ago (Ma); d'Oliveira Coelho et al., in review) had the morphological prerequisites to be capable of tool use (Almécija et al., 2015; Rolian & Carvalho, 2017). What is not known, however, is how early forms of tool

use were learned and transmitted across generations, and the implications of these processes on hominin cultural evolution. Comparative studies of extant nonhuman primate (hereafter "primate") populations are required to model the evolutionary trajectories and technological adaptations of early hominins (McGrew, 1992b; Tooby & DeVore, 1987). Such modelling provides helpful resolution for interpreting the behaviours underlying the formation of the time-averaged archaeological record (King, 2020; Kinzey, 1987).

Chimpanzees (*Pan troglodytes* spp.) remain a relevant referential model to understand the ontogenetic processes associated with developing technological proficiency in humans because: i) they are our closest biological and behavioural relatives (Foley & Gamble, 2009), ii) they are the only nonhuman species to ubiquitously show complex and sequential technological behaviour (Rolian & Carvalho, 2017), and iii) their stone tool use (for cracking nuts) shows similarities with percussive Oldowan technology (see section 3.3.3; Carvalho et al., 2008; Carvalho & McGrew, 2012).

A plethora of research has established variation in technological behaviour in wild primates, including in bearded capuchins (*Sapajus libidinosus*; Falótico et al., 2021), white-faced capuchins (*Cebus capucinus imitator*; Goldsborough et al., 2024), Burmese long-tailed macaques (*Macaca fascicularis aurea*, Gumert et al., 2011; Tan et al., 2015), Sumatran orangutans (*Pongo pygmaeus abelii,* van Schaik et al., 2003), chimpanzees (Boesch & Boesch, 1981; Estienne et al., 2017; Lonsdorf, 2005), and in captive bonobos (*P. paniscus*, Boose et al., 2013; Gruber et al., 2010).

Despite this, the cause(s) of individual variation are hitherto poorly understood and lack long-term investigations, although ontogenetic explanations have been previously posited (Koops, Furuichi, Hashimoto, et al., 2015; Lonsdorf, 2005). Given the importance of tool use, in particular percussive technology, in hominin evolution (see section 2.1.4; Benito-Calvo et al., 2015; de Beaune, 2004; Harmand & Arroyo, 2023), it is important to understand the extent of, and processes contributing to, individual variation in technological efficiency.

Such variation has direct consequences for energy expenditure, resource acquisition, and daily energy allocation to other fitness related activities, such as mating, defence, and grooming (Gruber et al., 2021; Kraft et al., 2021). This is also true for the energetic costs incurred through learning to use tools over prolonged periods, as any energy savings can be spent elsewhere (Gruber et al., 2021). As such, this will also inform our understanding of individual differences in social learning, something which could directly impact the evolutionary fitness of individuals (see section 3.1.4; Biro et al., 2013).

1.2 THESIS OUTLINE

1.2.1 Research Questions and Aims

The research presented in this thesis addresses the following three questions in turn:

1. Do chimpanzees vary in the efficiency of their stone tool use at the individual level, beyond any differences relating to age or sex?
2. Does variation in the period during which chimpanzees learn how to use stone tools predict the subsequent technological efficiency of individuals?
3. Do wild chimpanzees select conspecifics from whom to learn how to use stone tools based on specific characteristics?

Answering these questions entails three broad aims:

1. Develop a comprehensive inter-generational data set of the stone tool behaviour of the Bossou chimpanzee population to provide a long-term record of the material culture of the critically endangered population and subspecies.
2. Establish a stable and reliable measure of chimpanzee nut-cracking efficiency.
3. Demonstrate the key value of long-term video archives for answering questions on social learning in skill acquisition in a long-lived species.

1.2.2 Thesis Structure

Following an extensive review of the current literature (Chapters 2 and 3), and an introduction to the research context and methods (Chapter 4), the empirical contributions

of this thesis will then be addressed in turn. In a series of three papers, this project investigated how individual differences in technological efficiency arose in the wild chimpanzee population of Bossou, Guinea (West Africa). The research used 25 years (1992–2017) of archival video footage of the wild chimpanzee community, which provided a unique opportunity to conduct a large-scale, longitudinal analysis.

The first study (Chapter 5) tested whether variation exists in the nut-cracking behaviour across all the individuals ≥ 6 years old within the community, moving beyond typical age-sex class investigations. The second study (Chapter 6) aimed to explain the possible cause(s) of this potential variation. For this, it assessed whether divergent social learning experiences—from *both* the learner (≤ 5 years old) *and* the selected conspecific modelling the behaviour ("the model")—predicted subsequent nut-cracking efficiency. Finally, the third study (Chapter 7) tested whether particular characteristics of potential nut-cracking models affected the likelihood of learners peering at them.

The thesis ends with a discussion of the main contributions of the research, as well as its limitations and some proposed future research directions (Chapter 8). A significant contribution this research makes is the establishment of stable individual-level variation in the efficiency of chimpanzee stone tool use. In turn, the finding that variation stems from divergent experiences during skill development contributes to debates on social and cultural learning processes in wild primates, and has applications to current applied challenges in conservation policy. Moreover, the behavioural data presented throughout offers insights into the potential transmission processes underlying early hominin lithic technology, which has relevance for modelling hominin cultural and technological evolution more generally. Not least, this thesis reiterates the central importance of long-term research of known individuals in their natural environments to address evolutionarily pertinent questions.

2

THE BIG PICTURE

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2.1 EARLY HOMININ TOOL USE

Tool use, defined as the practice of using extra-somatic, unattached materials to produce modifications to oneself, others, objects, or the environment (Beck, 1980), is associated with significant—and diagnostic—cognitive, motor, and life-history shifts in the hominin lineage (Bril et al., 2015; Kaplan et al., 2000; Wynn et al., 2011). By enabling the expansion into new ecological niches, technology had profound impacts on hominin biological evolution (Schick, 2013).

Although the archaeology of plant-based tools is currently being pioneered (Luncz, Braun, et al., 2022; Pascual-Garrido, 2018; Pascual-Garrido & Almeida-Warren, 2021), the archaeological record is biased toward lithic techno-complexes given the durability of stone (McGrew, 1992a; Pascual-Garrido et al., 2023). The piecemeal fossilised wood evidence is also comparatively much younger than that of stones. For example, the earliest wooden artefact (a polished wooden plank; *Salix* sp.) from Gesher Benot Ya'aqov, Israel, is dated to 240–750 thousand years ago (ka; Belitzky et al., 1991), and the earliest structural use of wood is dated to 456 ka (Barham et al., 2023). Conversely, the earliest stone artefacts are suggested to be over 3 Ma (Harmand et al., 2015). Such biases mean that our insights into the earliest hominin behaviours are centred around the use of lithic technologies. Indeed, Proffitt et al. (2023) argued that 'intentional stone flake technology represents our lineage's first definitive behavioural feature' (p. 5).

The Palaeolithic, which marked the first foray into stone technology by hominins, spanned from the emergence of Lomekwian technology at 3.3 Ma (Harmand et al., 2015) to approximately 12 ka with the emergence of the Holocene. See Figure 1 for a timeline of early hominin technological evolution.

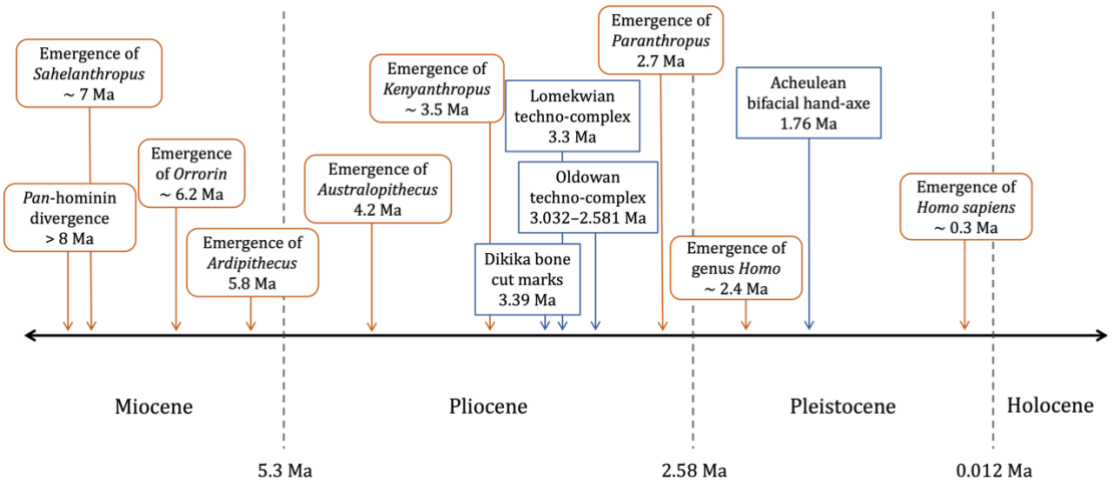


Figure 1. Timeline showing the current earliest dates of each hominin techno-complex. *Note*: Orange rounded squares indicate dates for fossil specimens of hominin species, and blue squares indicate the current first appearance dates of techno-complexes (Bobe & Reynolds, 2022).

Currently, indirect evidence of stone tool use dates to 3.39 Ma at Dikika, Ethiopia. McPherron et al. (2010) reported the discovery of two ungulate and bovid bones with 12 apparent stone tool cut marks aimed at flesh removal and marrow extraction, and implicated *A. afarensis* as percussive stone tool users. While these artefacts have been widely debated—with some arguing that more evidence is required before conclusions of stone-assisted butchery are made (Domínguez-Rodrigo & Alcalá, 2016)—Thompson et al.'s (2015) comparison of the taphonomy of the two bone specimens with other assemblages from the Hadar Formation at Dikika ruled out trampling damage as the most parsimonious explanation for the cut marks on the two bones. The authors also noted that the specimens are contemporaneous with the oldest stone tools found to date.

Indeed, Harmand et al. (2015) presented discoveries from the Lomekwi 3 site in West Turkana, Kenya, of *in situ* stone cores and flakes dating to 3.3 Ma—branded "Lomekwian technology". The artefacts sit within the chronological and geographical range of *Kenyanthropus platyops* and suggest that hominins were knapping stone (reducing lithic cores; Semaw, 2006) ~700 ka before the emergence of the first well-established stone industry entitled "Oldowan".

But Lomekwian technology is not without controversy. Toth & Schick (2018) warned that this technological outlier should be interpreted with caution as the artefacts may have been Oldowan tools redeposited in older sediments and hence not a unique techno-complex. Archer et al. (2020) further critiqued the claims that the Lomekwi cores and artefacts were *in situ*, concluding that Harmand et al.'s (2015) statements were 'dubious' and 'unwarranted' (p. 5). They called for further 'unambiguous evidence' (p. 5) before the 3.3 Ma age can be accepted.

Oldowan tools were characterised as being intentionally modified stone cores used for cutting and pounding (De La Torre, 2011), and were commonly manufactured from volcanic lavas, quartz, and quartzite (Toth & Schick, 2015). Recent archaeological findings place Oldowan tools associated with *Paranthropus* sp. in Nyayanga, Kenya, 3.032–2.581 Ma, extending the late Pliocene geographic range beyond the Afar Triangle in Ethiopia (Plummer et al., 2023). Indeed, previous research placed the first appearance of Oldowan tools in Gona from 2.6–2.5 Ma (Semaw et al., 1997) and then in Ledi-Geraru from 2.61–2.58 Ma (Braun et al., 2019). Plummer et al., (2023) recovered 330 stone artefacts, with the highest frequency being used for pounding activities (see section 2.1.4 for details on the ubiquity of percussion in early lithic techno-complexes). The team also excavated hippopotamid bones that show cut marks indicative of butchery. Use-wear analysis of three associated stone flakes evidence the use of these tools for animal tissue processing. Further bovid bone evidence shows the hominins were pounding and cutting carcasses for meat and marrow. Quartzite and rhyolite percussive tools were also used to process plant tissues, such as soft and fibrous tubers.

Such variation in foraging tasks highlights the flexibility of Oldowan technology, and the adaptive advantage hominins would have experienced by using these stone tools (Plummer et al., 2023). As illustrated in Figure 2, the Oldowan encompassed a heterogeneous group of technologies and was not a uniform techno-complex (Braun & Hovers, 2009; Toth & Schick, 2018). Carbonell et al., (2009) formulated a model of the Oldowan whereby they proposed

a progression from homogeneity to *variability* (in method), *diversity* (in system), and then *multiplicity* (of tool type) with the appearance of Acheulean tools at ~1.76 Ma (Toth & Schick, 2015). Recent research quantified the hammerstone striking angle used during stone knapping from 12 flake assemblages from Koobi Fora, Kenya, dated from 1.95 to 1.4 Ma (Li et al., 2023). The researchers found that the hominins were applying more perpendicular strikes to control the size of the subsequent flakes by 1.56 Ma, which overlapped with the Oldowan-Acheulean transition in Koobi Fora. This finding suggests that these tool users possessed more advanced understandings of the mechanics involved for efficient tool production, shedding light on the cognitive and technological capabilities of hominins during the Oldowan-Acheulean transition.

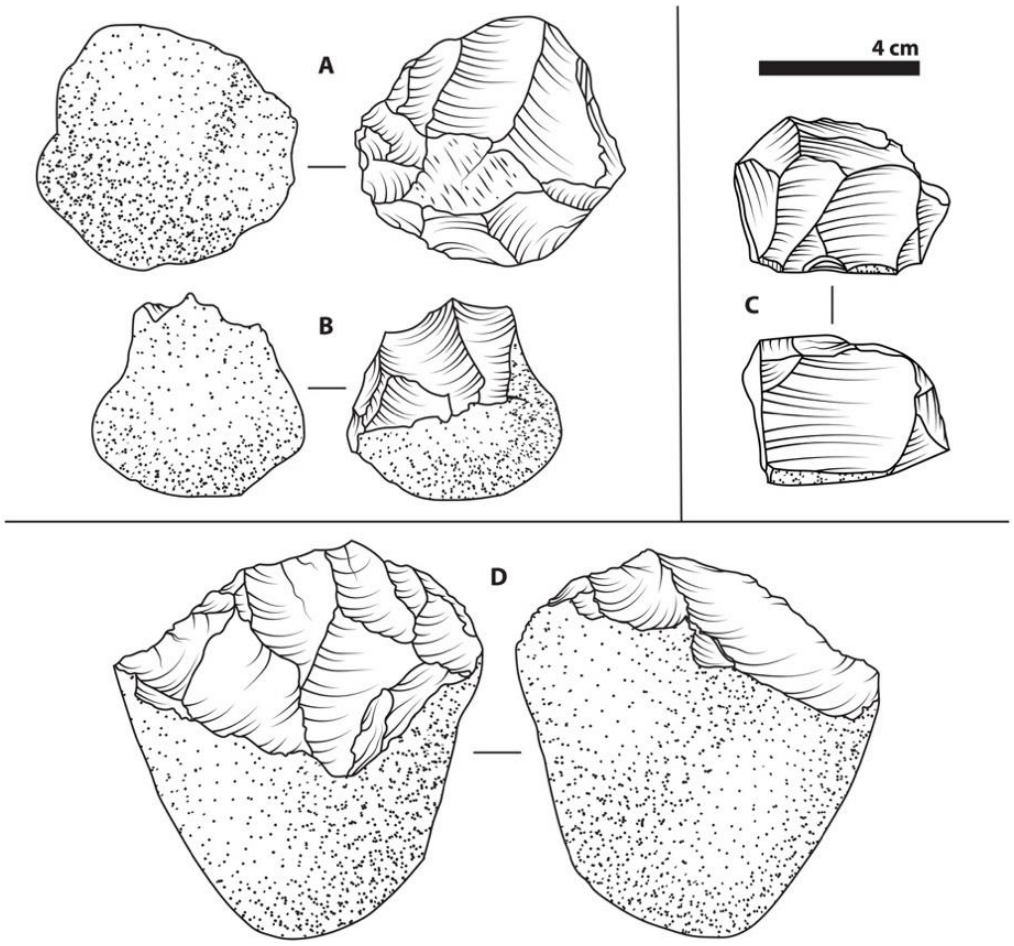


Figure 2. Illustrations of Oldowan stone tools from different time periods and sites: (A) and (B) 2.6–2.5 Ma from Gona, Ethiopia, (C) 1.7 Ma from Melka Kunture, Ethiopia, and (D) 2.3 Ma from Hadar, Ethiopia. Reprinted from "Early knapping techniques do not necessitate cultural transmission," by Snyder, W. D., Reeves, J. S., and Tennie, C., 2022, *Science Advances*, p. 2. This work is licensed under CC BY 4.0.

2.1.1 *Acquisition and Transmission of the Oldowan*

In their review of the cognitive implications of Oldowan technology, Toth & Schick (2018) argued that the expansion into this technological niche transitioned hominins into a 'new evolutionary stage' (p. 3), allowing for enhanced food processing and more complex social and communicative behaviours. This was facilitated by the capacity and inclination to learn faithfully from others (Boyd et al., 2011). This has been termed the "cultural niche", whereby the ability to accumulate modifications in tools (as well as in beliefs and practices) that cannot be invented individually through acquiring knowledge from others explains human adaptability (Boyd et al., 2011).

What is unknown from the early archaeological record, however, are the specific learning mechanisms and strategies involved in the transmission and acquisition of the skills required to make and use Oldowan tools. Pargeter et al. (2023) noted that,

> Stone tool skill-learning has been understudied even though (1) the most salient cognitive demands of tool-making should occur during learning, and (2) variation in learning aptitude would have provided the raw material for any past selection acting on tool-making ability. (p. 127)

Therefore, investigating the social transmission of early techno-complexes will assist in our understanding of the cognitive suite of early technological hominins (Braun, 2012). In turn, it will enable assessments of selective social learning in cultural learning, with the selection of successful "teachers" enabling adaptive information to be acquired by "pupils" (Boyd et al., 2011). Such selective social learning is discussed in more detail in section 3.1.3.

Running experiments on modern humans is one means through which to test how Oldowan tools were learnt and transmitted intergenerationally. There is a growing body of literature in this area, focusing on knapping tool manufacture (e.g., Moore & Perston, 2016; Pargeter et al., 2019; Putt et al., 2014; Stout et al., 2019). For example, researchers have claimed that the teaching of stone technology co-evolved with language in hominins. Morgan et al. (2015) tested whether five social learning mechanisms—reverse engineering, imitation/ emulation, basic teaching, gestural teaching, and verbal teaching—were capable of

transmitting Oldowan knapping techniques. The authors found that transmission was significantly improved when teaching was involved and was the most successful when verbal instructions could be provided. Moreover, performance along the transmission chain decreased much more rapidly when no teaching was involved, indicating that key information regarding the technique was lost faster when teaching was absent.

Morgan et al. (2015) concluded that 'Oldowan tool making would have created a continuous selective gradient leading from observational learning to more complex verbal teaching' (p. 5). Although the time allowed to learn the technique in the experiment (5 minutes) was far shorter than in natural settings, it nonetheless illustrates the importance of teaching for successfully transmitting Oldowan technology along a transmission chain. This would have heightened the selection pressure for more complex cognition in hominins (Braun, 2012).

Conversely, a more recent study sought to ascertain whether early knapping techniques could be learnt by individual trial-and-error learning. Snyder et al. (2022) motivated 25 knapping-naïve participants to make and use a cutting tool to obtain a monetary reward. Each participant was tested over a 4-hour period, with no "cultural information" (i.e., social demonstration, verbal instructions, or written instructions). All participants individually re-innovated early knapping techniques, which the authors argued suggests that hominin knappers did not need cultural information to learn to make and use Oldowan tools.

But the methodology used in this research substantially reduces the certainty of that conclusion. Of the 25 knapping-naïve participants, only two were naïve to stone technology in general. Given that the experimental task (which required cutting a rope to access a €10 note) included the provision of the raw materials necessary for stone tool production, arguably the remaining 23 participants did have prior cultural information. Moreover, the participants were required to wear safety equipment (e.g., gloves) to adhere to health and safety requirements, which may have primed (through cultural information) that a sharp object would be involved in the task. Finally, the raw materials provided (a painted glass hemisphere, a granite block, and a local river cobble) were not ecologically valid for

Oldowan technology, further hindering the validity of the inferences drawn from the findings. Therefore, on the basis of this research alone, it cannot be concluded that Oldowan tool production techniques can be re-innovated by naïve individuals.

Following their experiment testing the effects of individual differences in cognitive and motor capacities and learning conditions on knapping skill acquisition, Pargeter et al., (2023) concluded that future experimental designs must include younger participants, and explicitly incorporate the teacher's skill and their interpersonal relationships with the learners. Indeed, Shea (2006) noted the invisibility of children's tool use in the archaeological record, despite the fact that young knappers would have learned in social contexts and so their artefacts (including the greater number of flaked by-products they produced) will be among the currently excavated assemblages. Although controlled laboratory experiments on adults can inform our understanding of the role different forms of training plays on skill acquisition, long-term research in naturalistic settings of young individuals learning to make and use stone tools is key for advancing our understanding of the acquisition and transmission of the earliest hominin lithic tools. It is important to assess who learners choose to learn from when given the choice so that the evolutionary trajectory of cultural traits can be explored (discussed in section 3.1.4). This goal can be realised through behavioural observations of modern analogues.

2.1.2 *Modelling Hominin Technological Behaviour*

Given that behaviour is archaeologically invisible, models must be employed to draw inferences of the evolutionary trajectories and technological adaptations of hominins. Tooby & DeVore (1987) differentiated between two types of modelling: referential and conceptual. Referential modelling involves drawing inferences about a referent through investigation of an extant species or phenomenon, while conceptual models are theories whose concepts and variables are used to understand behaviour.

Tooby & DeVore argued that conceptual models are required to reconstruct hominid behavioural evolution, as referential models i) are disproportionately focused on the earliest, most ape-like stages of hominin evolution, and ii) overemphasise similarities between species, rather than differences. Issues can arise when focusing on similarities as they could be the result of convergent evolution, the process whereby adaptation to similar environments lead to shared characteristics rather than homology (i.e., common descent; Berdugo, 2019; Lewin & Foley, 2004).

Even so, primate referential models are frequently used due to their analogous (i.e., common attribute; Moore, 1998) and homologous relationships to hominins (Sussman & Hart, 2015). Notwithstanding the drawbacks of using referential modelling, estimates of the *Pan*-hominin LCA suggest it was a comparable size, had a similar diet, and occupied similar habitats to extant chimpanzees (Grabowski et al., 2018; Muller, 2017; Pilbeam & Lieberman, 2017). In fact, Pilbeam & Lieberman (2017) disagreed with the contention that *Pan* models are referential, rather concluding from their review of molecular, anatomical, and fossil evidence of the LCA that chimpanzees can be used as conceptual models given the extensive similarities between them.

Moreover, chimpanzee nut-cracking (described in detail in section 3.3) has potential relevance for understanding hominin percussive technology. Goren-Inbar et al. (2002) described lithic and palaeobotanical evidence demonstrating that the hammer-and-anvil composites used by extant chimpanzees for cracking nuts resemble assemblages produced by Early–Middle Pleistocene hominins in Gesher Benot Ya'aqov. Also, Proffitt et al.'s (2022) recent research compared the stone tool use of the Djouroutou chimpanzees in the Taï National Park, Côte d'Ivoire, to that of Bossou chimpanzees and hominin percussive tools. The researchers found variation in the use-wear patterns between the chimpanzee communities, but that their stone tools fell 'within the range of dimensions, percussive damage, and techno-morphological criteria used to identify some archaeological anvils in the Plio-Pleistocene archaeological record' (p. 19).

Moreover, archaeological evidence has established a "Chimpanzee Stone Age" from 4,300 ka in the Taï National Park (Mercader et al., 2007). The researchers found behaviourally modified stones with attached food deposits indicative of chimpanzee manipulation, which suggests percussive technology could have arisen prior to the *Pan*-hominin divergence as opposed to being an invention along the hominin lineage.

This evidence suggests that primates can inform our understanding of the evolutionary origins of technology, particularly the use and acquisition of Oldowan tools by early hominins (Sayers & Lovejoy, 2008; Stanford, 2012; Whiten et al., 2009). Moreover, Rolian & Carvalho (2017) argued that the existence of derived traits in the *Pan* and hominin lineages suggests that convergent evolution is unlikely to explain the complex tool use observed across chimpanzee (see section 2.2) and wild-born bonobo populations. Therefore, using chimpanzee models alongside primate and hominin archaeological evidence provides a more robust understanding of the evolutionary origins of hominin technological behaviour (Haslam et al., 2009).

In addition to the relevance of chimpanzee models for hominin behaviour, investigating chimpanzee tool use also informs our understanding of chimpanzee learning, development, and material culture. Bründl et al.'s (2020) longitudinal analysis of motor, social, and communicative developmental milestones in infant chimpanzees from Taï established that fine motor traits (precise phalangeal, hand, and foot movements, including tool use) emerge later in development, with nut-cracking emerging on average at 3.3 years.

Importantly, the researchers found that these later emerging traits exhibit larger degrees of inter-individual variation, potentially resulting from environmental influences (Bründl et al., 2020). In their review of primate development, Bard & Leavens (2014) reiterated the importance of the early-life experiences on behavioural outcomes in hominoids. Given that differences exist in chimpanzee tool use (see section 2.2.3), it is a useful case study for furthering our understanding of primate behavioural variation and the role of the

developmental socioecological environment in shaping this variation. As such, understanding the socioecological context within which early hominins were becoming increasingly reliant on stone tools, and the way this context facilitated the social transmission of tool skills, will provide key insights into how and why individual variation in efficiency of tool use developed.

2.1.3 *The Move to the Ground*

Current evidence suggests that the original hominin condition was arboreal (White et al., 2009), with the key hominin trait of bipedalism evolving in an arboreal context (Drummond-Clarke et al., 2024; Venkataraman et al., 2013). Habitat changes, ecological shifts, and reduced predation pressures enabled the transition to increasingly terrestrial living around 4 Ma (Eppley et al., 2022; Foley & Gamble, 2009; Hammond et al., 2022; Hammond et al., in review). This move to the ground facilitated the increased reliance on stone tools (Young et al., 2015). In fact, Meulman et al. (2012) argued that a 'terrestriality premium may have been a major pacemaker of hominin technological evolution' (p. 58). Fossil evidence suggests that early stone tool using hominins were at least semi-terrestrial (Foley & Gamble, 2009; Young et al., 2015), lending support to the claim that 'their tool use has probably also been subject to the terrestriality effect' (Meulman et al., 2012, p. 65).

This association between terrestriality and tool use is illustrated among extant technological primates. In fact, the species who demonstrate the most habitual tool use—bearded capuchins, long-tailed macaques, and chimpanzees—are also more terrestrial than other primates (Meulman et al., 2012). Among the great apes, Meulman et al. (2012) argued that the significantly more complex tool variants found in chimpanzees compared to orangutans is best explained by the former being more terrestrial than the latter. Indeed, the most complex technological behaviours (defined by Meulman et al. as 'tool-use variants that include at least two tool elements, flexibility in manufacture or use, and that skills are acquired in part by social learning,' p. 58) found in chimpanzees occur on the ground,

including cracking oil palm nuts (*Elaeis guineensis*) using a stone hammer-and-anvil composite and ant-dipping using plant-based tool sets (Matsuzawa, 2011b; Sanz et al., 2010). Heldstab et al.'s (2016) research exploring the relationship between manipulation complexity and relative brain size among 36 primate species found that terrestriality (including semi-terrestriality) mediates the positive correlation (see Figure 3). Terrestrial substrate use also frees species to use both hands during a task, which is key for complex tool use (that is, tools comprised of at least two components, which are used flexibly according to the task requirements, and where the skill is acquired at least partly through social learning; Meulman et al., 2012).

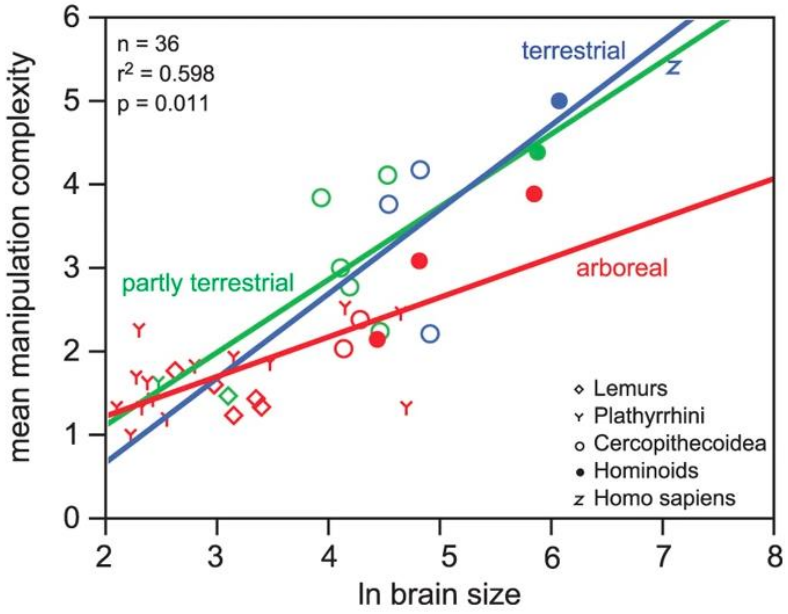


Figure 3. Relationship between log brain size and mean manipulation complexity for differing types of substrate use. Reprinted from "Manipulation complexity in primates coevolved with brain size and terrestriality," by Heldstab, S. A., Kosonen, Z. K., Koski, S. E., Burkart, J. M., van Schaik, C. P., and Isler, K., 2016, *Scientific Reports*. This work is licensed under CC BY 4.0.

Meulman et al. (2012) proposed that among extant species with a predisposition to use tools when foraging, and who demonstrate social tolerance, terrestriality facilitates three key aspects of tool use: innovation, accumulation, and social learning. Typically, there are more close-range learning opportunities available whilst on the ground, meaning that learners can observe individuals other than their mother. Indeed, Biro et al. (2003) found that chimpanzees learning to crack nuts in Bossou (where the behaviour is entirely

terrestrial) were more inclined to observe non-maternal models as they got older, rather than their mother. No research to date has sought to explain how learners in Bossou select *which* conspecific(s) to observe beyond age-class preferences (Biro et al., 2003), and whether social learning strategies, such as learning from more proficient individuals (Laland, 2004), play a role in the selection. Meulman et al. (2012) also noted that learners have greater ease of access to discarded tools used by expert conspecifics, as the tools are not lost after falling from trees.

Thus, terrestriality not only increases the number of observational learning opportunities, but also facilitates stimulus enhancement through access to conspecifics' tools. As stone tools are durable, it is possible for tools to be used many times and for learners to reuse tools used by knowledgeable conspecifics (Biro et al., 2006; Carvalho et al., 2009; Fragaszy et al., 2013). Percussive stone tools were amongst the earliest forms of technology, and so provide a rich context for understanding early hominin sociocultural learning and cognition.

2.1.4 Percussive Technology

Percussive technology, defined as 'the use of tools to strike surfaces and objects, their functionality deriving from the impacts involved' (Whiten et al., 2009, p. 420), was central to many qualitative shifts in hominin evolution (de Beaune, 2004; Wynn et al., 2011). Although there is consensus that percussive tools predated knapped tools, the origins and evolution of percussive technology, and the transition from percussive to knapping tools, are debated.

One early hypothesis was formulated by Marchant & McGrew (2005). The authors proposed a scenario following an investigation into the percussive techniques used by chimpanzees to open baobab fruits (*Adansonia digitata*) at Mont Assirik, Senegal. They postulated that anvil-only hard-shelled fruit cracking by an arboreal ape was the starting point, followed by a transition to increased terrestriality and the potential use of stone anvils, facilitating the

extraction of a wider range of resources (known as "passive hammer percussion"; Harmand & Arroyo, 2023). In this scenario, a shift to the use of hammer-and-anvil composites followed, with lithic composites potentially creating sharp-edged flakes which could be used for cutting during animal butchery. Indeed, Mercader et al.'s (2002) ethnoarchaeological investigation of chimpanzees in the Taï National Park found that their nut-cracking behaviour produced unintentional cortical flakes. Marchant & McGrew (2005) argued that the final shift toward knapping required a 'cognitive leap' from accidental to purposeful flaking (p. 349).

This stepwise scenario oversimplifies what we know to be complex evolutionary processes. For example, there would have been variation between populations based on ecological differences and the pre-existing behavioural repertoires of groups. Indeed, flakes may have been produced but not regarded as a tool, especially in settings where items (e.g., meat, skin, *etc.*) could be cut with the individuals' teeth. In their review of the relevance of primatology for understanding archaeology, Harmand & Arroyo (2023) argued that social and ecological factors likely influence the presence of passive hammer and hammer-and-anvil percussion techniques in chimpanzees, rather than there having been a linear evolution as proposed by Marchant & McGrew (2005).

Carvalho et al. (2009) highlighted that reusing the same tool combinations in stone composites (as in the case of the stone hammer-and-anvil composite used by chimpanzees to crack nuts in Bossou) increases the likelihood of fracture. The authors hypothesised that this may have created the first accidental flakes, with the use of the same pounding tools forming the cores of the first knapping technologies. Indeed, wild bearded capuchin monkeys (*Sapajus libidinosus*) 'deliberately break stones, unintentionally producing recurrent, conchoidally fractured, sharp-edged flakes and cores that have the characteristics and morphology of intentionally produced hominin tools' (Proffitt et al., 2016, p. 85). Similarly, long-tailed macaques in Phang Nga Bay, Thailand, frequently produce unintentional conchoidal flakes whilst using a stone hammer-and-anvil to crack oil

palm nuts which fall within the morphological range of variation of intentional Oldowan and Lomekwian tools (Proffitt et al., 2023). This illustrates that flaked technology is not exclusive to the hominin lineage.

Luncz, Arroyo, et al., (2022) tested this hypothesis—which they called the "by-product hypothesis"—through field experiments with 20 bearded capuchin monkeys in Tietê Ecological Park, Brazil, in which the archaeological signature of nut-cracking was assessed. The researchers found that high quality anvils (ironstone) produced more complete unintentional flakes (22.2%) than medium (quartzite; 10.9%) and low (cherty siltstone; 0%) quality anvils. Moreover, there were no discernible differences between the capuchin's high-quality-anvil produced flakes and experimental freehand knapped flakes in properties including weight, elongation, and internal platform angle.

These findings broadly support the by-product hypothesis, although Luncz, Arroyo, et al., (2022) noted some key points of refinement: i) raw material quality impacts the number of flakes produced, ii) the properties (e.g., shape and weight) of the anvil affects the assemblage, and iii) the skill (or lack thereof) of the tool user may determine the number of opportunities for flaking to occur, with mis-hits increasing the frequency of unintentional flake production. The authors concluded that their research 'highlights that under certain circumstances, the "by-product hypothesis" represents a valid scenario for the emergence of stone flake production' (p.13).

Percussive behaviour in the Order Primates can inform our understanding of hominin pounding tools. Examples of percussive technology in monkeys include nut-cracking with stone tools in bearded capuchins (Falótico et al., 2024; Fragaszy et al., 2004), white-faced capuchins opening Halloween crabs (*Gecarcinus quadratus*) and coconuts (*Cocos nucifera*) with hammerstones and anvils (Barrett et al., 2018), and Burmese and common long-tailed macaques (*M. f. fascicularis*) opening marine resources (such as rock oysters, *Saccostrea forskali*, and sea almonds, *Terminalia catappa*) and oil palm nuts with stone tools (Gumert

et al., 2011; Luncz et al., 2017; Muhammad et al., 2023; Tan et al., 2015). Among the great apes, two wild gorillas were observed hitting hand-held pieces of a termite mound together (Masi et al., 2022). The authors argued that this represents the evolutionary precursor to free hand percussion.

Percussion is also found in all chimpanzee subspecies across 18 locations, although the majority of sites (12/18) are West African chimpanzees (*P. t. verus*; Harmand & Arroyo, 2023). Chimpanzees show three types of percussive actions: *passive hammer percussion*, using a *hammer-and-anvil*, and *cleaving*, although the one instance of cleaving (of large and fibrous *Treculia africana* fruit; Koops et al., 2010) was based on indirect observations (Harmand & Arroyo, 2023). Passive hammer percussion involves using one hand to hit the food item against a hard passive object, such as a root or immobile stone (Harmand & Arroyo, 2023). For example, adult male chimpanzees in Fongoli, Senegal, hit nutrient-dense baobab fruit against an anvil (the tree trunk or branch, or a stone found on the ground) to obtain the seeds, which they then reingest (Lindshield et al., 2021). This is classified as "proto-tool use" (Pruetz et al., 2021). Although the chimpanzees routinely use both passive hammer percussion and their teeth to open the fruit, percussion is likely more efficient than using solely teeth and hands and may also reduce damage to the teeth over the lifespan (Pruetz et al., 2021).

Hammer-and-anvil percussion involves using an active hammerstone to hit a food item placed on a passive anvil (Harmand & Arroyo, 2023; Matsuzawa, 1994). Using a stone hammer-and-anvil has been reported in West African chimpanzees to crack nuts, defined as 'delivering a blow to a nut in such a way that the shell cracks leaving the kernel intact' (Bril et al., 2009, p. 220). This behaviour is described in detail in section 3.3.

The study of percussive technology in extant primates continues to provide insights into the behavioural repertoire and diversity of wild populations, and provides a useful heuristic for the study of hominin technological behaviour (Harmand & Arroyo, 2023; McGrew, 2010).

Investigating chimpanzee tool use, and variation found between individuals, is essential for interpreting the hominin archaeological record.

2.2 CHIMPANZEE TOOL USE

Every chimpanzee community studied thus far (see Figure 4) uses non-lithic or lithic technology for a range of purposes, including, subsistence, hygiene, and display (Berdugo, 2019; Kühl et al., 2016; Whiten et al., 1999). For example, chimpanzees in the Goualougo Triangle, Republic of Congo, use leafy twigs for rain cover (Sanz & Morgan, 2007), and the Ngogo community in Kibale National Park, Uganda, engage in leaf-clipping displays, which are mostly used by males to solicit females (Watts, 2008).

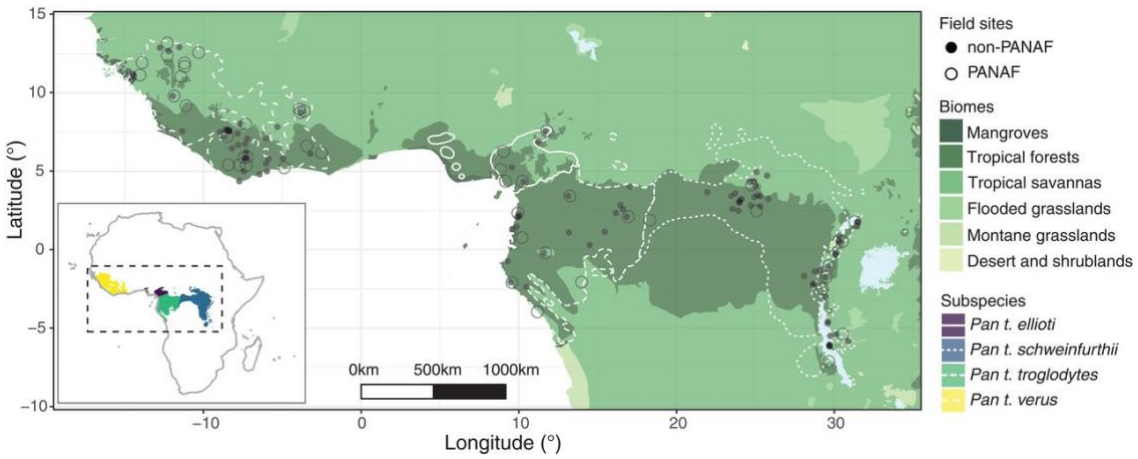


Figure 4. The distribution of the four subspecies of *Pan troglodytes* in Africa, with the locations of the 46 chimpanzee communities included in the Pan African Programme (PanAf), and a further 106 communities for which there is published research (non-PanAf). From "Human impact erodes chimpanzee behavioral diversity," by Kühl, H. S., Boesch, C., Kulik, L., Haas, F, et al., 2019, *Science*. Reprinted with permission from AAAS.

Regarding subsistence, access to embedded and high-quality resources is achieved by using tools (Sanz & Morgan, 2013). This is known as extractive foraging. For example, chimpanzees across sites termite fish, whereby they insert a long and flexible plant probe, such as a twig or bark, into a mound to retrieve the attached termites (Boesch & Boesch, 1990; Bogart & Pruetz, 2008; Goodall, 1964; Sugiyama & Koman, 1979b). They similarly use plant tools to harvest honey and ants (Bessa et al., 2021; Estienne et al., 2017; McGrew, 1992a). For example, the Goualougo chimpanzees use a specialised tool set—a long and

thick sapling to perforate the nest followed by a smaller herb stem for extraction—to retrieve army ants (*Dorylus* spp.; Sanz et al., 2010). Additionally, as discussed above, chimpanzees use pounding tools for pestle-pounding (Ohashi, 2015; Yamakoshi & Sugiyama, 1995), nut-cracking (Boesch & Boesch, 1983; Luncz et al., 2018; Matsuzawa, 2011b), and for predation on tortoises (*Kinixys erosa*; Pika et al., 2019).

2.2.1 Hypotheses Explaining Tool Use

Koops & Sanz (2022) argued that 'linking variation in tool-use behaviour in extant species to particular ecological and socio-cognitive differences is a key method for identifying drivers of the evolution of tool use' (p. 251). Fox et al. (1999) proposed the "necessity" and "opportunity" hypotheses as two non-mutually exclusive ecological explanations for the differences in the frequency of technological behaviour in great ape populations. The necessity hypothesis suggests that resource scarcity drives tool use as it allows extractive foraging during periods of low food abundance (Sanz & Morgan, 2013). Conversely, the opportunity hypothesis suggests that repeated exposure to the target extractable resources and tool materials motivates tool use (Sanz & Morgan, 2013). A further ecological hypothesis proposed to explain animal tool use is Rutz & St Clair's (2012) "relative profitability hypothesis". This hypothesis, originally conceptualised for New Caledonian crow (*Corvus moneduloides*) tool use, proposes that extractive foraging technologies are selected for when their profit margin exceeds that of non-extractive foraging techniques (Sanz & Morgan, 2013).

Fox et al. (1999) also proposed the "limited invention hypothesis", which emphasises the cognitive and social origins of tool use. This hypothesis postulates that 'tool behaviour may be invented only rarely and/or may have difficulty spreading and being maintained' (p. 113). Bandini & Harrison's (2020) review of chimpanzee innovation explained that behavioural variants are indeed rarely cemented into the group's behavioural repertoire despite the relative frequency of novel actions arising in the wild.

Sanz & Morgan's (2013) research on the ecological and social correlates of chimpanzee tool use in the Goualougo Triangle found that chimpanzees compensated with increased intake of leaves during periods of low fruit abundance, as opposed to increasing rates of tool use (contrary to the predictions of the necessity hypothesis). The authors did, however, find support for the opportunity hypothesis, and observed that the relatively small party sizes maintained throughout bouts of tool use facilitated social interaction and tolerance. This work corroborates that of Koops et al. (2013), whose research on wild chimpanzees in Seringbara (Nimba Mountains, Guinea) found support for the opportunity hypothesis. Indeed, the researchers found that the lack of termite-fishing and nut-cracking in the community was best explained by the rarity of nut-producing tree species and *Macrotermes* mounds in their home range. Conversely, the abundance of army ants (*Dorylus* spp.), rather than food scarcity, explained the presence of ant-dipping in the Seringbara community.

Grund et al. (2019) experimentally tested the necessity and opportunity hypotheses by assessing the short-term effects of travel and foraging history in the Sonso community in Budongo, Uganda. They found that '"necessity" augments chimpanzees' likelihood of engaging with ecological "opportunities"' (p. 1136), suggesting the complementary influences of these two factors on extractive foraging behaviours. Moreover, Pruetz et al.'s (2021) investigation of the relevance of the three ecological hypotheses for tool-assisted *Galago* hunting, termite-fishing, and baobab cracking for the Fongoli chimpanzees found that, over the 10 years of data used, no one hypothesis could best explain the three tool use behaviours. In fact, the opportunity hypothesis was the best explanation for termite-fishing and tool-assisted hunting (although the relative profitability hypothesis was not tested for *Galago* hunting), and the necessity hypothesis best explained baobab cracking. As such, it appears that the underlying mechanism facilitating the use of tools by chimpanzees is likely to vary according to the resource, behaviour, and location.

The two species of *Pan*, chimpanzees and bonobos (the latter confined to the Democratic Republic of Congo, DRC) differ in their technological behaviour, with the tool use repertoire

of wild chimpanzees consisting of 42 behaviours compared to only 13 in bonobos (Furuichi et al., 2015). Koops (2023) reviewed the current evidence and noted that chimpanzees are biased towards using tools in food contexts, whereas bonobos predominantly use tools in social contexts. To date, there has only been one reported instance of tool use in a feeding context in wild bonobos—leaf-sponging to drink water—whereas 25 of the 42 technological behaviours in wild chimpanzees are for feeding purposes (Furuichi et al., 2015).

Bonobos use tools to obtain food in captivity (e.g., Schick et al., 1999; Toth et al., 1993), suggesting divergent behavioural characteristics rather than different underlying cognitive abilities (Furuichi et al., 2015). Furuichi et al. (2015) found that the necessity, opportunity, and limited invention hypotheses could not explain the differences in tool use between the Goualougo chimpanzees and Wamba bonobos, who both inhabit the forest of the Congo Basin. Although the relative profitability hypothesis could not be tested, the authors concluded that the differences between the *Pan* species were likely due to differences in the ancestral Pleistocene environments of both species. They suggested that the more fragmented and variable environments inhabited by chimpanzees placed a larger selection pressure on tool-assisted extractive foraging to obtain hard-to-access resources than bonobos would have experienced. A follow-up study found support for an intrinsic difference in motivation for tool-use between bonobos and chimpanzees, which likely occurred after the *Pan*-hominin divergence (Koops, Furuichi, & Hashimoto, 2015).

The technological behaviour of chimpanzees can be classified as "flexible", which involves 'the use of different types of tools in different contexts and to reach different types of rewards' (Boesch, 2013, p. 25). Flexible tool use requires higher cognitive abilities as it involves a greater amount of relational spatial reasoning, more complex decision-making processes, and a larger working memory capacity, and is acquired via learning processes (Hunt et al., 2013; Visalberghi et al., 2017). Although social learning capabilities are widespread in non-human animals (discussed in section 3.1.1), there are very few species known to exhibit flexible tool use (Boesch, 2013; Hunt et al., 2013; Visalberghi et al., 2017).

Visalberghi et al., (2017) explained that complex, flexible tool use has only developed in a small number of bird and primate species, including New Caledonian crows, Galapagos woodpecker finches (*Camarhynchus pallidus*), and chimpanzees. Conversely, "stereotyped" tool use—defined as a species-wide behaviour requiring little learning—can be observed at a higher frequency in animals, including invertebrates and fish (Hunt et al., 2013).

In order to investigate the positive selection toward efficient technological behaviour, it is important to understand the daily energy budgets and feeding ecology of chimpanzees.

2.2.2 Chimpanzee Feeding Ecology and Daily Energy Budgets

The feeding ecology of chimpanzees is heterogeneous, conditional upon the particular environmental parameters of the community's habitat. However, notwithstanding the varied ecological niches within which chimpanzees reside (for example, savannahs and forest-mosaics, Hockings et al., 2009; Pruetz, 2006), chimpanzees are ripe fruit specialists (Humle, 2011a; McLennan, 2013; Wrangham et al., 1998), with diverse yet largely frugivorous diets predominating across the species (Yamagiwa & Basabose, 2006).

Moreover, chimpanzees are omnivores, with combinations of vertebrate, invertebrate, and plant-based resources comprising their diet (Milton, 1999). Chimpanzees hunt vertebrates, such as red colobus monkeys (*Colobus badius*) and bushbuck (*Tragelaphus scriptus*), across various sites (Wood & Gibly, 2017). Fongoli chimpanzees were observed crafting spears from sticks through a five-step process to extract bushbabies (*Galago senegalensis*) from inside tree hollows (Pruetz & Bertolani, 2007), although not all hunts are tool-assisted (Pruetz et al., 2015). Regarding invertebrates, chimpanzees consume ants (e.g., Sugiyama, 1995), termites (e.g., Sanz & Morgan, 2007; Yamamoto et al., 2013), and crabs (*Liberonautes* spp.; Koops et al., 2019).

The activities of any given 24-hour period vary across chimpanzee populations, but the proportion of behaviours exhibited can be averaged to establish a "typical" chimpanzee day. Pruetz & McGrew (2001) compiled data from 50 years of observation time from six long-

term wild chimpanzee field sites (Bossou, Budongo, Gombe, Kibale, Mahale, and Taï) and constructed an average 24-hour cycle (see Figure 5). Other than sleep (50%), foraging behaviour (including finding, extracting, processing, and ingesting the resources) predominates the average chimpanzee day (27.5%) across sites.

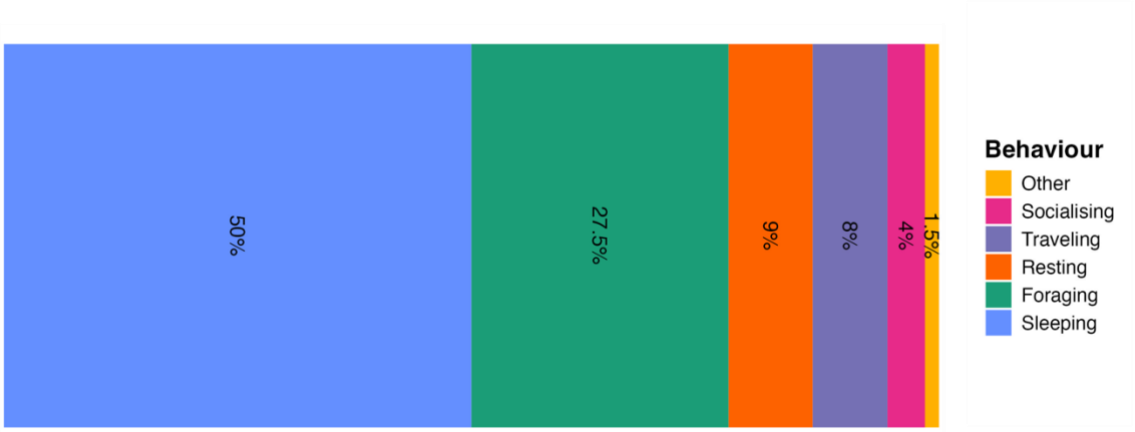


Figure 5. Chimpanzee behaviour across an average 24-hours. Data from "The Care and Management of Captive Chimpanzees," ed. L. Brent, by Pruetz, J. & McGrew, W., 2001, p. 18, San Antonio, American Society of Primatologists.

Although the categories identified in Figure 5 are not necessarily mutually exclusive (for example, foraging can also be social), there are potentially large selection pressures on achieving extractive foraging behavioural efficiency (Gruber et al., 2021). This is perhaps particularly likely given the sizeable proportion of the day dedicated to foraging. For example, the Goualougo chimpanzees have a complex "brush-tipped" termite-fishing probe to improve foraging efficiency (Sanz et al., 2009). Increased technological efficiency may allow for excess energy to be allocated to other fitness-enhancing behaviours, including socialising, mating, and rest. To date, daily energy budgets have been constructed as community averages, and variation between individuals in their energy expenditure have been overlooked. In Chapter 5, I argue that understanding the extent and cause of individual-level variation in extractive foraging techniques is essential for understanding variation in factors known to impact evolutionary fitness.

2.2.3 Variation in Chimpanzee Technological Behaviour

Inter- and intra-population variation in extractive foraging tool use is found across all chimpanzee communities, including differences in technological strategies and efficiency. For example, although chimpanzees across Africa fish for termites (Boesch & Boesch, 1990; Bogart & Pruetz, 2008; Goodall, 1964; Sugiyama & Koman, 1979b), and dip for ants and honey (McGrew, 1992a), the techniques vary according to community. For example, Koops et al. (2015) concluded that the ant-dipping tool length differences between two neighbouring chimpanzee sites (M- and S-group) in the Kalinzu Forest, Uganda, are likely cultural in origin. Similarly, Pascual-Garrido (2019) found differences in termite-fishing tools between the neighbouring Kasekela and Mitumba communities in Gombe, and concluded that this reflected different cultural knowledge.

Boesch et al. (2020) conducted ethnographic research in ten chimpanzee sites across Africa on the termite-fishing behaviours used for both aerial and underground termite nests. Using camera-trap footage, the researchers established that 14 of the 17 unique elements of aerial termite-fishing were dissociated from the local ecology, instead being socially transmitted, whilst for underground termite-fishing, 16 of the 21 behavioural elements were socially determined. The techniques used for both types were found to vary substantially between communities, with there being significantly more between-community variation than within-community variation (Boesch et al., 2020). For example, the "lean elbow" technical element for underground termite-fishing was only observed in Korup, Cameroon, whereas "head stick" was only detected in Campo Ma'an, Cameroon. The authors concluded that chimpanzees demonstrate a technological "etiquette" defined by their social group, suggesting that the sequences of technical elements are transmitted socially via high-fidelity learning processes.

Behavioural variation between four adjacent communities in Cantanhez National Park, Guinea-Bissau, has been established. Bessa et al. (2022) combined direct, indirect, and

remote camera trap data to construct behavioural profiles of the unhabituated chimpanzee communities and found that 18 of the 22 identified behaviours were 'putatively cultural' (p. 10). Of these, five behaviours were confirmed at only one site, for example, honey-dipping in Madina and fluid-dipping in Lautchandé. Both of these behaviours are extractive foraging techniques involving creating a probe from a twig. However, the putatively cultural behaviours found spanned different domains, including social and communicative.

Moreover, nut-cracking only occurs in West Africa despite the raw materials and nuts being present elsewhere (Biro et al., 2006; McGrew et al., 1997; Whiten et al., 1999). Also, the known nut-cracking populations vary in the tool materials (lithic or non-lithic) and cracking locations (arboreal or terrestrial) used (Carvalho & McGrew, 2012). Even among these populations, there are intergroup differences in cracking efficiency, resulting from differences in, for example, hammer selection and kinetic power dynamics (Luncz et al., 2018). For example, Luncz et al.'s (2012) research in Taï established that three neighbouring chimpanzee communities differed in their hammer selection for cracking *Coula edulis* nuts. The groups had different ways of selecting their hammers (i.e., regarding the size and material) in response to the seasonality of the nuts. For example, the South group continued to use stone hammers as the season progressed—despite their relative inefficiency—whereas the North and East groups switched to using wooden hammers. Given the ecological similarity (e.g., in terms of rainfall and raw material availability), and the frequent genetic transfer between the three communities, the authors suggested that these differences were cultural.

Individual differences in technological behaviour, notably regarding frequency and efficiency, also exist *within* chimpanzee communities. For example, Estienne et al.'s (2017) research on chimpanzee honey extraction in the Loango National Park, Gabon, found individual differences in the extractive foraging technique relating to the grip used during nest perforation, which was unaffected by the hardness of the soil.

Furthermore, at all sites where sex differences have been investigated, females are consistently more frequent and efficient tool users in foraging tasks than males (Berdugo, 2019), which is ubiquitous throughout the genus *Pan* (Gruber et al., 2010). In Gombe, females extract more termites per dip than males (Lonsdorf et al., 2004). However, Pandolfi et al.'s (2003) reanalysis of McGrew & Marchant's (1999) study on laterality in termite-fishing in 16 Gombe chimpanzees found that adult males collected 64% more termites per minute than adult females, owing to making more withdrawals per minute rather than extracting more termites per fish.

The apparent switch from female infants being more frequent and proficient termite fishers to adult males engaging in the behaviour more frequently and with greater success demonstrates the need for longer term projects assessing technological engagement throughout the life span. This would provide clarity as to whether this sex difference change is a typical occurrence, or whether it is an artifact of underlying individual differences in the proficiency of—and propensity to—termite-fish in Gombe.

In Taï, females crack coula and panda (*Panda oleosa*) nuts more efficiently than males (defined in terms of nuts per minute and hits per nut; Boesch & Boesch, 1981, 1984). Conversely, males in Bossou select, use, and transport stone tools more than females, with similar differences existing between adults and juveniles, respectively (Carvalho et al., 2008). Bain et al. (2021) used a novel behavioural automation algorithm on the nut-cracking behaviour in Bossou, and found adult male chimpanzees spent a greater proportion of their time cracking compared to adult females. However, this research did not investigate any differences in nut-cracking efficiency, other than a rudimentary measure of bout duration which compared the average time spent striking the nut ahead of eating the kernel. At present, no research has holistically assessed the presence and causes of individual variation in stone tool efficiency in wild chimpanzees.

2.2.4 Causes of Variation in Chimpanzee Technological Behaviour

As research on individual-level variation is lacking, the various hypotheses proposed to explain variation in chimpanzee technological behaviour are focused on the previously established sex differences in tool use across chimpanzee communities (see Table 1).

Table 1. Hypotheses explaining the potential causes of sex differences in chimpanzee technological behaviour, arranged according to Tinbergen's (1963) four questions.

Question	Hypothesis	Explanation	Tool type
Functional	Dependency on Nutritional Content	Females rely on the calories and nutrients of nuts more than males do (Boesch & Boesch, 1984)	Nut-cracking
		Females need micronutrients from tool-assisted insectivory, which males may get from hunting (Gibly et al., 2017; McGrew, 1979)	Tool-assisted insectivory
	Offspring-Friendly Techniques	Nut-cracking can be performed alongside dependent offspring, with more efficient mothers having higher reproductive success (McGrew, 1992a)	Nut-cracking
Phylogenetic	Uniparental Teaching	Mothers bias transmission towards daughters to ensure intergenerational cultural transmission of the skill (Zefferman, 2016)	Various*
Mechanistic	Social Interest	Females prefer solitary subsistence strategies whereas males prefer group-based strategies (Boesch & Boesch, 1984)	Nut-cracking
	Concentration	Males have shorter attention spans than females (Boesch & Boesch, 1984)	Nut-cracking
	Motor Abilities	Males find control of tools harder than females because of greater strength (Boesch & Boesch, 1984)	Nut-cracking
	Cognitive Abilities	Females are better at planning tool use (Boesch & Boesch, 1984)	Nut-cracking
Ontogenetic	Preparation for Tool Use	Differential use of objects in development affects later object manipulation (Koops, Furuichi, Hashimoto, et al., 2015)	Ant-dipping

	Social Learning	Divergent learning of the skill affects subsequent behavioural efficiency (Lonsdorf, 2005)	Termite-fishing

Notes: * = Not exclusive to chimpanzee tool use. Table adapted from "Why do female chimpanzees become more frequent and efficient nut crackers? An investigation into the developmental origins of the female bias in chimpanzee nut-cracking," by Berdugo, S., 2019, *University of Oxford*.

This thesis is concerned with the ontogenetic explanations for explaining individual variation in stone tool efficiency, as the other hypotheses specifically aimed to explain sex differences. Although the ontogenetic hypotheses were also originally developed to explain sex differences, they are broadly applicable to individual-level differences.

The "preparation for tool use" hypothesis was originally formulated for the ant-dipping tool context following the finding that male infants in Kalinzu, Uganda, manipulated sticks and woody vegetation more than females, but that this manipulation was mainly play-based (Koops, Furuichi, Hashimoto, et al., 2015). Conversely, female infants manipulated the objects in ways seen to be preparing them for acquiring the ant-dipping skill, such as breaking and plucking. The assumption, therefore, was that the female bias in technological behaviour stems from different experiences manipulating objects during infancy. However, this hypothesis does not explain why such variation might exist.

As such, this thesis develops the social learning hypothesis, which originally explained the female bias in termite-fishing efficiency in the Kasekela chimpanzee community in Gombe (Lonsdorf, 2005). Lonsdorf's (2005) 4-year study of mother-infant dyads found that female infants peered at their mothers more, spent more time termite-fishing, and subsequently successfully termite-fished earlier than male infants (see Figure 6). Mothers do not differ in the tolerance (such as allowing their offspring to steal a tool or peer) they show towards male and female infants (Lonsdorf, 2006). This is perhaps surprising, as tolerance can mediate the number of learning opportunities available to infants (van Schaik et al., 1999, 2003).

An important next step would be to determine whether there are between-mother differences in tolerance shown towards learners, rather than simply within-mother differences, and whether such differences correspond to subsequent variation in proficiency between the learners. This would build on Humle et al.'s (2009) finding that mothers in Bossou varied in the number of opportunities they provided their infants to learn to ant-dip, and that infants of "high opportunity" mothers started to dip earlier and made fewer dipping errors than infants of "low opportunity" mothers.



Figure 6. An infant chimpanzee from the Kasekela community in Gombe peering at their mother termite-fishing. Photograph credit: Alejandra Pascual-Garrido.

In fact, van Schaik et al., (1999) hypothesised that primates, including hominins, were able to evolve to use complex tools because of exposure to social learning opportunities within socially tolerant populations. A longitudinal investigation assessing the role of tolerance, opportunity provision, and learner peering (i.e., 'attentive close range watching'; Schuppli

et al., 2016, p. 87) will shed light on how cultural forms are transmitted intergenerationally, and whether these experiences produce variation in technological abilities in adulthood.

Having established the theoretical and empirical underpinnings of the research presented in this thesis, I now turn to reviewing the literature specific to social learning and chimpanzee nut-cracking. These provide the context for the empirical contributions of this thesis, which aim to address gaps in our knowledge relating to the "big picture" outlined in this Chapter.

3

CHIMPANZEE SOCIAL LEARNING AND THE NUT-CRACKING CONTEXT

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To investigate the role of the developmental period in generating variation in technological behaviour, it is essential to differentiate between different forms of learning, as well as the capacity and reliance on particular mechanisms and strategies used in wild populations acquiring naturally occurring behaviours, such as using stone tools to extract nut kernels.

3.1 LEARNING MECHANISMS

3.1.1 *Individual and Social Learning*

Individual learning (synonymous with "asocial learning") occurs when individuals change how they behave in response to a particular experience in the absence of social interaction (Boyd & Richerson, 1985; Heyes, 1994). Heyes (1994) outlined the three categories of experiences that can lead to asocial learning: i) a single stimulus, ii) a relationship between two stimuli, as in Pavlovian conditioning, and iii) a response-reinforcer relationship, through which the response of the individual will become more or less likely in the future. For example, individuals can learn via trial-and-error, whereby they update their technique based on the outcome of previous practice attempts.

The "costly information hypothesis" posits that individuals will rely on social learning when the energetic and time costs of asocial learning are high (Boyd & Richerson, 1985). A behaviour is said to have been socially transmitted when 'a behavioural trait previously mastered by individual *A* has an enduring positive causal influence on the occurrence of that trait in individual *B* when individual *A* engages in the behaviour' (Hoppitt & Laland, 2013a, p. 6). Social transmission occurs via three causal pathways: i) observation, ii) exposure to products, or iii) verbal or written instruction (Hoppitt & Laland, 2013a).

As well as these causal pathways, social transmission can be classified according to the mechanism employed (Galef, 1988; Heyes, 1994; Hoppitt & Laland, 2013b). For example, *stimulus enhancement* occurs when observing a demonstrator or their products draws the observer's attention to an object, thereby increasing the likelihood of them also manipulating that object (Heyes, 1994). *Local enhancement* occurs when an observer's

attention is drawn to a particular location because of a demonstrator's presence in that location (Thorpe, 1956). *Social facilitation* is the phenomenon whereby the mere presence of spectators influences an individual's behavioural frequency or intensity (Zajonc, 1965). *Emulation* is the process whereby, following observation of a demonstrator, an observer performs actions that result in the same, or a similar, outcome (Tomasello, 1990). *Imitation* is the process whereby, following observation of a demonstrator, an observer performs the same sequence of actions as the demonstrator (Tomasello et al., 1993).

Individual and social learning may rely on the same underlying cognitive processes (Heyes, 1994). Heyes (2012) explained that social and asocial learning both employ associative learning mechanisms, and that social learning is simply associative learning where the 'input mechanisms (perceptual, attentional, and motivational processes) are phylogenetically or ontogenetically tuned to other agents' (p. 193). This is supported by simulations demonstrating that associative learning can give rise to various forms of social learning, including stimulus and local enhancement and imitation (Lind et al., 2019).

Moreover, neuroscientific evidence suggests that social learning shares the same neural and computational circuitry as asocial learning (Olsson et al., 2020). For example, Burke et al. (2010) investigated whether individual and observational learning of actions and outcomes are both represented by brain regions related to reinforcement learning. Results of their fMRI experiment found that observing the successes and failures of others shares the same neural mechanisms as individually experienced prediction error, 'consistent with the idea that it is evolutionary efficient for general learning mechanisms to be conserved across individual and vicarious domains' (p. 14435).

Irrespective of the underlying cognitive processes and neurological circuitry, social learning is found across the Animal Kingdom, in both vertebrates and invertebrates (Hoppitt & Laland, 2008; Reader & Biro, 2010). For example, bumblebees (*Bombus terrestris*) learned a novel behaviour that could not be learned via trial-and-error from a conspecific (Bridges

et al., 2024). Blue tits (*Cyanistes caeruleus*) acquired a novel two-action foraging task by observing a trained demonstrator, rather than via asocial learning or local enhancement (Aplin et al., 2013). Among primates, ring-tailed lemurs (*Lemur catta*) solved a two-action puzzle feeder task using social learning (Kendal, Custance, et al., 2010), and infant Javan gibbons (*Hylobates moloch*) learn about their diet through food transfers from their mothers (Yi et al., 2020). In fact, social learning is described as being "pervasive" in lifetime development across the Order Primates, with individuals first learning from their mother, then from their groupmates, and finally, for individuals who disperse from their natal group, from new conspecifics entirely (Whiten & van de Waal, 2018).

3.1.2 *Chimpanzee Social Learning*

Chimpanzees learn a large array of behaviours socially (Whiten, 2017). For example, Hobaiter et al.'s (2014) social network analysis found that the spread of a novel moss-sponging behaviour in the Budongo chimpanzees (Uganda) was best explained by social rather than individual learning. There are also large time investments into socially-mediated learning of extractive foraging techniques, with ant-dipping taking a mean of 2.5 years to learn (Humle et al., 2009) and nut-cracking ca. 4 years (Matsuzawa, 1994).

There is little evidence, however, of active teaching (whereby the teacher incurs a cost whilst informing the student; Caro & Hauser, 1992) in chimpanzees (Hoppitt et al., 2008; Whiten, 2017), although Boesch (1991) presented anecdotal evidence of two instances of active teaching of nut-cracking by mothers in Taï. Musgrave et al. (2020) also found evidence of mothers teaching infants in Goualougo termite-fishing, as measured through tool transfers (imposing costs on the donor via loss of their tool and reduced feeding). Transfer rate was significantly more frequent in Goualougo compared to Gombe, Tanzania, which has a comparatively less complex form of termite-fishing. However, Whiten (2020) raised concerns of the validity of this teaching claim. He argued that Musgrave et al.'s (2020) observations do not demonstrate an intent to educate, and that, since the infants initiated

the tool transfers, the behaviour is likely enhanced scrounging tolerance or an attempt to reduce 'intense offspring pestering' (p. 803).

Thus, although more evidence is required to conclude chimpanzees engage in active teaching *per se*, it is clear that infants learn their technological behaviour at least in part socially, particularly from a maternal model. Legare (2017) advocated that this makes chimpanzees 'an ideal comparative sample' (p. 7881) for furthering our understanding of the evolutionary origins of the role of ontogenetic processes on hominin cognition. Moreover, investigating who young wild chimpanzees learn from and when throughout the learning period of complex technological behaviours sheds light on the role of network structure and social tolerance in knowledge transfer and skill acquisition (Coussi-Korbel & Fragaszy, 1995; Migliano et al., 2017; van Schaik et al., 1999).

3.1.3 Social Learning Strategies

Social learning enables faster behavioural acquisition than individual learning, but this is traded-off against the fact that the information may not be the most accurate or up-to-date (Boyd & Richerson, 1985; Kendal et al., 2005). As such, it is adaptive to employ social learning strategies to guide *when* to learn information socially, and *who* to learn from (Laland, 2004). Table 2 lists the 12 specific strategies originally outlined by Laland (2004).

Table 2. "When" and "who" social learning strategies.

Strategy type	Social learning strategy
When	Copy when established behaviour is unproductive
	Copy when asocial learning is costly
	Copy when uncertain
Who	Copy the majority
	Copy if rare
	Copy successful individuals
	Copy if better
	Copy if dissatisfied
	Copy good social learners
	Copy kin
	Copy "friends"
	Copy older individuals

Notes: Reprinted from "Social learning strategies," by Laland, K. N., 2004, *Learning & Behaviour*, 32 (1), p. 5, Springer Nature. *Reproduced with permission from Springer Nature.*

Of the first category, Kendal et al. (2005) reviewed evidence of "when" social learning strategies in fish, birds, and mammals, and found that, across taxa, social and public information is used when individuals are uncertain or when it is too costly to acquire information individually. For example, nine-spined sticklebacks (*Pungitius pungitius*) copy the feeding patch used by others when they have no relevant personal information (*copy when uncertain*; Coolen et al., 2003). Minnows (*Phoxinus phoxinus*) use a *copy when asocial learning is costly* strategy when foraging under a perceived threat of predation (Webster & Laland, 2008).

Laland (2004) outlined nine "who" strategies, including *copy the majority*, *copy successful individuals*, and *copy kin*, of which humans have been shown to employ experimentally both online (e.g., Brand et al., 2020) and in-person (e.g., Atkisson et al., 2012; Henrich & Broesch, 2011; Mesoudi, 2011; Wood et al., 2012, 2013). Watson et al. (2018) reviewed the current evidence of wild and captive primates using social learning strategies, discussed in detail in Chapter 7.

Of the nine "who" strategies outlined by Laland (2004), only one—*copy the majority* (i.e., conform)—has been investigated in wild chimpanzees. Luncz et al. (2018) found that female chimpanzees migrating into a community in Taï National Park conform to the nut-cracking technique employed by their new community, even if it means giving up a more efficient technique (in terms of number of strikes to crack a nut and the rate of nut intake). Moreover, to date, no preferences based on model-specific characteristics (such as *copy successful individuals*, *copy kin,* and *copy older individuals*) have been studied for the development of extractive foraging behaviours in wild chimpanzees, other than research showing that Bossou chimpanzees only peer at individuals in the same age class or older (Biro et al., 2003).

It is essential to determine whether social learning strategies guide the acquisition of tool use in the wild given the importance of such strategies in enabling cultural inheritance and

evolution (Heyes, 2016, 2017). Not least, investigating social learning in natural settings is crucial for gaining ecologically valid insights into processes known to shape biological, cognitive, social, and cultural evolution (Kendal, Galef, et al., 2010).

3.1.4 Social Learning can Shape Evolutionary Trajectories

Social learning plays a pervasive role in biological, social, technological, and cultural evolution. In terms of biological evolution, the need to learn a vast array of information socially placed a selection pressure on a longer period of childhood in hominins (Kaplan et al., 2000; Schuppli et al., 2012). This period of high dependency demonstrates the interconnection between the evolution of culture, life history, and cooperation (Schuppli et al., 2012). Indeed, Coussi-Korbel & Fragaszy (1995) noted that social learning is intimately related to social dynamics. Learners not only need to sustain their attention on the model for the duration of the behaviour, but the models must also be tolerant to prolonged and recurrent proximity. Van Schaik et al. (1999) argued that this tolerance provided the necessary conditions for primates, including hominins, to evolve to use tools.

In fact, Rapaport & Brown (2008) argued that social learning was the cornerstone in enabling hominins to specialise on ever more varied and hard-to-access resources, prompting technological advancement and reliance. Social learning is a critical component for the development of culture, enabling the acquisition of skills which would not be possible through individual learning alone (van Schaik, 2010). However, social learning and individual learning are also intimately connected during the process of cultural evolution. Boyd & Richerson (1985) explained that,

> … cultural transmission of the initial phenotype and its subsequent modification by [individual] learning combine to produce a force increasing the frequency of the variants favoured by learning, even in the absence of natural selection. This effect is the essence of guided variation. (p. 95)

Yet, these variants developed via individual learning are not transmitted to the subsequent generation (Boyd & Richerson, 1988). Rather, vertical (via kin) or oblique (via non-kin) social learning processes are required for cultural traits to be inherited (Danchin et al.,

2011). Therefore, social and asocial learning are complementary to one another, and are often both used when acquiring a skill (Richerson & Boyd, 2020).

Heyes (2016) argued that social learning strategies, specifically *metacognitive* social learning strategies, can also contribute to cultural evolution as they promote high-fidelity copying. Learning "who knows" the behaviour best encourages fine-grained transmission of knowledge from only a select few models and reduces the amount of asocial learning that is incorporated in by the learner. This allows small innovations to be accurately transmitted to many individuals within a population, thereby supporting cultural evolution.

Finally, although there are species-typical forms of social learning for particular skills, there is growing evidence that social learning mechanisms and strategies vary systematically across individuals (Mesoudi et al., 2016). For example, individual variation in social learning has been found during experiments in wild great tits (*Parus major*) and blue tits (Aplin et al., 2013, 2017). Such individual differences in social learning have also been found in humans (e.g., Miu et al., 2020) and primates (e.g., Barrett et al., 2017). This variation can have profound effects on evolutionary processes. Indeed, Mesoudi et al. (2016) argued that,

> … it can have significant evolutionary consequences, potentially driving populations to behavioural equilibria different to what we would expect if social learning were under tight genetic control, and casting doubt on the validity of a phenotypic gambit approach that ignores the extent and causes of individual variation. (p. 216)

Given the central importance of social learning in evolutionary trajectories, it is critical to explore the mechanisms through which complex behaviours are transmitted and maintained within populations. Although it is undeniable that humans have a qualitatively distinct reliance on social learning among the Animal Kingdom, whether or not humans are alone in being cultural is subject to ongoing, and heated, debate.

3.2 THE "CHIMPANZEE CULTURE WARS"

There is a longstanding debate regarding whether a "golden barrier" (Gould, 1999) exists between human and nonhuman animals regarding certain cognitive and behavioural characteristics. The extent to which human uniqueness is expected—and privileged—in primatological research sways the null hypothesis. Culture is often wielded as a core criterion for transcending the barrier (McGrew, 2003).

There are disagreements across the psychological and anthropological disciplines regarding the uniqueness of culture—dubbed the "Chimpanzee Culture Wars" (Langlitz, 2020; McGrew, 2003). The cultural biases and preconceptions of the researchers are deeply embedded into this debate (De Waal, 2003). This has historically split the field along the fault lines of the two broad primatological paradigms: Japanese primatology and Western primatology.

The nonhuman capacity for culture is firmly within the system of knowledge of Japanese primatology (De Waal, 2003; Kutsukake, 2011; Langlitz, 2020). This paradigm, founded by Kinji Imanishi, is said to have 'never been contaminated by feelings of superiority or an aversion to acknowledging humanlike characteristics in animals' (De Waal, 2003, p. 294). Conversely, Western primatologists have typically contested the notion of cultural animals, assuming that scientific provisioning and individual learning form the backbone of supposed cultures (De Waal, 2003). These paradigms also differ in methodological approaches. Japanese primatology focuses on long-term field research backed by detailed descriptions of behaviours and use of provisioning, whereas Western primatology emphasises rigorous hypothesis testing (Kutsukake, 2011).

3.2.1 Cultural Learning and the Ratchet Effect

The early battleground of the chimpanzee culture war was in the experimental research testing the social learning capabilities of captive chimpanzees and comparing them to humans. Early work from Tomasello et al., (1987) tested whether captive chimpanzees

across two age groups (4–6-year-olds and 9-year-olds) could learn how to use a metal T-bar to access an out-of-reach food item by observing a trained chimpanzee demonstrator. In the control condition, the chimpanzees were exposed to the tool, but the demonstrator (who was present in an adjacent cage) did not model the behaviour. As the tool performance of the 9-year-olds did not improve after training, the researchers focused on the results of the seven younger chimpanzees.

Tomasello et al. found that no young chimpanzees in the experimental condition imitated the demonstrator, but rather used emulation learning: observing the demonstrator taught them that the T-bar could be used as a tool (i.e., product-focused learning), but they did not copy the way the tool was used (i.e., process-focused learning). The chimpanzees in the control condition manipulated the tool, but did not use it to retrieve the food. From these results, Tomasello et al. concluded that observation of a model is important in the acquisition of tool use behaviours in chimpanzees, but that no imitation is involved.

A follow-up study by Nagell et al. (1993) compared how 4–8-year-old captive chimpanzees and 2-year-old human infants learned to use a rake-like tool from a human demonstrator. Mirroring Tomasello et al.'s conclusions, Nagell et al. suggested that the emulation of the chimpanzees and the imitation of the human infants reflected species-wide differences in social learning processes, resulting in chimpanzee tool use traditions being looser than human cultural traditions. As such, the authors concluded that this explained why chimpanzees accumulate very few innovations over time, whereas this is common in human material culture.

Based largely on these two experimental studies, Tomasello et al. (1993) proposed that cultural learning—'learning in which the learner is attempting to learn not *from* another, but *through* another' (original emphasis; p. 496)—is a form of social learning that only humans possess. They argued that the human capacity for high-fidelity behavioural transmission acts as 'the psychological basis for cultural evolution,' as it allows for

modifications to accumulate over time (p. 495). This cumulative culture is termed the "ratchet effect". Whiten (2022) recently called this the "imitative copying hypothesis" (p. 223).

Three distinct, and ontogenetically incremental, social learning processes are said to underpin human cultural learning: imitative learning, instructed learning, and collaborative learning. Instructed learning, like imitative learning, is a form of cultural transmission. It involves children learning about how the adult understands the task through purposeful instruction. Collaborative learning, on the other hand, is a process of 'cultural creation or co-construction' (p. 501), whereby peers work together to problem solve. As other species, including chimpanzees, supposedly lack these qualities, Tomasello et al. concluded that they do not have the ratchet effect. As such, humans are argued to be quantitatively and qualitatively different from chimpanzees (Tomasello, 1999). High-fidelity imitative learning is regarded to be a prerequisite to cumulative culture.

The distinctions drawn between chimpanzee and human learning mechanisms have garnered much attention. For example, research found that captive chimpanzees were more likely to copy the outcome of a demonstrator's actions (emulation), whereas human children were more likely to faithfully reproduce their actions (imitation; Call et al., 2005). Moreover, chimpanzees emulated a human demonstrator using a tool to access a reward from a clear puzzle box but imitated their actions (even when they are causally irrelevant) when the box was opaque (Horner & Whiten, 2005). Human infants imitated the demonstrator in both conditions. The researchers concluded that chimpanzees are therefore capable of imitative learning, but that emulation may be more adaptive in certain circumstances as it allows for efficient and generalisable behaviours.

3.2.2 The Zone of Latent Solutions

In 2009, the culture debate was expanded, with humans being said to possess the ability to 'ratchet up the ratchet' (Tennie et al., 2009, p. 2412). Here, along with the supposedly unique

human ability to copy behavioural processes and not just outcomes, humans are seen to have three cooperative processes: teaching, social imitation (i.e., motivations to conform), and normativity (i.e., punishment for non-conformity; Tennie et al., 2009). These three processes are said to 'give human cultural traditions their extraordinary stability, cohesion, and cumulativity' (p. 2412).

Conversely, as chimpanzees are not seen as possessing any of these capacities and tendencies, Tennie et al. hypothesised that all cultural behaviours are in fact traits that are within the physical cognitive skills of every individual within the species. This underpins the "zone of latent solutions" (ZLS) hypothesis (Tennie et al., 2009; Tennie, Bandini, et al., 2020), which is considered a 'more specific offshoot' of the imitative copying hypothesis (Whiten, 2022, p. 232). Tennie et al., (2009) argued that all currently known cultural traits found in chimpanzees can be independently individually re-innovated and learned, either readily or under specific conditions. In fact, Tennie, Hopper, et al. (2020) claimed that if a culturally naïve individual were placed on a "cultural island" (i.e., with no access to cultural information), they could nonetheless acquire the focal skill. They further argued that the behavioural variation between chimpanzee communities represents different expressions of the same total repertoire of behaviours available to all chimpanzees. Under the ZLS hypothesis, only humans can copy behaviours that lie outside of their so-called ZLS.

Similarly, proponents of the ZLS hypothesis propose that Palaeolithic technologies could have been latent solutions for the early stone tool using hominins, and that the null hypothesis should be that high-fidelity social learning mechanisms were not employed in tool production (Tennie et al., 2016, 2017). However, this "resetting" of the null hypothesis for the cultural transmission of early stone tools, along with the other elements of the ZLS hypothesis, have been highly criticised and are subject to ongoing debates.

3.2.3 Critiques of the Zone of Latent Solutions Hypothesis

The critiques of the imitative copying hypothesis and ZLS hypothesis are manyfold, surrounding both the theoretical underpinnings and the empirical approaches taken to test the hypotheses' assumptions. For example, in response to Tomasello et al.'s (1993) original proposals, Heyes (1993) argued that imitation does not require perspective-taking, such as in the case of mimicry. Moreover, Boesch (1993) questioned how the imitative capabilities found in enculturated (i.e., those adapted to human-like culture) chimpanzees could have arisen if there had been no selection pressure acting on the ability.

More recently, Whiten (2022) critiqued the ZLS hypothesis, noting the unfalsifiability of its central tenets, which precludes it as a 'useful scientific hypothesis' (p. 216). Whiten also refuted the contention that if a chimpanzee independently re-innovates a cultural behaviour, then that is evidence that the behaviour is within the ZLS. All cultural traits must have been invented by an individual who did not observe another individual producing the behaviour (Gruber & Biro, 2023; Whiten, 2022). Thornton & Mesoudi (2023) argued that it is more productive to investigate the drivers and constraints on innovation. They noted that motivation prompts innovation, rather than innovators necessarily being cognitively different from non-innovators. Within this, they explained that developmental conditions may mediate the benefits of innovating, and so it is important to investigate differential experiences during skill development to identify the socioecological contexts that encourage individuals to innovate.

The empirical work claiming to support the ZLS hypothesis has also been critiqued. A key criticism involves the recurrent use of small samples of captive chimpanzees engaging in artificial tasks (Gruber & Biro, 2023). For example, Neadle et al. (2020) tested whether 13 zoo-housed task-naïve chimpanzees could learn to use a log to open macadamia nuts either individually or from a human model. No chimpanzees throughout the research acquired the skill, which the authors claimed neither supported nor countered the claim that unenculturated chimpanzees (i.e., those not adapted to human-like culture) can re-innovate

nut-cracking. However, the study suffers from a lack of ecological validity, and neglects the fact that nut-cracking is often used to access fallback foods during periods of low fruit availability (Yamakoshi, 1998).

More broadly, using chimpanzees with a history of engaging in experimental tasks and who are in physical environments with little stimulation likely increases the chances of the individuals using the introduced tools (Gruber & Biro, 2023). Gruber & Biro (2023) argued that 'setting the threshold at two "genius" individuals to claim that a given behaviour remains in the ZLS is arbitrary and convenient' (p. 86).

3.2.4 *Nut-Cracking as a Cultural Trait*

Nut-cracking is a cultural behaviour, with some communities lacking the behaviour entirely despite possessing the required raw materials (Biro et al., 2003; McGrew et al., 1997), and others differing in aspects such as hammer selection (Luncz et al., 2018). This cultural variation is thought to explain the inability of two female Bossou chimpanzees, Pama and Nina, to crack nuts, as they are believed to have migrated from neighbouring communities that do not engage in nut-cracking (Matsuzawa, 2011b). Instead of nut-cracking, Nina and Pama scrounged pieces of kernel extracted by their groupmates (Matsuzawa, 2011b).

Experimental research demonstrated that nut-cracking using a stone hammer-and-anvil composite was not individually innovated in the wild Seringbara chimpanzee population which neighbours the Bossou community and, until recently, shared gene flow. Koops et al. (2022) conducted four field experiments across two sites over the course of three years that directly tested the ZLS hypothesis. Each experiment built incrementally from the last and provided the wild chimpanzees with the materials required for nut-cracking. Experiment 1 introduced stones (with varying properties, but all in the ranges used by Bossou chimpanzees) and dried oil palm nuts (stimulus/local enhancement). Experiment 2 additionally provided locally sourced ripe oil palm fruit (stimulus/local enhancement). In experiment 3, the set-up remained the same but cracked oil palm nuts were positioned on

top of the stones such that they were clearly visible (end-state emulation). Experiment 4 mimicked the first experiment, but with coula rather than oil palm nuts (stimulus/local enhancement).

Koops et al. (2022) found that no chimpanzees cracked (or attempted to crack) nuts across all experimental set ups, despite 99 individual chimpanzee visits. Of these, only 19 explored the materials. The authors argued that this suggests that neither stimulus/local enhancement nor end-state emulation are adequate social learning processes for nut-cracking with stone tools to be acquired in the wild population. The authors concluded that a competent conspecific is required to demonstrate the nut-cracking technique and motivate the learner to engage in the behaviour. As such, 'nut-cracking falls outside the ZLS of chimpanzees and may thus qualify as a culture-dependent trait' (p. 491).

Tennie & Call (2023) questioned this conclusion, claiming that the Seringbara chimpanzees lacked motivation to engage adequately with the test, and that the majority of the chimpanzees were too old to have innovated the skill. However, Koops et al. (2023) refuted these claims in their response, highlighting that not only had there been multiple immature chimpanzees in their experiments, but also that Tennie & Call (2023) had conflated what they called "test motivation" with pre-existing knowledge that the nut kernels were edible. Koops et al. (2023) noted that,

> First, one has to discover that nuts are edible, which is extremely unlikely without one first being cracked. Second, one has to learn a highly complex tool use technique. This combined difficulty may well be what places nut cracking outside the chimpanzee ZLS. (p. 165)

The research presented in this thesis takes the view that chimpanzee nut-cracking technology lies outside of their zone of latent solutions.

3.3 NUT-CRACKING

Nut-cracking is an extractive foraging strategy aimed at obtaining an energy- and nutrient-dense kernel, and is achieved through the use of either a wooden or stone hammer and anvil to hit the hard external shell (Boesch & Boesch, 1983; Matsuzawa, 2011b). Izar et al. (2022) used multi-dimensional nutritional geometry to determine the energetic and macro-nutritional components of wild bearded capuchins' diets. The researchers found that using stone hammers to open palm nuts (*Orbignya* sp.) increased the monkeys' energy gain by 50%, and enabled a more fat-, carbohydrate-, and energy-rich diet. The authors argued that,

> … tool use could have provided significant energetic and nutritional benefits for early hominins even when the forms of tooling were technically simple, and tooling was a small proportion of overall foraging activity. (p. 4090)

The nutritional and energetic payoffs of using tools to crack nuts are likely equally beneficial for chimpanzees. Indeed, oil-palm kernels are also high calorie (663 kcal/100g; Matsuzawa, 2003) and rich sources of carbohydrates, protein, lipids, and fibre (Bryson-Morrison et al., 2020). But 'efficiency improves when nut shells are fractured without smashing the inner kernel, so that the latter can be easily and quickly collected and consumed' (Sirianni et al., 2019, p. 107). Indeed, Boesch & Boesch (1981) noted that incorrectly judging the kinetic energy of a strike can result in the kernel being smashed—making it barely edible—and so this is a key skill that must be learned. Precision is also required to reduce the risk of fracture (Sirianni et al., 2019). As such, there are three outcomes to a nut-cracking bout, and they vary in their energetic payoffs: whole kernel is extracted, kernel is extracted but smashed, and no kernel is extracted. Any factor improving cracking efficiency, and the learning process, would potentially be subject to positive selection (Gruber et al., 2021).

A key determinant of the energetic benefits of tool use are the properties of the materials selected (Sirianni et al., 2019). Tool characteristics are known to partially determine the efficiency of nut-cracking. Luncz et al.'s (2018) comparative analysis of three communities in Taï found that lithic hammers were more efficient than non-lithic hammers. Also, Schrauf

et al. (2012) found that, among lithic hammers, heavier stones were preferentially used by captive chimpanzees at the Great Ape Research Institute (Okayama, Japan) for striking macadamia nuts (*Macadamia* sp.), and that heavier stones (1200g) necessitated fewer strikes per nut than lighter hammers (300g and 600g).

The drive for more efficient foraging behaviour promotes cumulative cultural evolution (Gruber et al., 2021). Schofield et al. (2018) defined cumulative culture as 'a modification (change in the sequence or form of behavioural elements) of a cultural trait (i.e., acquired via social learning) that enhances its complexity, efficiency, security, or convenience' (p. 114). The components of security (i.e., risk and food security) and convenience (i.e., time and energy to complete a task) are seen as the key adaptive components of efficiency, whereby more efficient behavioural forms increase the net benefits (in terms of the risk, energy, and time payoff) of an action sequence (Schofield et al., 2018). Therefore, in principle, over time nut-cracking techniques which increase the efficiency of the behaviour will be favoured.

3.3.1 *Geographic Distribution*

To date, nine chimpanzee communities (see Figure 7) are known to engage in nut-cracking technological behaviour. This behaviour occurs both arboreally and terrestrially, depending on nut species, hammer type, and location (Boesch & Boesch, 1983; Carvalho et al., 2008; Sugiyama & Koman, 1979b). Of these nine sites, eight are west of the N'Zo-Sassandra river, Côte d'Ivoire, and one claim is to its east in the Ebo forest, Cameroon (Morgan & Abwe, 2006). The N'Zo-Sassandra river was previously considered an information barrier, limiting the spread of the behaviour and thus producing a culture-zone of nut-cracking populations confined to West African chimpanzees (Morgan & Abwe, 2006; Wrangham, 2006).

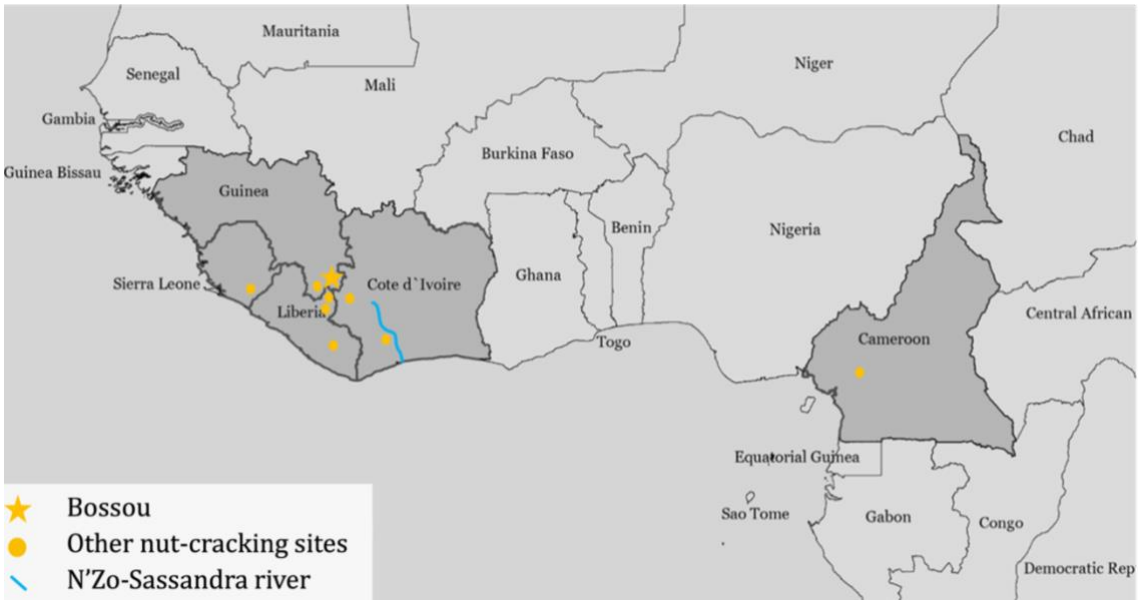


Figure 7. Map of the locations of the nine chimpanzee communities known to engage in nut-cracking behaviour. Image credit: Susana Carvalho.

Morgan and Abwe's (2006) report of both auditory and visual (albeit partly obscured) evidence of *Coula edulis* nut-cracking by chimpanzees in Cameroon (*P. t. ellioti*) contradicts this hypothesis. However, direct evidence of nut-cracking in the Ebo forest has hitherto not been obtained (Koops et al., 2022; Kühl et al., 2019). Koops et al. (2022) reasoned that, regardless of whether nut-cracking is present in Cameroon or not, the fact that nut-cracking has only been invented once or twice in wild populations indicates its difficulty to re-innovate.

3.3.2 *Nut-Cracking in Bossou, Guinea*

The Bossou chimpanzees crack nuts using a stone hammer-and-anvil composite (Carvalho et al., 2009; Matsuzawa, 2011b; Sugiyama & Koman, 1979b), with a composite being defined as 'a tool constructed through the purposeful association of two or more objects (transformed or not) that need to be used in combination in order to function and to achieve a specific goal' (Carvalho et al., 2008, p. 159). Carvalho et al.'s (2009) experimental investigation of the reuse of particular stone tools in Bossou found that 46% of the observed composites were used twice and one composite was reused 29 times, suggesting that the hammer-and-anvil combinations were preferentially selected by the chimpanzees.

The behaviour is complex, requiring coordinated action of both hands (and occasionally a foot for added stability) to manoeuvre the three objects (hammer, anvil, nut) during a nut-cracking bout (Sugiyama et al., 1993). Nut-cracking is also entirely a terrestrial activity in Bossou. The number of hits required to successfully open the nutshell was previously found to reach an asymptote in adulthood (Biro et al., 2006), and the movement of adult crackers was considered to be stereotyped (Biro et al., 2003). However, this finding is constrained to a measure of hits per nut which is only one measure of nut-cracking efficiency, and no research has sought to replicate this finding.

There is also individual-level laterality, resulting in exclusive handedness during nut-cracking (Humle & Matsuzawa, 2009). The only observed change in handedness occurred in 1996 when Fana (an adult female) switched to using her right hand following paralysis in her left arm (Biro et al., 2003). Biro et al.'s (2003) 16-year longitudinal analysis of nut-cracking acquisition in Bossou demonstrated that, despite there being no relationship between mother and infant handedness, there was near-perfect correspondence in laterality between siblings (13 of 14 dyads observed). There are no significant age or sex differences, although the chimpanzees exhibited a right-hand bias across nut-cracking, pestle-pounding, anti-dipping, and algae-scooping (Humle & Matsuzawa, 2009).

The Bossou nut-cracking behaviour conforms to the "chaîne opératoire" conceptual framework (Carvalho et al., 2008), which charts the operational sequential stages of lithic technologies, which are 'raw-material selection, blank production, tool production, tool use, recycling or maintenance, and discard' (Carvalho et al., 2008, p. 148). Carvalho et al.'s tool and microwear analysis in Bossou found that the most used raw material was diorite, despite granite being more frequently available, suggesting active selection of tool raw materials. Hammers were also significantly wider and lighter than anvils, although no significant differences were recorded regarding height and length of the stones. Together, this suggests that the chimpanzees assign a specific function to, and strategically select, stones depending on their characteristics (Carvalho et al., 2008).

Recent landscape-scale research by Almeida-Warren et al. (2022) sought to establish the broader technological landscape of the Bossou chimpanzees, namely tool site selection, use, and inactivity. The researchers used transects and quadrat methods to establish the availability and distribution of plant foods, oil palm nut trees, and raw materials, and conducted surveys to determine the presence of nesting sites and the location of water sources. Almeida-Warren et al. (2022) found that, not only did nut trees and raw materials need to be present for nut-cracking to occur at a particular location, but that being close to other food trees and nesting sites (< 250 m) also predicted nut-cracking. Moreover, all nut-cracking sites were between 40–300 m from water. Therefore, when nut-cracking, the Bossou chimpanzees are connected to the broader landscape.

Further detail on the Bossou chimpanzees, as well as on the location, ecology, and research history is provided in section 4.1.

3.3.3 *Similarity to Oldowan Technology*

As outlined in section 2.1.2, the chimpanzee stone tools used to crack nuts shares affinities with the Oldowan techno-complex, and hence remain relevant referential models of early hominin tool use. Braun et al. (in review) experimentally introduced four novel lithic materials (dacite, carbonatite, granite, and phonolite) into the Bossou community to investigate selectivity patterns, and similarity to Oldowan hominins from Kanjera South in western Kenya. They found that the chimpanzees selected hammer and anvil rocks according to their mechanical properties (hardness and strength), with hard rocks (dacite and granite) being selected for hammers and softer rocks (carbonatite) for anvils to maximise cracking efficiency (hits per nut). They also found that this selectivity pattern disseminated through the re-use of composite tools by juveniles and lower ranking individuals.

Moreover, Carvalho et al. (2008) established an operational sequence of 'stone selection for tool construction, transport, and utilisation' (p. 154), demonstrating a sequence of

stereotyped stages focused on realising a predetermined goal. This research further established similarities between this chimpanzee extractive foraging technology and that of the Oldowan techno-complex (Carvalho et al., 2008). This similarity was echoed by Almeida-Warren et al.'s (2022), whose research demonstrated that the Bossou chimpanzees' use of space resembles the "favoured places" model of hominin tool site formation, which proposed that tool sites were positioned at the heart of foraging locations, resulting in particular locations becoming technological hubs (Shick, 1987).

Reeves et al. (2023) noted the 'debate about the degree of tool variation that reflects the technical know-how of hominin tool makers and the social transmission of information *versus* the constraints imposed by the broader environmental constraints' (p. 2). Therefore, it is important to investigate the material consequences (for example, in terms of flaking or indentations on stones) of variation in stone tool efficiency to support interpretations of the archaeological remains.

3.3.4 *The Ontogeny of Nut-Cracking*

Primates, relative to other mammals, have slow life history strategies characterised by long growth periods and late age at first reproduction (Jones, 2011; Setchell, 2019). This slower rate of postnatal growth results in infants relying on their mothers to survive for a longer period.

Social learning, with the mother typically as the primary model, is critical for the acquisition of the nut-cracking skill in immature chimpanzees (Biro et al., 2003; Lonsdorf, 2013). Infants develop the ability to crack nuts through an "education by master-apprenticeship" learning process, which requires a highly tolerant model (the "master") for the learner (the "apprentice") to peer at, and a strong mother-infant bond (Matsuzawa et al., 2001). The term "peering" was first used in orangutan observational social learning research, and is defined as the 'attentive and sustained close-range watching of the activities of a conspecific' (Schuppli & van Schaik, 2019, p. 5, see section 4.2.3 for further detail on the definition of

peering). This "education by master-apprenticeship" process is analogous to the expert-apprentice learning system employed by human forager populations acquiring technological skills (Boesch et al., 2019).

Notwithstanding this prolonged social learning period, occurring via a range of stimulus and local enhancement and emulation, young chimpanzees also learn individually (Biro et al., 2003). Chimpanzee nut-cracking is acquired through a series of stages over a proposed period of 3–5 years (Biro et al., 2003), with each stage cumulatively building on the fundamental actions of the previous (Inoue-Nakamura & Matsuzawa, 1997). Although this age range was originally classified as a "critical period", Koops et al. (2023) have since questioned the use of this phrase in a cognitive sense, whereby individuals are seen as being unable to learn the skill beyond this period. Instead, they consider the learning period to be 'bounded by other variables' (p. 165), such as tolerance experienced from group mates and the provision of social learning opportunities. As such, the research presented in this thesis classifies the initial period of skill acquisition as the "early learning period" (hereafter "ELP"), during which the learner relies heavily on social learning within a generally tolerant environment. This period lasts until approximately age 5, and the post-early learning period ("post-ELP") encompasses individuals aged 6+.

Inoue-Nakamura & Matsuzawa (1997) followed the development of stone tool use in three infant chimpanzees in Bossou (Yolo, Fotaiu, and Vuavua) over four years to describe the stages of the nut-cracking learning process. They found that rates of nut and stone manipulation increased throughout the critical period, as did the proportional frequency of kernel scrounging. Also, the sequence of the five basic nut-cracking actions (taking nut, putting nut, holding stone, hitting nut, and eating kernel) became more formalised as a function of age. At 0.5 years old, only 45% of behavioural episodes involved a nut-cracking basic action, whereas at 1.5–2.5 years old three basic actions were present, which increased to four or five basic actions at 3.5 years. Stereotyped cracking sequences only emerged at 3.5 years old. However, this research had a very small sample size (n = 3) and could not

investigate whether any individual differences during the learning period corresponded to varying adult efficiency levels. See Figure 8 for photographs of a young chimpanzee learning the actions of nut-cracking.



Figure 8. An infant chimpanzee (Flanle) practising some of the basic actions of nut-cracking before he is able to perform a complete nut-cracking bout. Image credit: Tetsuro Matsuzawa.

Inoue-Nakamura & Matsuzawa (1997) also noted that the stages were facilitated by the infant's selected model. The proportion of peering at the mother decreased as the infants progressed through the learning period, being 100% of the time at 0.5 years old, and then only 14% of the time at 3.5 years old. This corresponds with Whiten & van de Waal's (2018) two-stage model of primate social learning within natal groups, whereby the mother is the primary model in early infancy, and the focus shifts to groupmates as individuals age. Their model built on Henrich & Broesch's (2011) two-stage model of cultural transmission in humans, whereby children first acquire information from their parents, and then update their knowledge by learning from other specifically-selected models. Indeed, the social network structure of hunter-gatherer populations maximises the efficiency of knowledge transmission and fosters cumulative cultural evolution (Migliano et al., 2017, 2020). This social network organisation allows young individuals to frequently interact with, and learn from, kin and non-kin (Chaudhary et al., 2024; Migliano et al., 2017).

Biro et al.'s (2003) three-part analysis incorporating extensive survey data with longitudinal records and field experiments found that infant chimpanzees are highly

selective in their choice of nut-cracking "master", with mothers being the predominant model of choice (90.2% of 203 observations). However, to date, no research has investigated whether social learning strategies dictate how non-maternal models are selected, or sought to replicate Inoue-Nakamura & Matsuzawa's (1997) findings in a larger sample. For example, two mothers in Bossou did not crack nuts but, nonetheless, their infants successfully acquired the skill from observing other conspecifics (Biro et al., 2006; Matsuzawa, 2003). Figure 9 shows a juvenile chimpanzee peering at a non-maternal model.

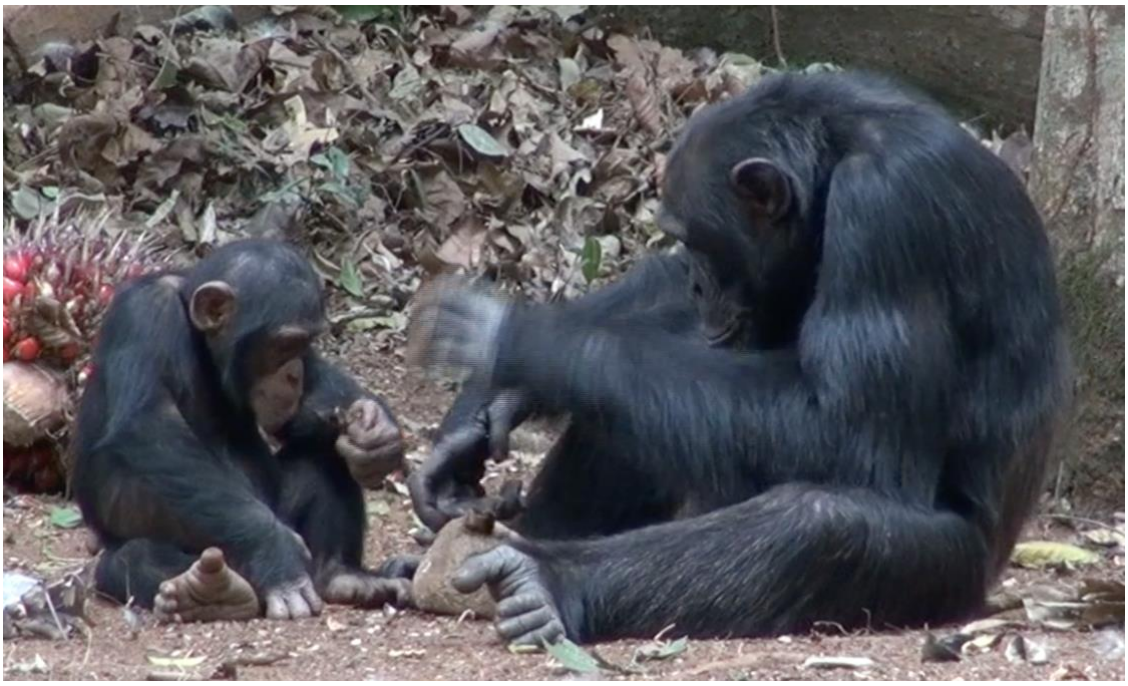


Figure 9. Juvenile chimpanzee Flanle peering at Peley, an unrelated older male, as he cracks and oil palm nut. Image credit: Tetsuro Matsuzawa.

Regardless of the selected model, the learning process involves remaining in close proximity (≤ 1 m) to the model, who tolerates infant scrounging, tool interaction, and peering (Biro et al., 2003; see Figure 10). In fact, van Schaik & Pradhan's (2003) mathematical model on tool-using skills demonstrated that populations with sufficient social tolerance and opportunities for social learning (indicated by degree of proximity to "expert" tool users) are more likely to possess complex skills such as tool use. Therefore, it is reasonable to hypothesise the variation in these dimensions will result in corresponding differences in technological proficiency (Humle et al., 2009; van Schaik et al., 2003).

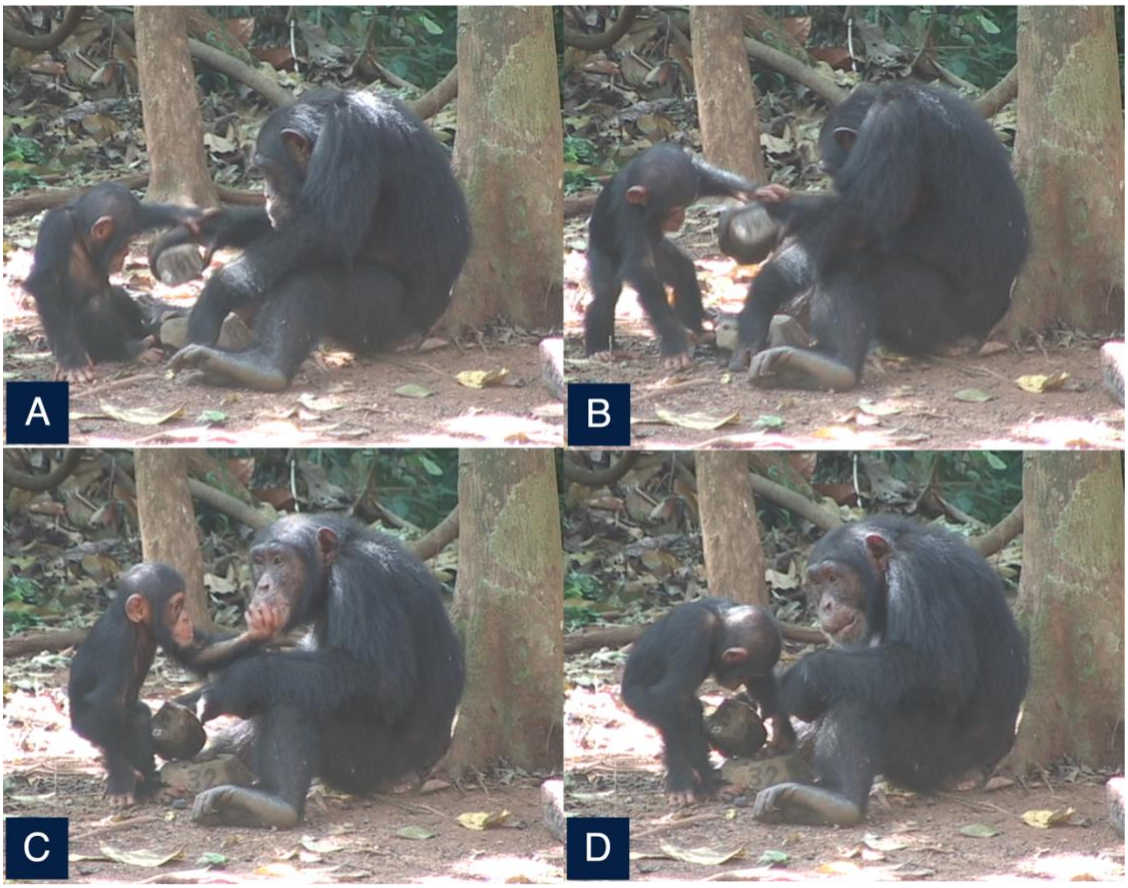


Figure 10. An adult female (Fanle) cracking an oil palm nut in the presence of her infant son (Flanle). The infant can be seen peering at the nut-cracking and interacting with his maternal model (images A and B) and scrounging the extracted kernel (images C and D). Fanle tolerates proximity, peering, interaction, and scrounging by Flanle. Image credit: Tetsuro Matsuzawa.

Previous research established that the Bossou chimpanzees reach adult-level nut-cracking competency at 10-years-old (Biro et al., 2003; Matsuzawa, 1994). Yet, to date, the post-ELP has not been investigated. Therefore, the research in this thesis considered the relevant behaviours (see section 4.2.3) for all post-ELP individuals, defined as chimpanzees aged 6 and over. This is based on the previously established period of social learning lasting until 5-years-old (Biro et al., 2003).

Moreover, the ontogeny of stone tool use to crack nuts is surprisingly understudied across the subfamilies of primates that engage in the behaviour (Cebinae, Cercopithecinae, and Homininae; see Figure 11). For capuchins (subfamily Cebinae), various species across the genera *Cebus* and *Sapajus* are known to use stone tools to crack nuts, but to date there have

been no long-term investigations into the acquisition of the skill and data are cross-sectional (Eshchar et al., 2016; Fragaszy et al., 2023; Resende et al., 2008, 2014). Research focused on the development of stone tool use in long-tailed macaques (subfamily Cercopithecinae) have so far only focused on using stone hammers to crack open oysters, and the findings are similarly derived from relatively short-term studies (1–2 years; Tan, 2017). However, longer-term studies are needed to fully understand the ontogeny of technological behaviour in primates, and to redress these gaps.



Figure 11. Ontogeny of stone tool use in West African chimpanzees, bearded capuchins, and long-tailed macaques. The colours represent the country-level range of stone tool use within each primate subfamily (yellow for Cebinae, orange for Homininae, and purple for Cercopithecinae). The labels show the locations, species, tools, resources, and learning periods for the populations where the development of the skill has been studied (Biro et al., 2003; Boesch & Boesch-Achermann, 2000; Boesch & Boesch, 1984; Eshchar et al., 2016; Resende et al., 2008, 2014; Tan, 2017).

3.4 THE NEED FOR LONGITUDINAL ONTOGENETIC RESEARCH

As chimpanzees' have long lifespans and correspondingly long learning periods for learning to use complex tools, longitudinal studies are essential for assessing the ontogeny of technology. Although more cost- and time-effective, cross-sectional studies cannot indicate how individuals and skills develop across the lifespan and they obscure any potential individual-level variation (Berdugo et al., 2023; Clutton-Brock & Sheldon, 2010; Kappeler et al., 2012). Long-term research allows for variation in fitness-enhancing traits, such as in the efficiency of extractive foraging, to be accurately assessed.

Importantly, observing individuals over the life span allows for tests of the stability of individual differences in technological proficiency. Mesoudi et al. (2016) called for 'more work… to track social learning within the same individual longitudinally' (p. 217), particularly in light of findings of individual learning of social learning (as discussed in section 3.1.4). It would also enable investigations into the transgenerational transfer of information within communities. However, tackling these topics is only possible with systematic data collection over multi-generational time spans.

3.4.1 The Importance of Long-Term Ethological Research

Long-term studies of known individuals are essential for advancing our understanding of ecology and evolutionary biology (Clutton-Brock & Sheldon, 2010). In their review of long-term, individual-based field research, Clutton-Brock & Sheldon (2010) argued that 'access to large numbers of recognisable individuals with known life histories spanning many years provides the possibility of asking (and answering) a wide range of novel questions that are otherwise inaccessible' (p. 570). Hayes & Schradin (2017) concurred, explaining that short-term research obscures the extent of variation and does not allow for accurate assessments of population dynamics in response to extreme environmental events. As such, they argued that long-term research is also essential for effective conservation strategies.

Clutton-Brock & Sheldon (2010) noted six research topics that benefit from such studies: development and ageing, evolution of life history stages, parental allocation of resources, network structures and social relationships, quantitative genetics, and phenotypic plasticity. For example, Bouwhuis et al.'s (2010) research using long-term data on great tits found that early life reproductive experiences and immigration status determined the rate of reproductive senescence in female birds. Longitudinal research also enables tests of the temporal nature of selection, with the strength, direction, and form of selection varying across time (Siepielski et al., 2009). As the existence of a selection pressure on a particular trait can also vary year-on-year, Siepielski et al. (2009) argued that long-term research is required to better understand these adaptive evolutionary dynamics.

Long-term ethological research has now been undertaken in a variety of taxa. For example, the Wytham Tit Project focused on great tits and blue tits was founded in 1947, the Serengeti Lion Project focused on *Panthera leo* commenced in 1966, and the Amboseli Baboon Research Project studying savannah baboons (*Papio cynocephalus*) started in 1971 (Clutton-Brock & Sheldon, 2010). Thanks to the pioneering work of Jane Goodall, chimpanzees have also been studied over multiple generations, starting with the chimpanzees in Gombe Stream National Park in 1960.

Chapman et al. (2017) reviewed the long-term field research on monkeys and highlighted the importance of these projects in advancing understandings of ecophysiology, social organisation, population ecology, and conservation. The 13 advantages Chapman et al. see long-term primate research as having are summarised in Table 3, below.

Table 3. Advantages and significance of long-term field studies on primates.

Factor	Advantages and significance
Life history studies	Allow documentation of the fitness values of specific life history and behavioural strategies
	Facilitate documentation of individual fitness if the study is of sufficient duration (i.e., < 60 years)
Informing short-term studies	Identify importance of rare ecological pressures (e.g., disease) on behaviour and population dynamics

	Illustrate if short-term studies are general
Documenting environmental variation	Provide an understanding of environmental variation and the strength of different selective pressures
	Illustrate variation in diet and social organisation
	Document the extremes of dietary flexibility
Evolutionary importance of extreme events	Identify if extreme events are important selective pressures of determinants of population size
	Identify fallback foods and essential foods
Population and community ecology	Document forest change and the impact on simian behaviour and population size
	Identify social drivers of behaviour and life history strategies that are independent of ecology
	Quantify the impacts of climate change
	Quantify the impacts of anthropogenic change and the time needed for ecosystem and simian population recovery

Note: Reprinted from "Long-term simian research sites: significance for theory and conservation" by Chapman, C. A., Corriveau, A., Schoof, V. A. M., Twinomugisha, D., & Valenta, K., 2017, *Journal of Mammalogy*, 98 (3), p. 653, by permission of Oxford University Press.

Given that chimpanzees are endangered (Humle et al., 2016), and that nut-cracking in is protected under the United Nations' Convention on the Conservation of Migratory Species of Wild Animals for being vital for the conservation of the West African chimpanzee subspecies (Expert Working Group on Animal Culture and Social Complexity, 2023), long-term field research on nut-cracking in Bossou is also vital for guiding conservation efforts.

3.4.2 Long-Term Chimpanzee Field Sites

There are six chimpanzee communities that have been under continuous investigation for over thirty years: Gombe (since 1960), Mahale (Tanzania, since 1965), Bossou (since 1976), Taï (since 1979), Kibale (since 1987) and Budongo (since 1990; Boesch & Boesch-Achermann, 2000). Other communities have now been observed for 20–30 years, including the Kahuzi-Biega (DRC, since 1994), Ngogo (since 1995), Semliki (Uganda, since 1996), Goualougo (since 1999), Fongoli (since 2001), and Nimba chimpanzees (since 2003). Research on the Cantanhez chimpanzees has been ongoing for approximately 20 years. The Loango (since 2005), Ebo (since 2005), Bulindi (Uganda, since 2006), Gishwati (Rwanda, since 2008), and Issa chimpanzees (Tanzania, since 2008) have been studied continuously

for almost 20 years. The locations of these long-term chimpanzee field sites are shown in Figure 12.



Figure 12. Google Earth satellite image of the locations of long-term chimpanzee field sites (May 2024, © 2023 Google). Blue placemarks with circles are the 30+ year field sites, orange placemarks with squares are the 20–30-year field sites, and the purple placemarks with diamonds are the <20-year field sites. Longitude and latitude coordinates from "Chimpanzee accumulative stone throwing," by Kühl, H., Kalan, A., Arandjelovic, M. et al., 2016, *Scientific Reports*, Supplementary Table 1. Map data attribution: Landsat / Copernicus Data SIO, NOAA, U.S. Navy, NGA, GEBCO IBCAO.

Many of these long-term field sites have also accumulated video records of wild chimpanzee behaviour, whether from remote camera traps or from camcorders. For example, the Taï Chimpanzee Project has a video archive spanning from 1992, and the Goualougo Triangle Ape Project has had camera traps positioned by termite mounds since 2003 (Sanz et al., 2004). The Pan African Programme: The Cultured Chimpanzee (known as "PanAf") makes use of camera traps at both long term and temporary research sites to conduct cross-community behavioural surveys and comparisons (Boesch et al., 2020; Kalan et al., 2020; Kühl et al., 2016, 2019; Vaidyanathan, 2011). The distribution of the PanAf camera trap network can be found in Figure 4 in section 2.2.

The formation of video archives and note digitisation by long-term field sites are now offering insights that would not be possible based on data from relatively short-term studies. For example, research using 19 years of footage from Taï found stable "social phenotypes" in 45 chimpanzees (Tkaczynski et al., 2020). Also, Rosati et al. (2020) utilised

78,000 hours of observations from 1995–2016 to investigate the social interactions of 21 male chimpanzees in Kibale National Park. The authors found that mutual friendships—into which more is invested, as indicated by longer and more equitable grooming bouts—increased with age whereas one-sided friendships decreased with age. These projects were only feasible given the presence of long-term observational data.

Similarly, the research presented in this thesis is only possible because of the long-term video data on the Bossou chimpanzees (see section 4.1.3, below). Bossou is the only site with a yearly video record (1988–2018) of known individuals habitually using stone tools in the same location during the same season, which allows for systematic ecologically and socially valid investigations of behavioural variability and social learning in the long-lived species (Kappeler et al., 2012; Matsuzawa, 2011a). This resource provides a rare opportunity to conduct longitudinal ontogenetic research and is thanks to the immense and sustained efforts of Tetsuro Matsuzawa as well as many field assistants and contributors over the decades.

4

LONG-TERM RESEARCH AT BOSSOU AND GENERAL RESEARCH METHODS

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The 25-year longitudinal research presented in this thesis focuses on the ontogeny of stone tool use in the Bossou chimpanzees. Prior to outlining the systematic collection of efficiency and social learning data, I will outline the field site, the video archive, and previous longitudinal research on the Bossou chimpanzees.

4.1 BOSSOU

Bossou has been recognised as an important chimpanzee field site since 1942, when French zoologist Maxime Lamotte led an expedition to explore the geography, flora, and fauna of the Guinean side of the Nimba Mountains (Humle, 2016; Kortlandt, 1986). Dutch primatologist Adriaan Kortlandt later conducted the first experimental research on the community in the early 1960s, with tests on anti-predator responses to stuffed leopards (Humle, 2016; Kortlandt, 1962).

Long-term field work in Bossou was started by Yukimaru Sugiyama from the Kyoto University Primate Research Institute, Japan, in November 1976 (Sugiyama & Koman, 1979a, 1979b). Tetsuro Matsuzawa joined the field site in February 1986, and commenced the longitudinal research on the nut-cracking behaviour of the community. The first field experiment (whereby experimental manipulations are performed in the natural setting) was conducted in February 1988 (Matsuzawa, 1994, 2011a). As such, the original research undertaken in Bossou has been ideologically and methodologically rooted in Japanese primatology, with the long-term observations and preconditional assumption of the non-uniqueness of culture to humans (Humle, 2016). Much of the subsequent research has been a hybrid of Japanese and Western primatology, with a combination of inductive and deductive reasoning being found in the questions posed and approaches used (Humle, 2016).

Bossou is the oldest long-term field site focused on the critically endangered West African chimpanzee species (the other being the Taï Chimpanzee Project) and also has the longest video record of West African chimpanzee behaviour (outlined in section 4.1.3). This makes

Bossou the ideal community to study the development of the skills required to use tools in the wild, and the source of individual variation in technological efficiency.

4.1.1 Bossou's Climate and Ecology

Bossou village is in the south-eastern Guinée Forestière region of the Republic of Guinea, close to the borders with Liberia and Côte d'Ivoire (7°38'71.7'N, 8°29'38.9'W). The region has a tropical wet seasonal climate, with two seasons: a short dry season (November–February) and a long wet season (March–October), with yearly temperatures ranging from 12°C–43°C and monthly precipitation ranging from 0–700 mm (Hockings et al., 2012; Humle, 2011a). Hills covered in primary and secondary forest, primarily consisting of terrestrial herbaceous vegetation, surround the village (see Figure 13 and Figure 14; Humle, 2011a). All of the primary forest (< 1 km^2) is located on Mont Gban, and largely consists of species including *Ficus mucuso* and *Cola cordifolia*, whereas the predominant secondary forest is comprised of species including oil palm and bush pineapple (*Myrianthus arboreus*; Humle, 2011a).

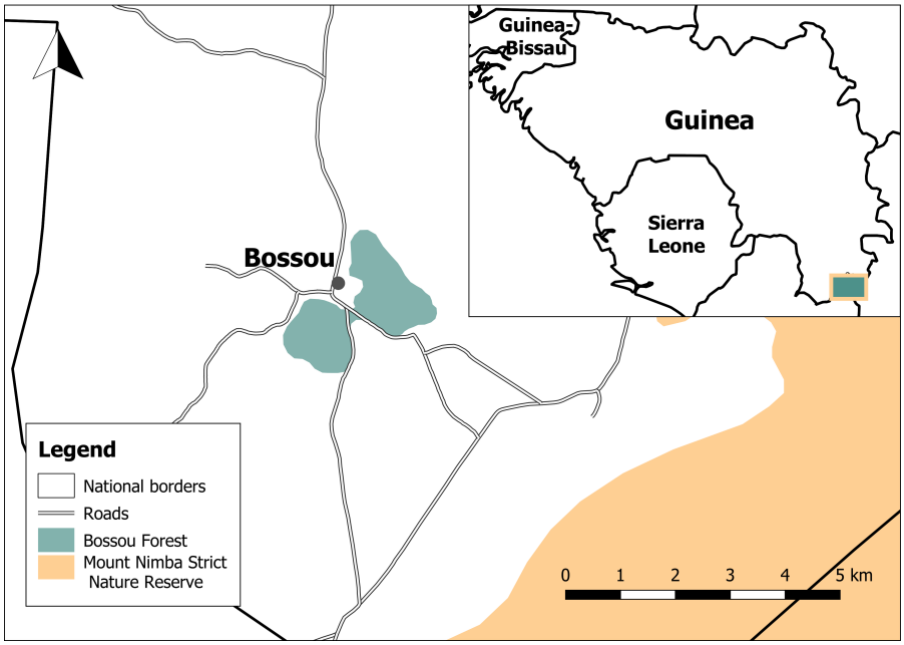


Figure 13. Map of Bossou forest and location in Guinea. Reprinted from "Landscaping the Behavioural Ecology of Primate Stone Tool Use," by Almeida-Warren, K., Didier Camara, H., Matsuzawa, T., and Carvalho, S., 2022, *International Journal of Primatology*. This work is licensed under CC BY 4.0.



***Figure 14*.** Photographs of Bossou village (top) and the surrounding forested and cultivated hills (bottom). Photograph credit: Katarina Almeida-Warren.

Bossou village's population is chiefly of the Manon ethnic group (Hockings et al., 2012), although there was a large influx of refugees into Bossou and the surrounding area during the Liberian civil war (Sugiyama & Fujita, 2011). The increased cultivation and construction that followed to accommodate the larger population resulted in significant deforestation and habitat degradation. The use of slash-and-burn agriculture is common in the area,

producing a mosaic habitat including guarded and abandoned cultivated fields and orchards (Hockings et al., 2009).

The chimpanzees neighbouring Bossou village ("the Bossou chimpanzees") reside in the primary and secondary forest, with a 15 km^2 home range and a 7 km^2 core area (Hockings et al., 2012). The chimpanzees are a totem animal for the Manon people, considered to be their ancestors reincarnated and hence have historically been protected (Matsuzawa, Humle, et al., 2011). Yet, by virtue of living in an anthropogenic landscape (Bryson-Morrison et al., 2016; Hockings et al., 2012), the chimpanzees encounter a variety of threats such as the construction of roads intercepting their home ranges and deforestation and degradation (Humle & Kormos, 2011). A 12 m wide road connecting the Guinea-Liberia border and Guinea's forested region dissects the village and chimpanzees' home range (Hockings, 2007). The road was expanded in December 2004, and is frequently used by large vehicles (Hockings, 2007). In fact, Wilson et al., (2014) noted that Bossou is the most intensely human-disturbed chimpanzee site.

4.1.2 The Bossou Chimpanzees

The Bossou community has always been relatively small, with 21 individuals being present in 1976 (Sugiyama & Koman, 1979b). Although the population size was always limited, it was within the normal range for chimpanzee populations (Wittig & Boesch, 2019). However, the community has been declining in size (see Figure 15), with only three chimpanzees currently remaining. A key cause of the population decline was the November 2003 flu-like epidemic which killed five chimpanzees, totalling more than a quarter of the population (Humle, 2011b). The population has not recovered since, further hindered by the geographically isolated location of the Bossou community, making immigration between groups by female chimpanzees a rare occurrence (Biro et al., 2006). In fact, although females have migrated out of Bossou, no female has entered the community for the entire duration it has been under investigation. Although the closest neighbouring

community, the Seringbara chimpanzees, are only 6 km away in the Nimba Mountains (7°37'50.0" N, 8°27'44.7" W), a stretch of savannah between the two communities impedes migration. This is despite the best efforts of the Green Corridor Project, which aimed to plant trees in this savannah to connect the communities (Matsuzawa, Ohashi, et al., 2011).

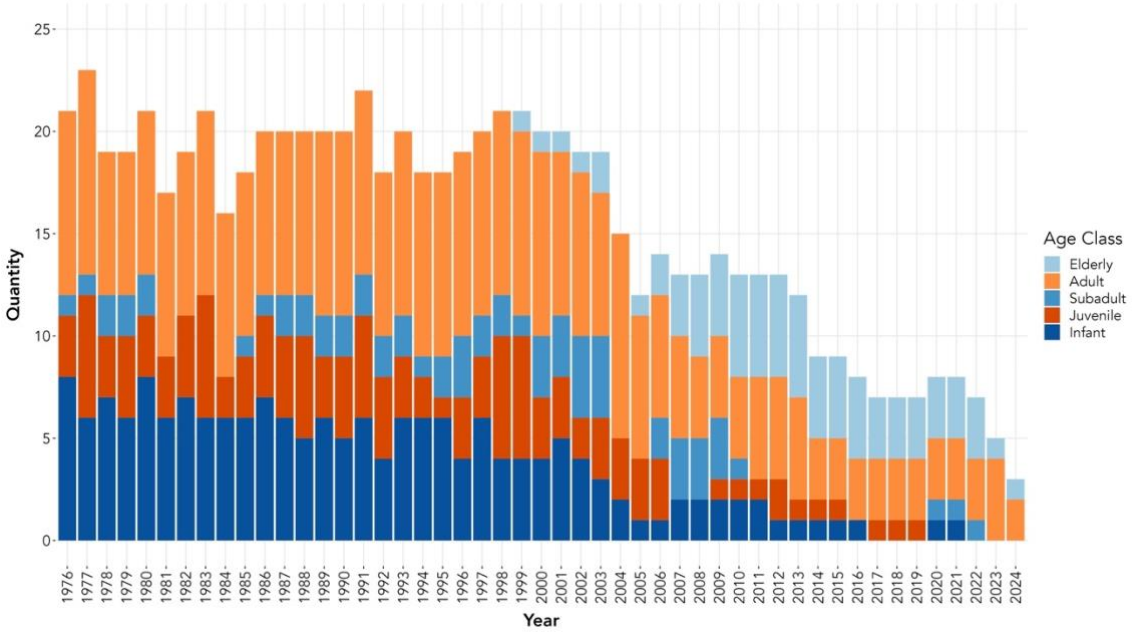


Figure 15. Demographics of the Bossou chimpanzee population from the founding of the field site to present. The number of infants (0–4 years old), juveniles (5–8 years old), subadults (9–12 years old), adult (13–48 years old), and elderly (49+ years old) are shown for each year. Figure reproduced from https://www.greencorridor.info/index.html.

The feeding ecology of the chimpanzees varies according to the season (Humle, 2011a). Fruit availability fluctuates throughout the year, with availability peaking from December–April and declining from May–November (Hockings et al., 2010). The chimpanzees eat over 200 plant species, culminating in 246 plant parts (Bryson-Morrison et al., 2020), as well as, for example, honey, ants (*Dorylus* sp., *Camponotus* sp., and *Oecophylla longinoda*), and adult termites (*Pseudacanthotermes* and *Macrotermes* sp.), but there are low rates of meat-consumption (Humle, 2011a). Crop-raiding of cultivated foods (17 varieties in total; Hockings, 2011) increases during periods of fruit scarcity (Hockings et al., 2009) and constitutes 8.8% of total feeding time (Hockings et al., 2010). Cultivated foods such as rice

pith (*Oryza* sp.) and maize (*Zea mays*) are geographically concentrated, and hence can be targeted for increased foraging efficiency (Hockings et al., 2009).

Oil palm (Manon name: *toun*) is a fundamental resource for the Bossou chimpanzees. It is naturally abundant in the region, with a density in the chimpanzees' core area of 7.2 oil palm trees per km^2 (Humle & Matsuzawa, 2004). The chimpanzees nest in oil palm trees and spend 23.9% of their feeding time during the rainy season eating oil palm parts, including the heart, petiole, fruit, and kernels (Humle, 2003).

Moreover, Yamakoshi (1998) found that cracking oil palm nuts is an important subsistence strategy, with it being one of three fallback strategies during periods of fruit scarcity, alongside oil palm pith and umbrella trees (*Musanga cecropioides*). However, further research is needed to confirm the role of necessity in the nut-cracking behaviour in Bossou, as alternative ecological explanations were not tested (Koops et al., 2014). Notwithstanding this, Yamakoshi (1998) observed that tools were used in 97.2% of instances of oil palm kernel foraging interactions, and simply biting the nut was attempted in only 2.8% of the kernel feeding time. This demonstrates the advantage of stone tool use for cracking nuts in this community.

4.1.3 The Bossou Archive

Since Tetsuro Matsuzawa's first field experiment in 1988, there have been yearly observations and recordings of the Bossou chimpanzees from within the "outdoor laboratory" (also known as the "Bureau")—a 7 m x 20 m clearing on Mont Gban which the chimpanzees pass through daily (7°38'41.5″ N, 8°29'50.0″ W; Biro et al., 2006; Carvalho et al., 2009; Matsuzawa, 1994, 2011a; Sousa et al., 2009). This has resulted in a long-term video archive of their behaviour, with a particular emphasis on their tool use (hereafter, "the Bossou archive"). In December 2009, a second experimental site located on Mont Guein, known as the "Salon", was established (7°38'39.2″ N 8°29'58.5″ W). No video from the Salon was used when collecting data on nut-cracking efficiency for this project to ensure

ecological variables were kept consistent across the data set. The list of Bossou chimpanzees found in the video archive can be found in Table S1 in Chapter 6.

The "laboratory" in "outdoor laboratory" highlights the experimental nature of the location, with the stones (with pre-established properties) and nuts being provisioned (Berdugo et al., 2023; Biro et al., 2006; Carvalho et al., 2009; Matsuzawa, 1994, 2011a). Despite the provisioning, the natural setting afforded by the outdoor laboratory increases the ecological and social validity of the emergent research findings (Matsuzawa, 2011a) as it protects against captivity bias, whereby the increased frequency and diversity of tool use in captive compared to wild chimpanzees results from, for example, more observation opportunities and time for practise (Haslam, 2013).

A grass screen along one edge of the clearing allowed for behavioural observations and video recordings to be relatively covert, although the chimpanzees were aware of the human presence (see Figure 16; Biro et al., 2006; Matsuzawa, 2011a). All observation sessions (7am–6pm; Biro et al., 2006) were videoed from multiple consistent positions using wide-, standard-, and zoom-angle lenses (Schofield et al., 2023). The tripod-mounted cameras were frequently panned and zoomed according to the individuals and behaviours of interest for researchers in given years (Schofield et al., 2019, 2023).



Figure 16. Photographs of observations at the outdoor laboratory. A camera records the behaviour of the chimpanzees present in the outdoor laboratory (A), whilst field researchers stand behind the grass screen (B). Photograph credit: Tetsuro Matsuzawa.

4.1.4 Previous Longitudinal Work from Bossou

Much of the previous research on the Bossou chimpanzees has made use of the long-term nature of the field site. For example, computational ethological research using 17 years of footage (amounting to 100 hours of video) from the Bossou archive established individual variation in association patterns over time, indicating differences in sociality among the Bossou chimpanzees (Schofield et al., 2023). Also, Rodrigues et al.'s (2022) research using data from three time periods, each a decade apart, found that communication occurred over twice as often during fusion than during fission and that such communication was more likely towards dominant individuals and non-kin.

On the technological behaviour of the Bossou chimpanzees, Humle's (2003) cross-sectional research on age-based variation in the efficiency of ant-dipping, nut-cracking, and pestle-pounding used data from 1995–2001. Results indicated that adults (> 11 years old) made more dips per minute and gathered more ants per minute than sub-adults (4–11 years old). Moreover, adults cracked more nuts per minute and required fewer strikes per nut than sub-adults, although there were no differences in the number of bad nuts (those with rotten kernels or where no kernel was extracted) cracked between the age classes. Adults and subadults did not differ in their pestle-pounding efficiency (total pounding rate, pounds per minute, and extraction time). Individuals who showed exclusive handedness in single-handed pestle-pounding were no more efficient than those who were non-exclusive, although they did spend more time extracting the crushed palm heart per extraction, suggesting they obtained more of the resource. Humle et al.'s (2009) subsequent research on the ontogeny of ant-dipping (detailed in section 2.2.4) used data from the Bossou wet season spanning 1997–2006.

Moreover, there is a history of longitudinal research on the development of stone tool use in Bossou, such as Inoue-Nakamura & Matsuzawa's (1997) research following three infants over four years, and Biro et al.'s (2003) 16-year study establishing the critical learning period and individual-level handedness (both discussed in sections 3.3.2 and 3.3.4).

This project furthers this by being the first to make use of a long-term video archive to address the developmental origins of *variation* in the nut-cracking behaviour in chimpanzees at the individual level. All previous research on the development of variation in technological behaviour has conducted primary field work (e.g., on chimpanzees: Estienne et al., 2019; Humle et al., 2009; Lonsdorf, 2005; Lonsdorf et al., 2004; and on long-tailed macaques: Tan, 2017), and often relied on cross-sectional research designs to compare the frequency and efficiency of tool use across individuals. Though primary fieldwork is beneficial as it allows the focal subjects to be continuously followed during an entire day, and contextual information (such as previous interactions) can be gathered alongside behavioural data, such work is constrained by time and resources, making longitudinal research spanning more than 3–4 years challenging. These issues are compounded by the fact that chimpanzees have slow life histories, meaning that tracking the same individuals across their lifetime requires access to a long-term field site.

As such, the Bossou archive is ideally suited for the present investigation as it allows for an ecologically valid, systematic, and in-depth longitudinal analysis of the ontogeny of stone tool use in Bossou across the lifespan (Biro et al., 2003, 2006; Matsuzawa, 2011a; Matsuzawa et al., 2001). It also completely avoids disturbance of wildlife and has minimal environmental impact.

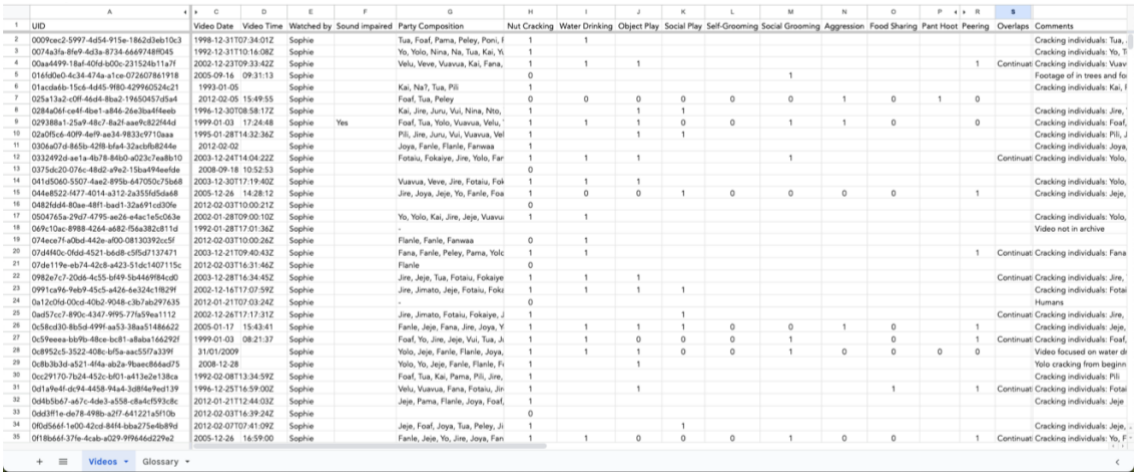
To date, the development and stability of variation in nut-cracking behaviour has not been investigated using long-term data. The research presented in this thesis is the first to take such a longitudinal approach to shed light on the mechanisms underpinning individual differences in behavioural efficiency in wild chimpanzees. This will contribute to theoretical understandings of the individual learning of social learning (Mesoudi et al., 2016), and the potential impact on energy allocation to other fitness-enhancing behaviours. Moreover, the research will further our knowledge of the social transmission of cultural traits in primates, which has implications for the field of technological and cultural evolution more broadly.

4.2 COLLECTING BEHAVIOURAL DATA FROM THE BOSSOU ARCHIVE

4.2.1 Video Data Systematisation

All original video tapes were organised and digitised by Daniel Schofield over the course of four months between February 2017 and April 2018 (Schofield, 2022). The complete 1988–2018 Bossou archive consists of 1840 files, totalling 1200 hours of footage and 11.44 terabytes (TB) of storage. Each year has an average of 31.5 hours of footage, with each video being 55 minutes long on average. Each video has a unique identifier (UID) made up of a random 128-bit string of numbers and lowercase letters (Schofield, 2022). All videos in the Bossou archive were stored on a 12 TB WD Elements External hard drive. Video files were formatted under Linux, so extFS for Mac 11 by Paragon Software (11.7.569; Copyright © 2023 Paragon Software GmbH) was used so the files could be read by MacOS.

Ahead of data collection, the entirety of the Bossou archive was catalogued in collaboration with Alexander Mielke (Queen Mary University of London; 59 videos reviewed by AM, 1190 videos reviewed by SB). This involved watching every video to determine the party composition in the outdoor laboratory, the presence of visible nut-cracking, and the names of any nut-cracking individuals (see Figure 17). From this cataloguing process, 966 of the 1185 videos from 1992–2017 were found to contain nut-cracking, totalling 832 hours of footage.



	A	C	D	E	F	G	H	I	J	K	L	M	N	O	P	R	S	
1	UID	Video Date	Video Time	Watched by	Sound impaired	Party Composition	Nut Cracking	Water Drinking	Object Play	Social Play	Self-Grooming	Social Grooming	Aggression	Food Sharing	Pant Hoot	Peering	Overlaps	Comments
2	009fcac2-5997-4d54-915e-1862d3eb10c3	1998-12-31T07:34:01Z		Sophie		Tua, Foaf, Pama, Peley, Poni, I	1	1										Cracking individuals: Tua, ,
3	0074a3fa-8fe9-4d3a-8734-6669748ff045	1992-12-31T10:16:08Z		Sophie		Yo, Yolo, Nina, Na, Tua, Kai, Yi	1											Cracking individuals: Yo, T
4	00aa4499-18af-40fd-b00c-231524b11a7f	2002-12-23T09:33:42Z		Sophie		Velu, Veve, Vuavua, Kai, Fana,	1	1	1							1	Continuat	Cracking individuals: Vuav
5	016fd0e0-4c34-474a-a1ce-072607861918	2005-09-16	09:31:13	Sophie			0					1						Footage of in trees and fo
6	01acda6b-15c6-4d45-9f80-429960524c21	1993-01-05		Sophie		Kai, Na?, Tua, Pli	1											Cracking individuals: Kai, I
7	025a13a2-c0ff-46d4-8ba2-19650457d5a4	2012-02-05	15:49:55	Sophie		Foaf, Tua, Peley	0	0	0	0	0	0	1	0	1	0		
8	0284a06f-ce4f-4be1-a846-26e3ba4f4eeb	1996-12-30T08:58:17Z		Sophie		Kai, Jire, Juru, Vui, Nina, Nto,	1		1	1								Cracking individuals: Jire,
9	02938ba1-25a9-48c7-8a2f-aaef9c822f4d	1999-01-03	17:24:48	Sophie	Yes	Foaf, Tua, Yolo, Vuavua, Velu,	1	1	1	0	0	1	1	0		0		Cracking individuals: Foaf,
10	02a0f5c6-40f9-4ef9-ae34-9833c9710aaa	1995-01-28T14:32:36Z		Sophie		Pli, Jire, Juru, Vui, Vuavua, Vel	1		1	1								Cracking individuals: Pli, J
11	0306a07d-865b-42f8-bfa4-32acbfb8244e	2012-02-02		Sophie		Joya, Fanle, Flanle, Fanwaa	1											Cracking individuals: Joya,
12	0332492d-ae1a-4b78-84b0-a023c7ea8b10	2003-12-24T14:04:22Z		Sophie		Fotaiu, Fokaiye, Jire, Yolo, Far	1	1	1			1					Continuat	Cracking individuals: Yolo,
13	0375dc20-076c-48d2-a9e2-15ba494eefde	2008-09-18	10:52:53	Sophie			0											
14	041d5060-5507-4ae2-895b-647050c75b68	2003-12-30T17:19:40Z		Sophie		Vuavua, Veve, Jire, Fotaiu, Fok	1	1	1									Cracking individuals: Yolo,
15	044e8522-f477-4014-a312-2a355fd5da68	2005-12-26	14:28:12	Sophie		Jire, Joya, Jeje, Yo, Fanle, Foa	1	0	0	1	0	0	0	0		1		Cracking individuals: Jeje,
16	0482fdd4-80ae-48f1-bad1-32a691cd30fe	2012-02-03T10:00:21Z		Sophie			0											
17	0504765a-29d7-4795-ae26-e4ac1e5c063e	2002-01-28T09:00:10Z		Sophie		Yo, Yolo, Kai, Jire, Jeje, Vuavu	1	1										Cracking individuals: Yolo,
18	069c10ac-8988-4264-a682-f56a382c811d	1992-01-28T17:01:36Z		Sophie		-												Video not in archive
19	074ece7f-a0bd-442e-af00-08130392cc5f	2012-02-03T10:00:26Z		Sophie		Flanle, Fanle, Fanwaa	0	1										
20	07d4f40c-0fdd-4521-b6d8-c5f5d7137471	2003-12-21T09:40:43Z		Sophie		Fana, Fanle, Peley, Pama, Yolo	1	1								1	Continuat	Cracking individuals: Fana
21	07de119e-eb74-42c8-a423-51dc1407115c	2012-02-03T16:31:46Z		Sophie		Flanle	0											
22	0982e7c7-20d6-4c55-bf49-5b446f984cd0	2003-12-28T16:34:45Z		Sophie		Jire, Jeje, Tua, Fotaiu, Fokaiye	1	1	1								Continuat	Cracking individuals: Jire,
23	0991ea96-9eb9-45c5-a426-6e324c1f829f	2002-12-16T17:07:59Z		Sophie		Jire, Jimato, Jeje, Fotaiu, Foku	1	1	1	1								Cracking individuals: Fotai
24	0a12c0fd-00cd-40b2-9048-c3b7ab297635	2012-01-21T07:03:24Z		Sophie		-	0											Humans
25	0ad57cc7-890c-4347-9f95-77fa59ea1112	2002-12-26T17:17:31Z		Sophie		Jire, Jimato, Fotaiu, Fokaiye, J	1			1							Continuat	Cracking individuals: Jire,
26	0c58cd30-8b5d-499f-aa53-38aa51486622	2005-01-17	15:43:41	Sophie		Fanle, Jeje, Fana, Jire, Joya, Y	1	1	1	1	0	0	1	0		1		Cracking individuals: Jeje,
27	0c59eeea-bb9b-48ce-bc81-a8aba166292f	1999-01-03	08:21:37	Sophie		Foaf, Yo, Jire, Jeje, Vui, Tua, Ji	1	1	0	0	0	1		0		1	Continuat	Cracking individuals: Foaf,
28	0c8952c5-3522-408c-bf5a-aac5577a339f	31/01/2009		Sophie		Yolo, Jeje, Fanle, Flanle, Joya,	1	1	1	0	0	1	0	0	0	0		Video focused on water di
29	0c8b3b3d-a521-4f4a-ab2a-9baec864ad75	2008-12-28		Sophie		Yolo, Yo, Jeje, Fanle, Flanle, Fi	1		1									Yolo cracking from beginn
30	0cc29170-7b24-452c-bf01-a413e2e138ca	1992-02-08T13:34:59Z		Sophie		Foaf, Tua, Kai, Pama, Pli, Jire,	1											Cracking individuals: Pli
31	0d1a9e4f-dc94-4458-94a4-3d8f4e9ed139	1998-12-25T16:59:00Z		Sophie		Velu, Vuavua, Fana, Fotaiu, Jir	1		1					1		1	Continuat	Cracking individuals: Fotai
32	0d4b5b67-a67c-4de3-a558-c8a4cf593c8c	2012-01-21T12:44:03Z		Sophie		Jeje, Pama, Flanle, Joya, Foaf,	1											Cracking individuals: Jeje
33	0dd3ff1e-de78-498b-a2f7-641221a5f10b	2012-02-03T16:39:24Z		Sophie			0											
34	0f0d566f-1e00-42cd-84f4-bba275e4b89d	2012-02-07T07:41:09Z		Sophie		Jeje, Foaf, Joya, Tua, Peley, Ji	1			1								Cracking individuals: Jeje,
35	0f18b66f-37fe-4cab-a029-99f646d229e2	2005-12-26	16:59:00	Sophie		Fanle, Jeje, Yo, Jire, Joya, Fan	1	1	0	0	0	1	0	0		1	Continuat	Cracking individuals: Yo, F

Figure 17. Screenshot of the catalogue of all videos in the Bossou archive in Google Sheets.

4.2.2 Piloting

Behavioural analysis was conducted using *Behavioural Observation Research Interactive Software* (BORIS v. 7.11.1)—a free, open-source software package for coding video observations, allowing for a fully customisable coding scheme (Friard & Gamba, 2016).

Prior to collecting the data, pilot research was conducted to familiarise myself with the BORIS interface and practise behavioural coding, refine the behavioural categories in the ethogram (outlined in 4.2.3), and familiarise myself with the Bossou chimpanzees to allow for accurate identification all individuals. During this time, I also collaborated with Daniel Schofield and the Visual Geometry Group, Department of Engineering Science, University of Oxford, to assist in the development of a model to automate the detection of nut-cracking strikes within the archive. This research was published in *Scientific Advances* (see Appendix A; Bain et al., 2021).

The pilot phase (outlined in Appendix B) was critical for ensuring and enhancing the feasibility, practicality, reliability, and validity of the project. Following its completion, Research Assistants were hired to act as hypothesis-blind, independent coders for the inter-rater reliability analyses. Research Assistants who had Windows operating systems used Linux Reader™ by DiskInternals to read the video files. Full details on the behavioural coding training they received can be found in Appendix C, and the analyses of the training data can be found in Appendix D.

4.2.3 Building on Existing Measures and Constructing Ethograms

To enable comparison with the published literature, established measurements of the behaviours of interest (e.g., efficiency, peering) were utilised and advanced.

Nut-cracking efficiency was originally measured by Boesch & Boesch (1984) as the mean number of hits per nut and the number of nuts cracked per minute. Humle (2003) extended this measure to include success rate, defined as the 'number of nuts, yielding an edible kernel, cracked per minute' (p. 286).

The present study used the measure of hits per nut (here, *strikes per nut*). As the camera in the video footage did not always focus on an individual for the entirety of their nut-cracking behaviour, the measure of nuts per minute was not appropriate. As such, a substitute measure of *bout duration* was used. A "bout" was defined as the continuous period of nut-cracking starting when the individual lifts the hammer stone to commence striking and ending when the hammer stone contacts the nut for the final time, involving the same hand, bodily posture, and nut (Neufuss et al., 2017). *Bout duration* measured the length of this continuous period (in seconds). Similarly, here *success rate* measured the proportion of bouts that ended in the whole and intact kernel being extracted ("successful"), the kernel being extracted but broken into multiple pieces ("smash"), and the kernel not being retrieved ("failed"). These reflect decreasing degrees of nut-cracking efficiency, as a smashed kernel takes longer to collect and consume than a whole kernel (Sirianni et al., 2019).

Two further measures of efficiency, which were previously used by Tan (2017) in Burmese long-tailed macaque stone tool use, were used: *displacement rate* and *tool switch rate*. *Displacement rate* (called "strike accuracy" by Tan, 2017) counted the number of times a hammer strike resulted in the nut being hit off the anvil. This indicates the frequency with which the kinetic energy needed to crack the nutshell is misjudged, which Bril et al. (2009) argued to be an important aspect of efficiency. *Tool switch rate* recorded the number of times the focal individual altered their tools whilst cracking nuts. Its inclusion was a proxy for assessing the quality of the tools being selected by the chimpanzees, which could not be controlled given the archival and observational nature of the research. This research is the first to apply both *displacement rate* and *tool switch rate* to chimpanzees.

Therefore, the measure of "efficiency" used in this project consisted of five separate components: *bout duration*, *strikes per nut*, *success rate*, *displacement rate*, and *tool switch rate*. Although distinct measures, I expected bout duration and strikes per nut to be positively correlated. However, these were expected to be perfectly correlated as bout

duration also encompasses components such as distraction. Also, the length of time to perform a single strike, and the amount of time between multiple strikes for the same nut, may also vary between individuals.

The complete definitions of the developmental measures can be found in Table 1 in Chapter 6. In orangutans, peering events are recorded if there is sustained close-range focus on a conspecific engaging in the target behaviour for at least 5 seconds (Schuppli et al., 2016). In Bossou, peering at older, knowledgeable nut-cracking conspecifics by young chimpanzees was previously characterised as an "observational episode", whereby the infant's face was orientated toward the model for ≥ 3 seconds from ≤ 1 metre away (Inoue-Nakamura & Matsuzawa, 1997). This definition was subsequently refined to require the fixed gaze to be on the model's hand or face for ≥ 3 unbroken seconds (Biro et al., 2003, 2006). However, the threshold of ≥ 3 unbroken seconds may be too conservative, as "checking" behaviours and moments of distraction intersecting the fixed gaze are neglected.

Given the importance of sustained attention in social learning (Coussi-Korbel & Fragaszy, 1995), the research in this thesis used a more liberal definition of peering: attentive watching of a knowledgeable conspecific. Moments of distraction did not stop a peering event being recorded; rather, they were themselves noted as occurring within the peering event. As such, a peering event could be of any length, as long as it occurred within a nut-cracking bout of a model (i.e., a peering event was never longer than the length of the model's bout). Also, as the tolerance of the model affects the ability to peer at close range (Coussi-Korbel & Fragaszy, 1995), being within 1 m of the model was not a necessary precondition to record a peering event. Instead, it was recorded as model tolerance to proximity.

See Table 4 for the ethogram of behaviours coded for this project. All data were collected in strict accordance with the relevant coding scheme (see Appendix E for the Efficiency Coding Scheme and Appendix F for the Development Coding Scheme).

Table 4. Ethogram of behaviours of interest.

Coding Scheme	Behavioural Category	Event Type	Definition
Efficiency	Start Bout	Point	The start of the continuous nut-cracking period. A bout will start soon after a new nut is placed on the anvil.
	End Bout	Point	The point when the continuous nut-cracking period finishes.
	Displacement	Point	A hammer strike results in the nut being hit off the anvil.
	Tool Switch	Point	The focal individual changes one or both parts of the tool composite (hammer or anvil) to a new tool or surface.
Development	Start Peering	Point	The start of the period when the focal subject's gaze is directly oriented towards a model's hand, arm, nut, or stone tool composite during a nut-cracking bout.
	End Peering	Point	When the focal subject's gaze is no longer oriented towards the model's hand or arm or towards the nut and stone tool composite.
	Start Opportunity	Point	When the focal's mother commences nut-cracking whilst the focal subject is in the outdoor laboratory.
	End Opportunity	Point	The focal's mother ceases to crack nuts whilst the focal subject is in the outdoor laboratory.
	Total Visibility	State	The continuous period of when the focal subject's mother is on camera whilst the focal subject is in the outdoor laboratory.

4.2.4 Data Collection in BORIS

For the main data collection, a BORIS project was created which allowed the ethogram and subject information to be established. The ethogram was built by adding "codes" to be annotated, with keyboard shortcuts allocated to each code to increase the speed of behavioural annotation. Codes that required additional information to be inputted were set as "point events" so that separate "modifiers" could be added to each event. Modifiers are attributes of behaviours that can only be inputted once the behaviour has been recorded. When a point event was recorded, the corresponding modifier checklist automatically appeared to input the additional relevant information (see Table 5). For example, when an *End Bout* event was recorded, the modifier pop-up would appear to document the *strikes*

per nut outcome of the bout for the *success rate* measure of efficiency and any *model tolerance* or *model intolerance* shown towards any learners attempting to peer during the bout (as shown in Figure 18, below). When the behavioural duration was of interest, but no modifiers were required, the code was set as a "state event".

Table 5. Modifiers used in BORIS for each coding scheme.

Coding Scheme	Behaviour	Modifier	Definition	Output options
Efficiency	Start Bout	Nut species	The nut species being cracked by the focal.	Single selection: Oil palm; Coula; Unknown
	End Bout	Complete bout	Whether or not the full bout was able to be recorded because of the video footage itself.	Single selection: Yes; No
		Number of strikes	The number of strikes performed by the focal individual on a nut in the whole nut-cracking bout.	Numerical: Observer inputs quantity
		Bout outcome	Outcome of the nut-cracking bout.	Single selection: Successful; Smash; Failed
		Learner	Whether or not there was a conspecific who was in their critical period (a "learner") present during the focal individual's nut-cracking bout.	Multiple selection: Peering; Interacting; Clinging and peering; Clinging; Present; Solo
		Maternal model	Whether or not the model is the learner's mother.	Single selection: None; Yes; No
		Model tolerance	Whether the model permitted any of the following learner behaviours within the nut-cracking bout.	Multiple selection: Not Applicable; Scrounge; Tool interaction; Model interaction; Tool re-use; Proximity
		Model intolerance	Whether the model expressed intolerance towards the learner.	Multiple selection: Not Applicable; Physical; Vocal
Development	Start Peering	Model name	The name of the individual the focal subject was peering	Single selection: Choice from list of names

		at during their nut-cracking bout.	
	Maternal model	Whether or not the model was the learner's mother.	Single selection: Yes; No
End Peering	Complete peering event	Whether or not the full peering episode was able to be recorded because of the video footage itself.	Single selection: Yes; No
	Whole bout	Whether or not the learner was peering for the whole nut-cracking bout.	Single selection: Unknown; Yes; No
	Model name	The name of the individual the focal subject was peering at during their nut-cracking bout.	Single selection: Choice from list of names
	Maternal model	Whether or not the model was the learner's mother.	Single selection: Yes; No
	Model tolerance	Whether or not the model permitted any of the following learner behaviours within the nut-cracking bout.	Multiple selection: Not Applicable; Scrounge; Tool interaction; Model interaction; Tool re-use; Proximity
	Model intolerance	Whether or not the model expressed intolerance towards the learner.	Multiple selection: Not Applicable; Physical; Vocal
End Opportunity	Complete opportunity	Whether or not the full opportunity was able to be recorded because of the video footage itself.	Single selection: Yes; No
	Learner behaviour	Which behaviour the infant was engaged in when their mother was cracking nuts.	Multiple selection: Solitary play; Social play; Object play; Behavioural Episode; Bout; Feeding; Drinking; Resting; Peering; Clinging; Unknown

	Scrounge events	How many times the focal subject took the kernel extracted by the maternal model to eat themselves. Only record these scrounge events where the focal subject took the kernel but *did not* peer at the nut-cracking bout	Numerical: Observer inputs quantity

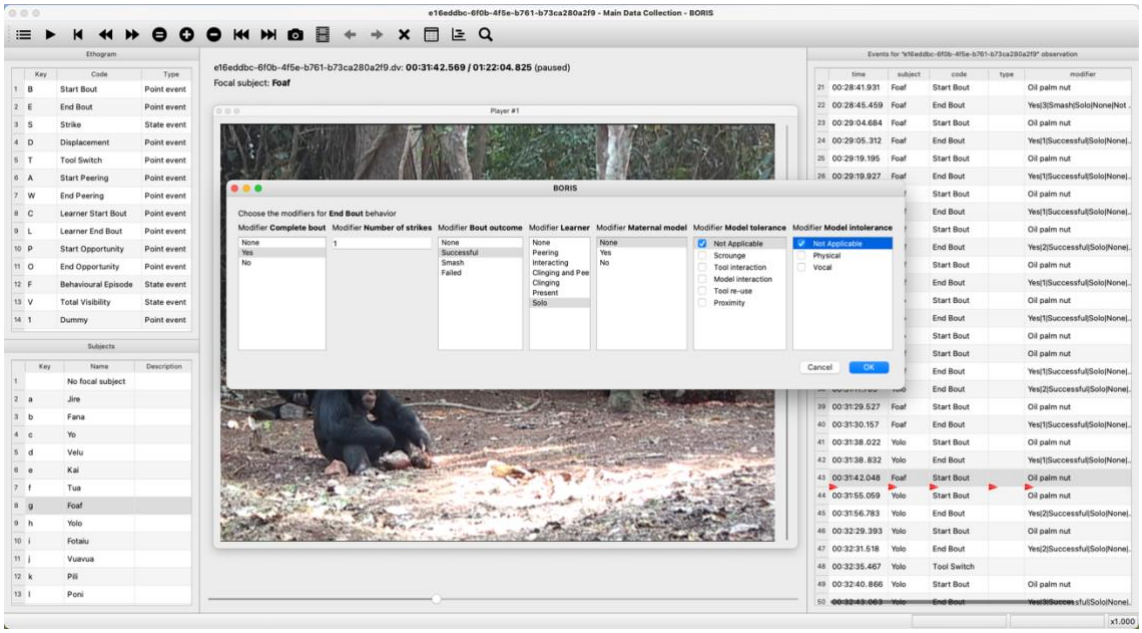


Figure 18. Screenshot of the "End Bout" modifier window in BORIS.

Once all behavioural codes and modifiers were inputted into the ethogram, the first video was uploaded as a new "observation" in BORIS. This video was selected using the protocol outlined in the Supplementary Information in Chapter 5. Where possible, the videos from the zoom- or standard-angle lens data were used for behavioural data collection. If the behaviour of interest was not visible, or became obscured, in this footage, the corresponding wide-angle lens footage was inputted to try to observe the complete behavioural sequence. If the behaviour was still incomplete or unobservable, the video was excluded (Berdugo et al., 2023). The UID of the video was used as the name for each observation, and the date and time of the original recording was inputted into BORIS.

Where behavioural duration was of interest, the exact frame in which the behaviour started and ended was recorded to increase the sensitivity of measurement. The data collection protocol of each study can be found in the corresponding manuscripts. The research presented here used the 1992–2017 footage, as the 1988–1991 footage lacked the quality required for accurate and reliable individual recognition and behavioural coding. The 2018 footage was excluded as recordings were exclusively taken from the Salon.

EMPIRICAL CONTRIBUTIONS

5

STABLE LONG-TERM INDIVIDUAL VARIATION IN CHIMPANZEE TECHNOLOGICAL EFFICIENCY

Under revision at *Nature Human Behaviour*

Stable long-term individual variation in chimpanzee technological efficiency

Berdugo, S.[1,2,3], Cohen, E.[1,2,4], Davis, A. J.[1,2,4], Matsuzawa, T.[5,6,7], & Carvalho, S. [2,3,8]

[1] Institute of Human Sciences, University of Oxford, Oxford, OX2 6NP, United Kingdom

[2] School of Anthropology and Museum Ethnography, University of Oxford, Oxford, OX2 6PE, United Kingdom

[3] ICArEHB, Interdisciplinary Center for Archaeology and Evolution of Human Behaviour FCHS, Universidade do Algarve, Faro 8005, Portugal

[4] Wadham College, University of Oxford, Oxford, OX1 3PN, United Kingdom

[5] Department of Pedagogy, Chubu Gakuin University, Gifu, 504-0837, Japan

[6] Division of the Humanities and Social Sciences, California Institute of Technology, Pasadena, CA 91125, United States

[7] College of Life Science, Northwest University, Xi'an 710069, China

[8] Department of Science, Gorongosa National Park, Sofala, Mozambique

Corresponding author

Sophie Berdugo, Institute of Human Sciences,

School of Anthropology and Museum Ethnography, University of Oxford,

Oxford, OX2 6PE, United Kingdom,

sophie.berdugo@anthro.ox.ac.uk

Abstract

Using tools to access hard-to-reach and high-quality resources initiated a fundamental adaptive shift in human and nonhuman primate cognitive and behavioural evolution. Variation in the efficiency of extracting calorie-rich and nutrient-dense resources, such as termites, honey, and nuts, directly impacts energy expenditure and potentially has significant repercussions for cultural transmission where model-based social learning strategies are employed during skill acquisition. Assessing variation in efficiency is key to understanding the evolution of complex behavioural traits in non-human primates. Yet, individual-level differences beyond age- and sex-class in primate extractive foraging efficiency have never been investigated. Here, we used 25 years (1992–2017) of video data of the Bossou chimpanzee community (Guinea), to investigate whether individual differences in nut-cracking efficiency exist across the life span of chimpanzees aged ≥ 6 years. Data from 3,882 oil palm nut-cracking bouts from over 800 hours of observation were collected. We found long-term stable and reliable individual differences in four (out of five) measures of efficiency. We found no sex effect, counter to previous research on a female bias in chimpanzee tool use. These life-long differences in extractive foraging impact daily energy budgets, which potentially have significant individual fitness and life history consequences. Additionally, the establishment of long-term individual variation in chimpanzee stone tool use has implications for interpreting archaeological records of hominins. Our findings highlight the importance of longitudinal data from long-term field sites when investigating underlying cognitive and behavioural diversity across individual lifespans and between populations.

Main

The importance of individual variation in cognition and behaviour is increasingly appreciated in research on nonhuman animals[1]. Such variation has ramifications at both the individual and population levels, with broader implications for life history[2–4], cultural evolution, and interpretations of the archaeological record[5] (see Figure 1). For example, a recent large-scale meta-analysis found individual variation in the migration timing of land-, water-, and seabirds, which impacts the breeding success and survival of a given migration[6].

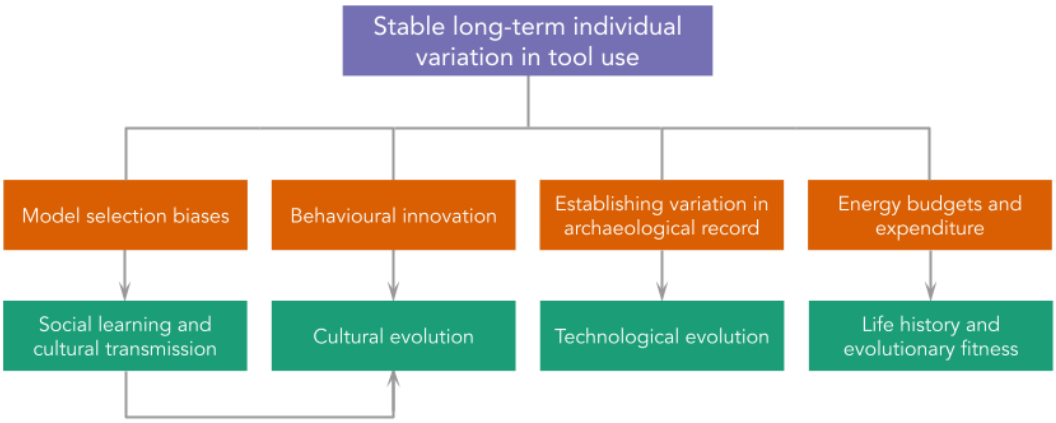


Figure 1. Implications of long-term stable individual variation in lithic technological behaviour.

Yet, although cognitive and behavioural variation has been reported, the research has mostly focused on one time-point for each individual or is limited to short time spans[1,7,8]. We argue that this approach does not reflect the true extent and patterns of variation within wild populations. Here, we aim to fill this knowledge gap and establish long-term stable and reliable individual differences in chimpanzee technological efficiency.

Firstly, persistent variation in the proficiency and efficiency with which individuals extract high quality resources from the environment directly impacts energy expenditure and individual fitness. An individual who is slow or inefficient at a given extractive-foraging technique relative to others in the population will have less time and energy for other fitness-enhancing tasks, thus incurring relative fitness costs[9]. This is particularly true for complex tool-assisted foraging tasks aimed at extracting high calorie resources, such as

wood-boring beetle larvae extraction by New Caledonian crows (*Corvus moneduloides*)[10], oyster-cracking by Burmese long-tailed macaques (*Macaca fascicularis aurea*)[7], and honey-dipping, termite-fishing, and nut-cracking by chimpanzees (*Pan troglodytes* spp.)[8,11,12]. Understanding the extent and causes of individual differences in extractive-foraging tasks is key for identifying variation in factors known to be relevant to evolutionary fitness.

Secondly, there is growing recognition that variation in tool use produces variation in the traces left in the archaeological record, particularly for the signatures produced during percussive behaviours[5]. For example, the number of unintentional flakes produced by wild bearded capuchin monkeys (*Sapajus libidinosus*) whilst cracking nuts with stones will vary according to the tool user, with the skill (or lack thereof) of the individual determining the frequency of mishits and subsequent flakes[13]. Investigating the archaeological signatures of known individuals can inform our understanding of hominin fossil sites and the context behind technological traces[5]. However, there is currently no research on individual-level variation in chimpanzee stone tool use, constituting a significant gap in our understanding of primate technological behaviour and its potential implications for hominin tool use.

Thirdly, identifying systematic variation in technological behaviour is crucial for investigating the factors influencing individual differences in behavioural acquisition via social learning. Indeed, although there are species-typical forms of social learning for particular skills, there is growing evidence that social learning mechanisms vary systematically across individuals[14]. Individual-level variation can develop from "individual learning of social learning", whereby differing experiences with previous social learning opportunities can result in different strategies being employed in the future, or the rate of learning being altered[14]. This phenotypic plasticity can facilitate faster adaptation to environmental changes, potentially having profound effects on evolutionary processes. This is particularly true where model selection and social learning biases guide behavioural acquisition[15–18]. For example, female migrant chimpanzees in the Taï National Park, Côte d'Ivoire, conform to the nut-cracking technique of their new community, even when their

previous technique was more efficient (in terms of strikes per nut and foraging speed)[17]. Therefore, assessing variation contributes to our understanding of cultural transmission, and the evolution of complex behavioural traits in primates[19].

Variation in technological behaviour in nonhuman primates is well established. For example, only male bearded capuchins use sticks as probing tools[20]. In chimpanzees, inter- and intra-population variation in tool use is found across all communities, including differences in technological strategies and efficiency. For example, ant-dipping tool lengths differ between the two neighbouring communities in the Kalinzu Forest, Uganda[21]. Chimpanzees in Loango National Park, Gabon, use different grip types to perforate nests during honey extraction, which is unaffected by the soil hardness[8]. In Gombe National Park, Tanzania, females commence termite-dipping earlier, engage in fishing more frequently, and retrieve more termites per dip than males[22].

In nut-cracking, females in Taï crack *Coula edulis* and *Panda oleosa* nuts more efficiently than males[23,24]. In contrast, males in Bossou, Guinea, select, use, and transport tools more frequently than females[25], and spend a significantly greater proportion of their time cracking oil palm (*Elaeis guineensis*) nuts compared to adult females[26]. The number of hits required to successfully open the nutshell was previously found to reach an asymptote in adulthood[27], and the movement of adult crackers was considered to be stereotyped[28]. However, this finding is constrained to a measure of strikes per nut, which is only one measure of nut-cracking efficiency. Moreover, no research has sought to replicate this finding, and the presence and stability of variation in nut-cracking behaviour has not been investigated using long-term data.

The combination of chimpanzees' long lifespans and the protracted early learning periods (hereafter, "ELP"; 3–5 years for nut-cracking in Bossou[28,29]) required to learn complex tool use necessitates longitudinal studies for assessing developmental trajectories and social learning. Although cross-sectional data can be useful for determining general developmental milestones, they do not allow for tests of individual variation across the

lifespan. By obscuring potential variability, this may result in generalisations about population- or species-typical development of a behavioural trait. Tracking the development of a skill across an individual's life course is key for understanding the ontogenetic processes involved—and potential variation in—fitness-enhancing traits, including extractive technologies.

This study assessed five measures (see Table 1) of post-early learning period (hereafter, "post-ELP") nut-cracking efficiency for 21 individuals present in a 25-year video archive of wild chimpanzees. "Post-ELP" was defined as chimpanzees aged 6 and over, based on the previously established period of social learning lasting until 5-years-old[28]. Data were gathered from all post-ELP individuals present in the archive for each year they were in the footage (see Figure 2). This research is the first to take such a longitudinal approach to investigate the presence of variation in primate extractive foraging. We also assess the *reliability* (internal consistency across efficiency measures) and *stability* (whether individual differences hold over time)[1] of such differences in a wild primate population.



Figure 2. Stills taken from the Bossou video archive. On the left, a six-year-old female chimpanzee, Fanle, cracks an oil palm nut in 2004, the year after finishing her early learning period. On the right, the same female chimpanzee cracks an oil palm nut in 2017 at the age of 20. Image credit: Tetsuro Matsuzawa.

Table 1. Definitions of efficiency measures.

Efficiency measure	Definition
Bout duration	The length of the continuous period (in seconds) of nut-cracking whereby the individual strikes a single nut on an anvil with a hammer stone involving the same hand, bodily posture, hand grip, and nut (the "bout")[53]. A bout starts in the frame when the hammer is lifted for the first strike of the nut on the anvil and ends in the frame when the hammer makes contact with the nut for the final time[43].
Strikes per nut	The number of hits required to open a single nut using a stone hammer and stone anvil[23].
Success rate	The outcome of the nut-cracking bout. A successful bout is one where the nut is cracked using the stone hammer and anvil composite and the full kernel is retrieved and eaten. A failed bout is one where the kernel is not retrieved or eaten by any individual. A smashed nut is one where the nut is opened but the kernel has broken into multiple pieces such that each piece must be eaten separately[34].
Displacement rate	The number of times a hammer strike resulted in the nut being displaced from the anvil[19].
Tool switch rate	The number of times the focal individual alters their tools whilst cracking nuts[19].

Results

Nut-cracking bouts. A total of 3,882 oil-palm nut-cracking bouts were recorded across 21 chimpanzees (12 females and 9 males; ages 6–60) over a 25-year period. Of these bouts, 318 (8.17%) ended in failure, 336 (8.66%) ended with a smashed kernel (which results in only partial retrieval of the kernel), and 3,228 (83.17%) ended in the successful retrieval of a whole kernel. Individuals' raw data can be found in Figures S1–5.

Individual variation. Analyses (see Tables S2–6) revealed that including random intercepts for individual chimpanzees improved model fit for all measures: *bout duration* ($\chi^2(1) = 369.49$, $p < 0.0001$), *strikes per nut* ($\chi^2(1) = 475.26$, $p < 0.0001$), *success rate* ($\chi^2(1) = 47.16$, $p < 0.0001$), *displacement rate* ($\chi^2(1) = 87.022$, $p < 0.0001$), and *tool switch rate* ($\chi^2(1) = 4.17$, $p < 0.05$). Age had a significant fixed effect on *bout duration* ($t = 7.724$, $p < 0.001$) and *strikes per nut* ($z = 8.51$, $p < 0.001$), *displacement rate* ($z = -2.40$, $p < 0.05$), and

tool switch rate (z = -2.462, p < 0.05). There was a significant fixed effect of sex for *tool switch rate* (z = -2.502, p < 0.05), but not for *bout duration* (t = 0.238, p > 0.05), *strikes per nut* (z = 0.407, p > 0.05), *success rate* (z = -0.1296, p > 0.05), or *displacement rate* (z = -1.029, p > 0.05).

Stability of variation. Next, we ranked the random intercepts for each multilevel model; random intercepts represent estimated individual-level effects on the outcome variable in the model. Lower ranks represent greater relative nut-cracking efficiency: fewer strikes per nut, shorter bout durations, and so on. Ranks ranged from 1 to 21 (the total number of individuals in the dataset, see Figure 3). Individual ranks for *bout duration*, *strikes per nut*, *success rate*, and *displacement rate* were moderately-strongly correlated (see Figure S6), meaning that when an individual was ranked highly on one of these measures, they also ranked highly in the other two. However, *tool switch rate* was only weakly–moderately correlated, suggesting it reflects a different underlying construct.

Reliability of variation. The consistency of the relative rank of each chimpanzee's random intercepts obtained in the *bout duration*, *strikes per nut*, *success rate*, and *displacement rate* models indicates reliable individual differences in nut-cracking efficiency. A two-way intra-class correlation (ICC) analysis also indicated good consistency, ICC(C,1) = 0.718, F(20,60) = 11.2, 0.543 < ICC < 0.857, p < 0.001. Including *tool switch rate* in the two-way ICC decreased the internal consistency of the efficiency measures (ICC(C,1) = 0.558, F(20,80) = 7.32, 0.366 < ICC < 0.751, p < 0.001), further suggesting it reflects a different underlying construct.

Inter-rater reliability. Two independent, hypothesis-blind coders reviewed 70 hours (8.41%) of footage for inter-coder reliability analyses. Unweighted Cohen's κ and ICC analyses indicated substantial–excellent agreement and consistency between coders (see Supplementary Information).

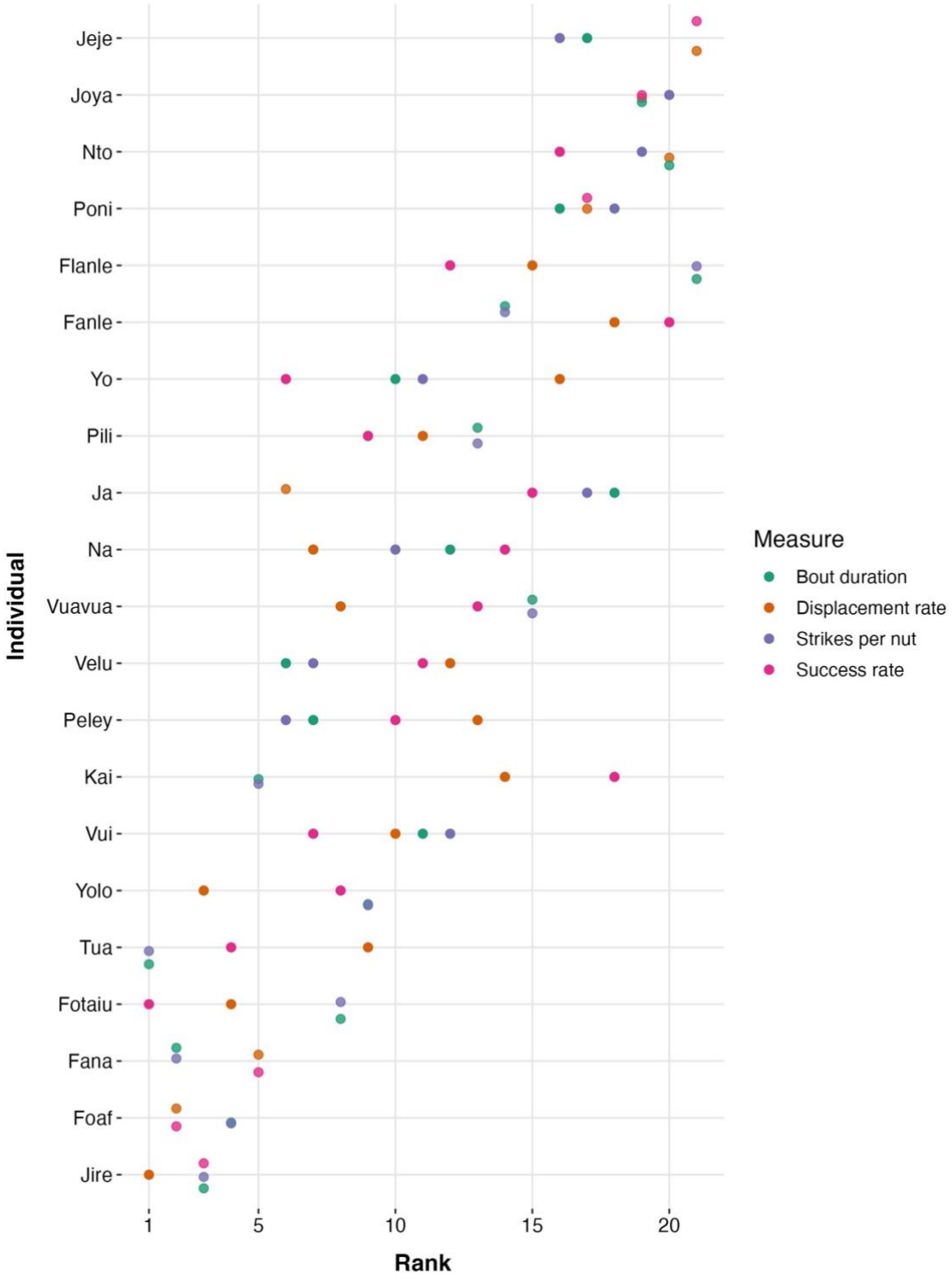


Figure 3. Ranked random intercepts from each multilevel model for the four stable and reliable measures of nut-cracking efficiency.

Discussion

This longitudinal research establishes the presence of stable and reliable systematic individual differences in the technological efficiency of wild chimpanzees. This finding highlights the necessity to move beyond exclusively using averages when investigating daily energy expenditure and activity budgets—factors with large implications for life history and foraging ecology in primates. Variation in time and energy expended for nut-cracking will produce variation in resource allocation to other fitness-enhancing traits. Thus, the extent of variation in nut-cracking efficiency may have large implications for other factors impacting survival and reproduction at the individual-level. In turn, this will inform our understanding of potential individual differences in social learning, which could directly impact the evolutionary fitness of individuals as well as the evolution of cultural traits.

Moreover, this research demonstrates individual variation in chimpanzee stone tool use. This finding reiterates the need to consider variation in the archaeological signatures left by percussive technological behaviours, with some individuals potentially contributing more to the record than others[5]. Research is now needed to ascertain the sources of this variation. A particular focus on the nut-cracking learning period is key given the known developmental drivers of variation in technological behaviour[22,30,31].

The ranked random intercepts for *bout duration*, *strikes per nut*, *success rate*, and *displacement rate* were closely correlated, but the raw scores were not perfectly correlated (r = 0.756 for the correlation between bout duration and strikes per nut). Indeed, longer bouts do not necessarily equate to more strikes per nut, with bout duration also being elongated from factors such as greater distractibility or taking longer pauses between strikes. This supports the view that each variable measured captured distinct aspects of "efficiency". Bout duration is an indicator of energy intake, as shorter bouts allow more kernels to be retrieved over the course of a feeding session. This may improve an individual's food security, as they will be at a competitive advantage compared to conspecifics in terms of access to more kernels. Also, longer bouts mean that the individual's

attention is focused on the task for a relatively longer period of time, such that there is reduced time to be allocated to fitness-enhancing behaviours such as defence, socialisation, and grooming. Conversely, the number of strikes required to retrieve the kernel and the success rate of the individual are indicators of energy expenditure relative to energy intake. The number of strikes per nut also dictates how convenient it is for the individual to use stones to open the nuts (rather than, for example, using their teeth or scrounging kernels), with more convenient techniques being favoured due to their increased efficiency[32]. For success rate, future research should investigate why chimpanzees choose to end a nut-cracking bout before the kernel is extracted and assess whether certain individuals stop bouts earlier than others (i.e., do not expend unnecessary energy and are hence more efficient).

Displacement rate measures the ability, or lack thereof, to judge the amount of kinetic energy required to strike a nut. Displacing the nut not only expends more energy than is required, but also elongates the bout duration, particularly if the individual has to travel to retrieve the nut. This also reduces the convenience of using tools. Primate archaeological research should investigate whether individuals with higher displacement rates are also more likely to fracture their stone tools, potentially resulting in unintentional flakes[33].

Furthermore, our results suggest that the number of times individuals adjust their tools during a bout reflects a different underlying process. Tool switch rate is a proxy measure for the individual's ability to select an efficient tool composite and position the stones in such a way to reduce the energetic effort required to extract the kernel. Given the importance of tool properties in determining the efficiency of the behaviour[17,34,35], learning to select the best tools is also an important aspect of successful foraging though our results suggest that it does not relate to how efficient the individual is at cracking nuts *per se*.

Unlike previous research, we found inconsistent effects of sex on technological efficiency. Sex had no significant effect on bout duration, strikes per nut, success rate, or displacement rate, but there was a significant effect on tool switch rate, with male chimpanzees switching

tools less frequently than female chimpanzees. This finding contradicts previous research establishing a female bias in technological behaviour across the genus *Pan*[36]. The lack of sex differences in this research may suggest that the mechanism(s) establishing a female bias in nut-cracking efficiency (measured as the mean number of strikes per nut and nuts per minute) in Taï[24] are not present in Bossou. However, it may be that the apparent female bias may be an artefact of short-term, cross-sectional analyses, and that the effect does not hold longitudinally. Further long-term research is required to determine whether this finding holds for other populations of nut-cracking chimpanzees.

Age had a significant fixed effect on bout duration, strikes per nut, displacement rate, and tool switch rate. Increasing age corresponds to longer bouts and more strikes per nut, which may reflect greater muscle weakness and the need for more rests in old age. Indeed, there have been many elderly chimpanzees in the Bossou population, with six individuals in the archive being aged 45+. Conversely, increasing age also corresponds to fewer nut displacements and fewer tool switches during bouts. This may reflect older individuals' greater proficiency at selecting appropriate tools, and better ability at judging the amount of kinetic energy required for each strike. More research is needed to assess the impact of old age on chimpanzee technological capabilities.

The presence of variation in the different measures of nut-cracking efficiency may indicate variation in the underlying cognitive and/or motor capacities. For example, longer bout durations may signify that certain individuals are prone to distraction rather than an individual being inherently less skilled. Therefore, the stable individual variation in nut-cracking efficiency may indicate that there are stable cognitive differences between the individuals, which potentially has implications for performance in other key fitness-enhancing behaviours. Future research should assess whether variation exists in other behaviours in the community to determine the extent of these cognitive differences.

The research is limited by two main points. First, despite the experimental nature of the outdoor laboratory, there are risks of confounding variables. For example, there is no

control for what else each individual has consumed in a day or levels of physical activity, both of which could influence motivations for cracking nuts[37]. However, footage selected for analysis was randomly sampled, representing a period of many years, in an attempt to amplify the signal-to-noise ratio.

Second, the outdoor laboratory is a field experimental set up, with nuts and stones being provisioned, and the experiments only occurring during the dry season (when there is high fruit availability). It could be argued that this decreases the validity of the findings and that they may not reflect the year-round nut-cracking efficiency of the individuals (such as in periods of low fruit availability). However, the nut-cracking that occurs in the outdoor laboratory is no different from the nut-cracking that the Bossou chimpanzees perform at the natural cracking site of Moblim (07°38'20.7'' N; 008°30'39.2'' W)[25]. Moreover, the location of the outdoor laboratory was specifically selected to be on Mont Gban's summit—the core of the home range for this chimpanzee community—to optimise the frequency of chimpanzees visiting the site[38,39]. This suggests that nut-cracking behaviour remains unchanged regardless of site location, reiterating the ecological validity of the outdoor laboratory.

Conclusion

This study systematically assessed individual differences in nut-cracking in the Bossou chimpanzees using a long-term video archive of 25 years to longitudinally investigate these differences. Our results establish stable and reliable individual-level differences across four measures of nut-cracking efficiency, shedding light on the underlying cognitive and behavioural diversity in the Bossou chimpanzees. This research contributes to a growing body of evidence finding stable cognitive abilities in great apes, and points to potential variation in the development of this extractive foraging skill. Future research should seek to establish the factors driving this individual variation.

Methods

Study site. Bossou is a village in south-eastern Guinea (7°38'71.7'N, 8°29'38.9'W), with a tropical wet seasonal climate and a predominant population of the Manon ethnic group[37,39]. The neighbouring chimpanzee community resides in primary and secondary forest, with a home range of 15 km^2, although their core area is 7 km^2. The chimpanzees in Bossou have been studied continuously since 1976, with 21 individuals being present[40]. The community has been declining in size since a flu-like outbreak in 2003[41]. The Bossou chimpanzees use a stone hammer-and-anvil composite to extract oil palm nuts[12,33,42], with individuals requiring complementary coordinated action of both hands to manoeuvre three objects (hammer, anvil, nut) during a nut-cracking bout[43].

Study materials. The Bossou chimpanzees have been recorded in every dry season (December–February) since 1988, resulting in a long-term video archive of their behaviour. Researchers observed and videoed the chimpanzees in the "outdoor laboratory"[28,38]—a 7 m x 20 m clearing in the core of the community's home range on Mont Gban (7°38'41.5″ N, 8°29'50.0″ W), which is passed through daily[28,33,38].

The outdoor laboratory is experimental in nature, with many of the available raw materials (with established weights and dimensions) and nuts being provisioned by the researchers[33]. Observations of behaviour within the outdoor laboratory occur from behind a grass screen along one edge of the clearing. All observation sessions were recorded using at least two standardised camera angles[33] (wide- and standard-angle lenses), optimising the viewing angles.

Data collection. Behavioural analysis was conducted using *Behavioural Observation Research Interactive Software* (BORIS, v. 7.11.1)[44]. Of the 1185 videos in the Bossou archive from 1992–2017, 966 videos contained visible nut-cracking bouts by at least one individual, amounting to 832 observation hours. Where possible, the videos from the standard-angle lens data were used for analysis. If behaviour was obscured in this footage, the equivalent video with the wide-angle lens was uploaded to attempt to observe the behaviour. If the

behaviour remained unobservable, the bout(s) were excluded. No footage was collected in 2001 or 2011, and so these are absent from the data set.

Data from each year each focal individual was present in the archive was collected. Multiple bouts (up to 20) per individual per year were recorded to establish the degree of within-individual variation in efficiency, while also producing more independent data points, allowing between-individual variation to be assessed. The full data collection protocol can be found in the Supplementary Information.

Ethical approval and permissions to conduct scientific research in the Bossou community were obtained by each contributor to the video archive from the Direction Générale de la Recherche Scientifique et de l'Innovation Technologique (DGERSIT) and the Institut de Recherche Environnementale de Bossou (IREB) in Guinea. The video footage was used with the permission of Tetsuro Matsuzawa and Kyoto University, Japan. No further ethical approval was required by the School of Anthropology and Museum Ethnography, University of Oxford, or the Social Science Division, University of Oxford.

Statistical analysis. All bouts where an infant was clinging to the focal subject were removed from analyses (n = 210), as this was exclusive to certain female chimpanzees (Fana, Fanle, Fotaiu, Jire, Pili, Velu, Vuavua, and Yo) and so could reduce the internal validity of the findings by altering the efficiency of these individuals. Removing these bouts ensured that all subjects were compared under equal circumstances. This left 3,672 bouts for analysis.

Only data for bouts in which a kernel was retrieved were included in the analyses for *bout duration* and *strikes per nut* (n = 3,367). Excluding the "Failed" bouts here ensured that the amount of time it took to access the energetic reward of the enclosed kernel was analysed. The full data set (n = 3,672) was analysed for *success rate*, *displacement rate*, and *tool switch rate*.

All analyses were performed using R (v. 4.3.2)[45] and RStudio (v. 2023.09.1+494) for MacOS. The significance level (α) was 0.05 for all analyses. Multilevel models were constructed to

test for individual differences in the five measures of efficiency. Individual chimpanzees comprised the level-two random factor, while age and sex were included as fixed effects. Simple models (without random effects) were constructed and compared against the multilevel models (see Tables S2–S6); ANOVAs were used to determine the model with the best fit. The ANOVAs (two-tailed) assessed whether including a random intercept for individual chimpanzees significantly decreased the model prediction error. The model with the smallest prediction error (according to AIC and -2-log-likelihood values) was selected for each of the five components of efficiency.

The linear mixed-effects model for *bout duration* was fitted using the *lme4*[46] and *lmerTest*[47] packages. Initially, a simple linear multilevel model (subject as a random intercept) was constructed, with age and sex as fixed effects. However, this model fit the data poorly, and so the normality of the outcome variable *bout duration* was assessed using a histogram. The data were found to be strongly right skewed, and so they were log transformed to normalise the distribution and correct for heteroskedasticity[48].

Given that the count data for *strikes per nut* did not contain zeros, zero-truncated poisson generalised linear (mixed) models (GL(M)Ms) were fitted using the truncated_poisson family in the *glmmTMB* package[49], with age and sex as fixed effects. However, the check_dispersion function from the *performance* package[50] detected overdispersion in the multilevel model (subject as a random intercept). As such, zero-truncated negative binomial GL(M)Ms were fitted with quadratic parameterisation.

As the data for *success rate* were ordinal, cumulative link models (CLMs) and cumulative link mixed models (CLMMs) were fitted using the *ordinal* package[51]. The 'outcome' factor was ordered to Failed, Smash, Successful, to account for the increasing degrees of efficiency with each increasing level of outcome[34]. The Hessian matrices were calculated for all models to allow the model summaries to be called. The number of quadrature points used in the adaptive Gauss-Hermite quadrature approximation was set to 7. Age was originally

included as a fixed effect but was removed as the model did not converge. Sex remained as a fixed effect.

Negative binomial GL(M)Ms were fitted for *displacement rate* and *tool switch rate* using the *glmmTMB* package. All models specified zero-inflation as being equal for all observations, given the substantial number of zeros in the data where an individual did not displace the nut (n = 2909) or switch their tools (n = 3308) in a bout.

The individuals' random intercepts were ranked for the *bout duration*, *strikes per nut*, *success rate*, *displacement rate*, and *tool switch rate* models, and a correlation matrix was constructed to determine whether they represent the same underlying construct. The two-way ICC used to assess the stability of individual variation was selected according to recommended guidelines[52].

Data availability

A minimum dataset can be found in the following public repository: https://github.com/arranjdavis/chimpanzee_nut_cracking_efficiency

Code availability

All analysis code needed to reproduce the results and figures reported in the paper and the Supplementary Information can be found in the following public repository: https://github.com/arranjdavis/chimpanzee_nut_cracking_efficiency

References

1. Bohn, M. *et al.* Great ape cognition is structured by stable cognitive abilities and predicted by developmental conditions. *Nat. Ecol. Evol.* (2023).
2. Pontzer, H. *et al.* Primate energy expenditure and life history. *Proc. Natl. Acad. Sci.* **111**, 1433–1437 (2014).
3. Kaplan, H. S., Hill, K., Lancaster, J. & Hurtado, A. M. A theory of human life history evolution: diet, intelligence, and longevity. *Evol. Anthropol.* **9**, 156–185 (2000).
4. Kraft, T. S. *et al.* The energetics of uniquely human subsistence strategies. *Science* **374**, (2021).
5. Pascual-Garrido, A., Carvalho, S. & Almeida-Warren, K. Primate archaeology 3.0. *Am. J. Biol. Anthropol.* 1–17 (2023).
6. Franklin, K. A. *et al.* Individual repeatability of avian migration phenology: A systematic review and meta-analysis. *J. Anim. Ecol.* **91**, 1416–1430 (2022).
7. Tan, A., Tan, S. H., Vyas, D., Malaivijitnond, S. & Gumert, M. D. There is more than one way to crack an oyster: identifying variation in Burmese long-tailed macaque (*Macaca fascicularis aurea*) stone-tool use. *PLoS One* **10**, e0124733 (2015).
8. Estienne, V., Stephens, C. & Boesch, C. Extraction of honey from underground bee nests by central African chimpanzees (*Pan troglodytes troglodytes*) in Loango National Park, Gabon: techniques and individual differences. *Am. J. Primatol.* **79**, e22672 (2017).
9. Biro, D., Haslam, M. & Rutz, C. Tool use as adaptation. *Philos. Trans. R. Soc. B* **368**, (2013).
10. Rutz, C. *et al.* The ecological significance of tool use in New Caledonian crows. *Science* **329**, 1523–1526 (2010).
11. Bessa, J., Hockings, K. J. & Biro, D. First evidence of chimpanzee extractive tool use in Cantanhez, Guinea-Bissau: cross-community variation in honey dipping. *Front. Ecol. Evol.* **9**, 1–14 (2021).
12. Matsuzawa, T. Stone tools for nut-cracking. in *The chimpanzees of Bossou and Nimba* (eds. Matsuzawa, T., Humle, T. & Sugiyama, Y.) 73–84 (Springer, 2011).
13. Luncz, L. V, Arroyo, A., Falótico, T., Quinn, P. & Proffitt, T. A primate model for the origin of flake technology. *J. Hum. Evol.* **171**, 103250 (2022).
14. Mesoudi, A., Chang, L., Dall, S. R. X. & Thornton, A. The evolution of individual and cultural variation in social learning. *Trends Ecol. Evol.* **31**, 215–225 (2016).

15. Henrich, J. & Gil-White, F. J. The evolution of prestige: freely conferred deference as a mechanism for enhancing the benefits of cultural transmission. *Evol. Hum. Behav.* **22**, 165–196 (2001).
16. Kendal, R. *et al.* Chimpanzees copy dominant and knowledgeable individuals: implications for cultural diversity. *Evol. Hum. Behav.* **36**, 65–72 (2015).
17. Luncz, L. V, Sirianni, G., Mundry, R. & Boesch, C. Costly culture: differences in nut-cracking efficiency between wild chimpanzee groups. *Anim. Behav.* **137**, 63–73 (2018).
18. Tan, A., Hemelrijk, C. K., Malaivijitnond, S. & Gumert, M. D. Young macaques (*Macaca fascicularis*) preferentially bias attention towards closer, older, and better tool users. *Anim. Cogn.* **21**, 551–5563 (2018).
19. Tan, A. From play to proficiency: the ontogeny of stone-tool use in coastal-foraging long-tailed macaques (*Macaca fascicularis*) from a comparative perception-action perspective. *J. Comp. Psychol.* **131**, 89–114 (2017).
20. Falótico, T., Bueno, C. Q. & Ottoni, E. B. Ontogeny and sex differences in object manipulation and probe tool use by wild tufted capuchin monkeys (*Sapajus libidinosus*). *Am. J. Primatol.* **83**, (2021).
21. Koops, K., Schöning, C., Isaji, M. & Hashimoto, C. Cultural differences in ant-dipping tool length between neighbouring chimpanzee communities at Kalinzu, Uganda. *Sci. Rep.* **5**, (2015).
22. Lonsdorf, E. V. Sex differences in the development of termite-fishing skills in the wild chimpanzees, *Pan troglodytes schweinfurthii*, of Gombe National Park, Tanzania. *Anim. Behav.* **70**, 673–683 (2005).
23. Boesch, C. & Boesch, H. Sex differences in the use of natural hammers by wild chimpanzees: a preliminary report. *J. Hum. Evol.* **10**, 585–593 (1981).
24. Boesch, C. & Boesch, H. Possible causes of sex differences in the use of natural hammers by wild chimpanzees. *J. Hum. Evol.* **13**, 415–440 (1984).
25. Carvalho, S., Cunha, E., Sousa, C. & Matsuzawa, T. Chaînes opératoires and resource-exploitation strategies in chimpanzee (*Pan troglodytes*) nut cracking. *J. Hum. Evol.* **55**, 148–163 (2008).
26. Bain, M. *et al.* Automated audiovisual behavior recognition in wild primates. *Sci. Adv.* **7**, eabi4883 (2021).
27. Biro, D., Sousa, C. & Matsuzawa, T. Ontogeny and cultural propagation of tool use by wild chimpanzees at Bossou, Guinea: case studies in nut cracking and leaf folding. in *Cognitive development in chimpanzees* (eds. Matsuzawa, T., Tomonaga, M. & Tanaka, M.) 476–506 (Springer, 2006).

28. Biro, D. *et al.* Cultural innovation and transmission of tool use in wild chimpanzees: evidence from field experiments. *Anim. Cogn.* **6**, 213–223 (2003).
29. Inoue-Nakamura, N. & Matsuzawa, T. Development of stone tool use by wild chimpanzees (*Pan troglodytes*). *J. Comp. Psychol.* **111**, 159–173 (1997).
30. Lonsdorf, E. V, Eberly, L. E. & Pusey, A. E. Sex differences in learning in chimpanzees. *Nat. Br. Commun.* **428**, 715–716 (2004).
31. Humle, T., Snowdon, C. T. & Matsuzawa, T. Social influences on ant-dipping acquisition in the wild chimpanzees (*Pan troglodytes verus*) of Bossou, Guinea, West Africa. *Anim. Cogn.* **12**, S37–S48 (2009).
32. Schofield, D., McGrew, W. C., Takahashi, A. & Hirata, S. Cumulative culture in nonhumans: overlooked findings from Japanese monkeys? *Primates* **59**, 113–122 (2018).
33. Carvalho, S., Biro, D., McGrew, W. C. & Matsuzawa, T. Tool-composite reuse in wild chimpanzees (*Pan troglodytes*): archaeologically invisible steps in the technological evolution of early hominins? *Anim. Cogn.* **12**, 103–114 (2009).
34. Sirianni, G., Luncz, L. V & Gratton, P. An energetic model of foraging optimization: wild chimpanzee hammer selection for nut-cracking. in *The chimpanzees of the Taï forest: 40 years of research* (eds. Boesch, C. & Wittig, R.) 104–124 (Cambridge University Press, 2019).
35. Schrauf, C., Call, J., Fuwa, K. & Hirata, S. Do chimpanzees use weight to select hammer tools? *PLoS One* **7**, 1–12 (2012).
36. Gruber, T., Clay, Z. & Zuberbühler, K. A comparison of bonobo and chimpanzee tool use: evidence for a female bias in the *Pan* lineage. *Anim. Behav.* **80**, 1023–1033 (2010).
37. Koops, K., Gaspard Soumah, A., van Leeuwen, K. L., Didier Camara, H. & Matsuzawa, T. Field experiments find no evidence that chimpanzee nut cracking can be independently innovated. *Nat. Hum. Behav.* **6**, 487–494 (2022).
38. Matsuzawa, T. Field experiments on use of stone tools by chimpanzees in the wild. in *Chimpanzee cultures* (eds. Wrangham, R. W., McGrew, W. C., De Waal, F. B. M. & Heltne, P. G.) 351–370 (Harvard University Press, 1994).
39. Matsuzawa, T. Field experiments of tool-use. in *The chimpanzees of Bossou and Nimba* (eds. Matsuzawa, T., Humle, T. & Sugiyama, Y.) 157–164 (Springer, 2011).
40. Sugiyama, Y. & Koman, J. Social structure and dynamics of wild chimpanzees at Bossou, Guinea. *Primates* **20**, 323–339 (1979).
41. Matsuzawa, T. & Humle, T. Bossou: 33 years. in *The chimpanzees of Bossou and Nimba* (eds. Matsuzawa, T., Humle, T. & Sugiyama, Y.) 3–10 (Springer, 2011).

42. Sugiyama, Y. & Koman, J. Tool-using and -making behaviour in wild chimpanzees at Bossou, Guinea. *Primates* **20**, 513–524 (1979).
43. Sugiyama, Y., Fushimi, T., Sakura, O. & Matsuzawa, T. Hand preference and tool use in wild chimpanzees. *Primates* **34**, 151–159 (1993).
44. Friard, O. & Gamba, M. BORIS: a free, versatile open-source event-logging software for video/audio coding and live observations. *Methods Ecol. Evol.* **7**, 1325–1330 (2016).
45. R Core Team. R: a language and environment for statistical computing. (2023).
46. Bates, D., Maechler, M., Bolker, B. & Walker, S. Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* **67**, 1–48 (2015).
47. Kuznetsova, A., Brockhoff, P. B. & Christensen, R. H. B. lmerTest package: tests in linear mixed effects models. *J. Stat. Softw.* **82**, 1–26 (2017).
48. Field, A., Miles, J. & Field, Z. *Discovering statistics using R*. (SAGE Publications, 2012).
49. Brooks, M. E. *et al.* glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *R J.* **9**, 378–400 (2017).
50. Lüdecke, D., Ben-Shachar, M. S., Patil, I. & Makowski, D. performance: an R package for assessment, comparison and testing of statistical models. *J. Open Source Softw.* **6**, 3139 (2021).
51. Christensen, R. H. B. ordinal - regression models for ordinal data. (2019).
52. Koo, T. K. & Li, M. Y. A guideline of selecting and reporting intraclass correlation coefficients for reliability research. *J. Chiropr. Med.* **15**, 155–163 (2016).
53. Neufuss, J., Humle, T., Cremaschi, A. & Kivell, T. L. Nut-cracking behaviour in wild-born, rehabilitated bonobos (*Pan paniscus*): a comprehensive study of hand-preference, hand grips and efficiency. *Am. J. Primatol.* **79**, e22589 (2017).

Acknowledgements

We thank the Direction Générale de la Recherche Scientifique et de l'Innovation Technologique (DGERSIT) and the Institut de Recherche Environnementale de Bossou (IREB) in Guinea for research authorisation. The video data for this research was provided by Tetsuro Matsuzawa and Kyoto University, Japan. The original video archive was digitised, organised, and systematised by Daniel Schofield, Department of Engineering Science, University of Oxford. Special thanks to all the field researchers and assistants at Bossou, specifically Henry Didier Camara, Cé Vincent Mami, Gouanou Zogbila, Boniface Zogbila, Jules Doré, Guana Goumy, Tino Camara, Pascal Goumy, Paquílé Cherif, Jiles Gondo Doré, and Marcel Doré. Thank you to all the researchers who contributed to the Bossou archive since its inception. Thank you to Alexander Mielke (Queen Mary University of London) for help cataloguing the Bossou video archive. Thank you to Dora Biro and Katarina Almeida-Warren for feedback. Thank you to Zhangzhuoran Dai and Victoire Martignac for being independent, hypothesis-blind coders for the inter-rater reliability analyses.

Author contributions

S.B. conceived of the study, designed and coordinated the study, collected data, analysed and visualised the data, and wrote the manuscript. **E.C.** provided supervision, participated in the design of the study, and commented on the manuscript. **A.J.D.** analysed and visualised the data and commented on the manuscript. **T.M.** collected the original data set and commented on the manuscript. **S.C.** collected the original data set, provided supervision, participated in the design of the study, and commented on the manuscript.

Funding

This research was supported by the Clarendon Fund (University of Oxford, UK), Keble College Sloane-Robinson Clarendon Scholarship (University of Oxford, UK), the Boise Trust Fund (University of Oxford, UK) to **S.B.**, and by the Ministry of Education, Culture, Sports, Science, and Technology (MEXT), Japan, (grant nos. 07102010, 12002009, 16002001, 20002001, 24000001, and 16H06283) to **T.M.**. The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Competing interests

The authors declare no competing interests.

Supplementary information is available for this paper.

Correspondence and requests for materials should be addressed to Sophie Berdugo.

Supplementary Information

Data collection protocol

First, all available footage was systematically reviewed to ascertain the party composition in each video, and verify which chimpanzees were visible cracking nuts in the footage. Following this, the videos' unique identifiers (UIDs) for each year were placed into ascending order and allocated an integer code starting from one, incrementally increasing by one. Vectors for each focal individual in each year were constructed in RMarkdown[1], each comprising the code for each video the individual was nut-cracking. Each vector was sampled without replacement to create a random order of video codes for all individuals. A seed was set to make the sequence of random codes replicable.

From this process, it became apparent that some individuals in the community (for example, Velu and Fana) were present and nut-cracking in the footage considerably less frequently than the other community members. To reduce potential bias introduced from the varying sample sizes for each subject, data from all nut-cracking bouts for the rare individuals (defined as being present and having observable nut-cracking bouts in ≤ 25% of videos for a given year) were collected. Where other chimpanzees had observable nut-cracking bouts in this footage, data from their bouts were also collected. This allowed for the effect of seasonality on nut hardness to be partially controlled. Thereafter, the videos were selected from the randomly ordered vectors (present and nut-cracking in > 25% of videos for a given year), starting from the least common of the remaining chimpanzees. This process continued until at least 20 nut-cracking bouts had been recorded for each individual.

Data from each year each individual was present in the archive was collected. Multiple bouts per individual per year were recorded to establish the degree of within-individual variation in efficiency, while also producing more independent data points, allowing between-individual variation to be assessed. This reduced the sampling error and random variation found between years, and hence amplified the signal-to-noise ratio. This was to ensure that the data collected were reliable, and representative of the true behaviour of the group.

Lastly, to ensure the measures of efficiency were recorded accurately, only bouts which were clearly visible (i.e., observable) were coded. Visible bouts were those where the focal individual was facing the camera and the nut, hammer, and anvil could be seen, and those where the individual was not directly facing the camera, but the nut, hammer, and anvil could be seen. At the end of each bout, whether to not the entirety of the bout could be observed was recorded. Incomplete bouts were removed prior to analysis. This reduced the risk of systematic bias being introduced into the sampling procedure by the recording period ending prior to the termination of the behaviour, or because the focal subject became occluded[2].

Subject information

Table S1. Focal subject information, with the years that they were observed cracking nuts in the Bossou archive during their post-learning period.

Subject	Sex	Nut-cracking hand	Observation years	Age (years)	Bouts observed
Fana	F	Right*	1992–2017	36–60	386
Jire	F	Left	1992–2017	34–59	346
Yo	F	Left	1992–2016	32–56	347
Tua	M	Left	1992–2012	35–55	338
Velu	F	Right	1992–2015	33–55	248
Kai	F	Right	1992–2002	42–52	164
Foaf	M	Right	1992–2017	12–37	416
Fanle	F	Right	2004–2017	6–20	234
Jeje	M	Left	2004–2017	7–20	236
Yolo	M	Left	1998–2009	6–17	208
Peley	M	Left	2005–2012	6–14	133
Pili	F	Right	1993–2000	6–13	102
Vui	M	Left	1992–1999	6–13	123
Vuavua	F	Left	1998–2004	6–12	106
Fotaiu	F	Right	1998–2003	6–11	90
Na	M	Right	1992–1996	7–11	82
Ja	F	Right	1992–1993	9–10	22
Poni	M	Right	2000–2002	7–9	41
Joya	F	Left	2010–2012	6–8	25
Flanle	M	Left	2014	6	14
Nto	F	Right	2000	6	11

Note: * = Switched to her right hand after her left arm became paralysed in 1996.

Model outputs

Table S2. Simple and multilevel model outputs for log bout duration efficiency measure.

	Log bout duration			**Log bout duration**		
Predictors	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*
(Intercept)	1.21	1.11–1.30	**<0.001**	0.59	0.18–1.01	**0.005**
Age	-0.01	-0.01–-0.00	**<0.001**	0.02	0.02–0.03	**<0.001**
Sex [Male]	-0.35	-0.42–-0.27	**<0.001**	0.07	-0.53–0.67	0.812
Random Effects						
σ^2				0.94		
τ_{00}				0.46 $_{\text{Subject}}$		
ICC				0.33		
N				21 $_{\text{Subject}}$		
Observations	3367			3367		
R^2 / R^2 adjusted	0.023 / 0.022			0.086 / 0.387		

Note: The confidence intervals are calculated using the standard error for the fixed effects. The random effects residual variance (σ^2) and intercept variance (τ_{00}) are presented.

Table S3. Zero-truncated negative binomial simple and multilevel model outputs for strikes per nut efficiency measure.

	Strikes per nut			**Strikes per nut**		
Predictors	*Incidence Rate Ratios*	*CI*	*p*	*Incidence Rate Ratios*	*CI*	*p*
(Intercept)	3.04	2.76–3.34	**<0.001**	1.68	1.14–2.47	**0.008**
Age	1.00	1.00–1.00	0.268	1.02	1.02–1.03	**<0.001**
Sex [Male]	0.71	0.66–0.77	**<0.001**	1.12	0.65–1.94	0.684
Random Effects						
σ^2				0.49		
τ_{00}				$0.39_{Subject}$		
ICC				0.44		
N				$21_{Subject}$		
Observations	3367			3367		
R^2 conditional / R^2 marginal	NA / 0.028			0.150 / 0.525		

Note: The confidence intervals are calculated using the standard error for the fixed effects. The random effects residual variance (σ^2) and intercept variance (τ_{00}) are presented.

Table S4. Cumulative link simple and multilevel model outputs for success rate efficiency measure.

	Success rate			**Success rate**		
Predictors	*Odds Ratios*	*CI*	*p*	*Odds Ratios*	*CI*	*p*
Failed|Smash	0.09	0.08–0.10	**<0.001**	0.09	0.07–0.12	**<0.001**
Smash|Successful	0.20	0.18–0.23	**<0.001**	0.21	0.17–0.27	**<0.001**
Sex [Male]	0.96	0.81–1.14	0.641	0.98	0.67–1.43	0.897
N				21_{Subject}		
Observations	3672			3672		
R^2 Nagelkerke	0.000			NA		

Table S5. Simple and multilevel zero-inflated negative binomial model outputs for displacement rate efficiency measure.

	Displacement rate			**Displacement rate**		
Predictors	*Incidence Rate Ratios*	*CI*	*p*	*Incidence Rate Ratios*	*CI*	*p*
(Intercept)	0.56	0.47–0.65	**<0.001**	0.43	0.30–0.62	**<0.001**
(Intercept)	0.56	0.47–0.65	**<0.001**	1.51	1.38–1.69	
Age	0.98	0.98–0.98	**<0.001**	0.99	0.98–1.00	**0.016**
Sex [Male]	0.79	0.68–0.92	**0.002**	0.81	0.54–1.21	0.303
(Intercept)	1.60	1.45–1.80		0.43	0.30–0.62	**<0.001**
(Intercept)	1.60	1.45–1.80		1.51	1.38–1.69	
Zero-Inflated Model						
(Intercept)	0.00	0.00–Inf	0.994	0.00	0.00–Inf	0.993
Random Effects						
σ^2				1.68		
τ_{00}				0.16 $_{\text{Subject}}$		
ICC				0.09		
N				21 $_{\text{Subject}}$		
Observations	3672			3672		
R^2 conditional / R^2 marginal	NA / 0.056			0.020 / 0.104		

Note: The confidence intervals are calculated using the standard error for the fixed effects. The random effects residual variance (σ^2) and intercept variance (τ_{00}) are presented.

Table S6. Simple and multilevel zero-inflated negative binomial model outputs for tool switch rate efficiency measure.

	Tool switch rate			**Tool switch rate**		
Predictors	*Incidence Rate Ratios*	*CI*	*p*	*Incidence Rate Ratios*	*CI*	*p*
(Intercept)	0.19	0.15–0.24	**<0.001**	0.18	0.14–0.25	**<0.001**
(Intercept)	0.19	0.15–0.24	**<0.001**	1.32	1.21–1.50	
Age	0.99	0.98–1.00	**0.002**	0.99	0.98–1.00	**0.014**
Sex [Male]	0.66	0.53–0.83	**<0.001**	0.68	0.50–0.92	**0.012**
(Intercept)	1.33	1.22–1.51		0.18	0.14–0.25	**<0.001**
(Intercept)	1.33	1.22–1.51		1.32	1.21–1.50	
Zero-Inflated Model						
(Intercept)	0.00	0.00–Inf	0.995	0.00	0.00–Inf	0.995
Random Effects						
σ^2				2.43		
τ_{00}				0.04 $_{\text{Subject}}$		
ICC				0.02		
N				21 $_{\text{Subject}}$		
Observations	3672			3672		
R^2 conditional/ R^2 marginal	NA / 0.017			0.016 / 0.031		

Note: The confidence intervals are calculated using the standard error for the fixed effects. The random effects residual variance (σ^2) and intercept variance (τ_{00}) are presented.

Inter-rater reliability

Two independent, hypothesis-blind coders were recruited to test the between-observer reliability of the five efficiency components. This took place following the pilot research to ensure that 1) the coding scheme was finalised prior to the main data collection, and 2) that the coding scheme was consistent throughout the investigation, as any ambiguities in the behavioural category definitions were clarified *a priori*. This was important for reducing potential disagreement, and hence increasing reliability, between coders.

Both independent coders received thorough training for using the coding scheme and the BORIS software. Thereafter there was no consultation between coders, although the identity of the individuals in the videos were provided to assist with the accuracy of the behavioural coding.

The videos for reliability analysis were randomly selected to reduce the risk of bias. A combined total of 70 hours of observation was completed by the independent coders.

Cohen's κ was calculated to determine the extent of agreement between coders for *success rate* as the measure was categorical. All statements of the strength of the agreement between the coders are in accordance with standardised benchmarks[3].

Numerical data were compared using intraclass correlations (ICCs). Here, two-way random-effects models were used. The type was selected to be "single rater" since measurements were not averaged across the *k* number of raters. Finally, 'definition' varies depending on the variable. *Strikes per nut*, *displacement rate*, and *tool switch rate* were selected as "absolute agreement" to check if scores matched exactly across coders. *Bout duration* was selected as "consistency" to determine the extent to allow for systematic error[4]. All statements of the strength of the agreement between the coders are in accordance with standardised guidelines[4].

Analyses were performed using the *irr* package[5]. ICC scores to assess the absolute agreement between the three raters can be found in Table S7. For *bout outcome*, the agreement between the three coders was substantial, $\kappa = 0.771$, and greater than what

would be expected by chance, z = 19.5, p <0.001. For *bout duration*, a single-rater, consistency, two-way model ICC analysis found ICC(C,1) = 0.991, F(424,424) = 214, 0.989 < ICC < 0.992, p < 0.001, indicating excellent consistency.

Table S7. ICC calculations using single-rating, absolute agreement, two-way random-effects models.

		95% Confidence Interval		F Test with True Value 0			
	ICC	Lower bound	Upper bound	Value	*df1*	*df*2	Sig.
Strikes per nut	0.986	0.984	0.989	147	424	424	**<0.001**
Displacement rate	0.893	0.872	0.91	17.6	424	424	**<0.001**
Tool switch rate	0.708	0.652	0.755	6.03	424	305	**<0.001**

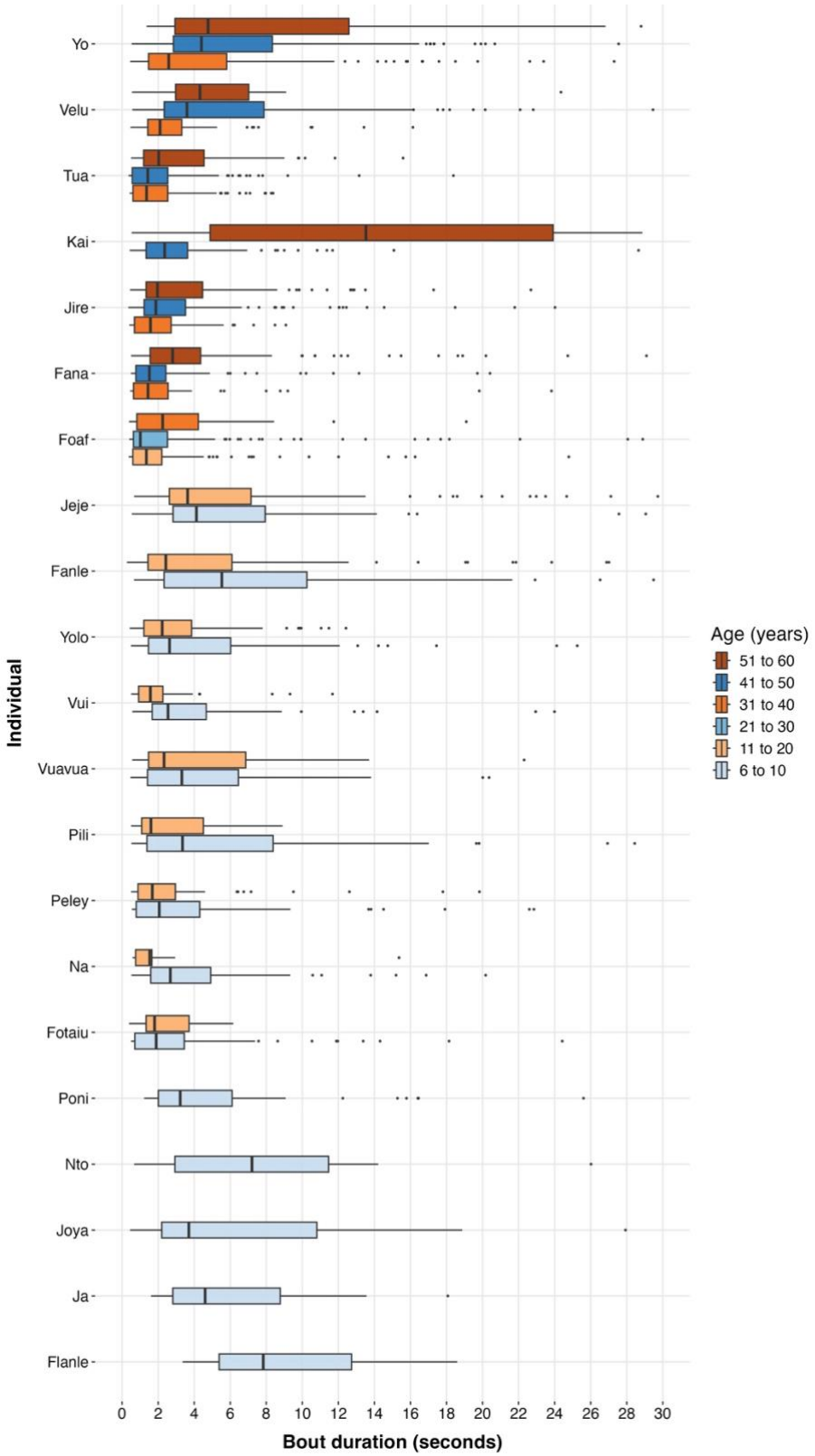


Figure S1. Stacked boxplots illustrating the intra-individual development of nut-cracking bout duration (in seconds) for each age class the chimpanzee is visible in the archive after their early learning period (aged 6 years and older). Where the chimpanzee was in the video archive over multiple age classes, older ages are stacked on top of younger age classes.
Note: Boxplots show the lower quartile, median, and upper quartile of values for each age class for each individual. The whiskers show the minimum and maximum values, and dots show the outliers.

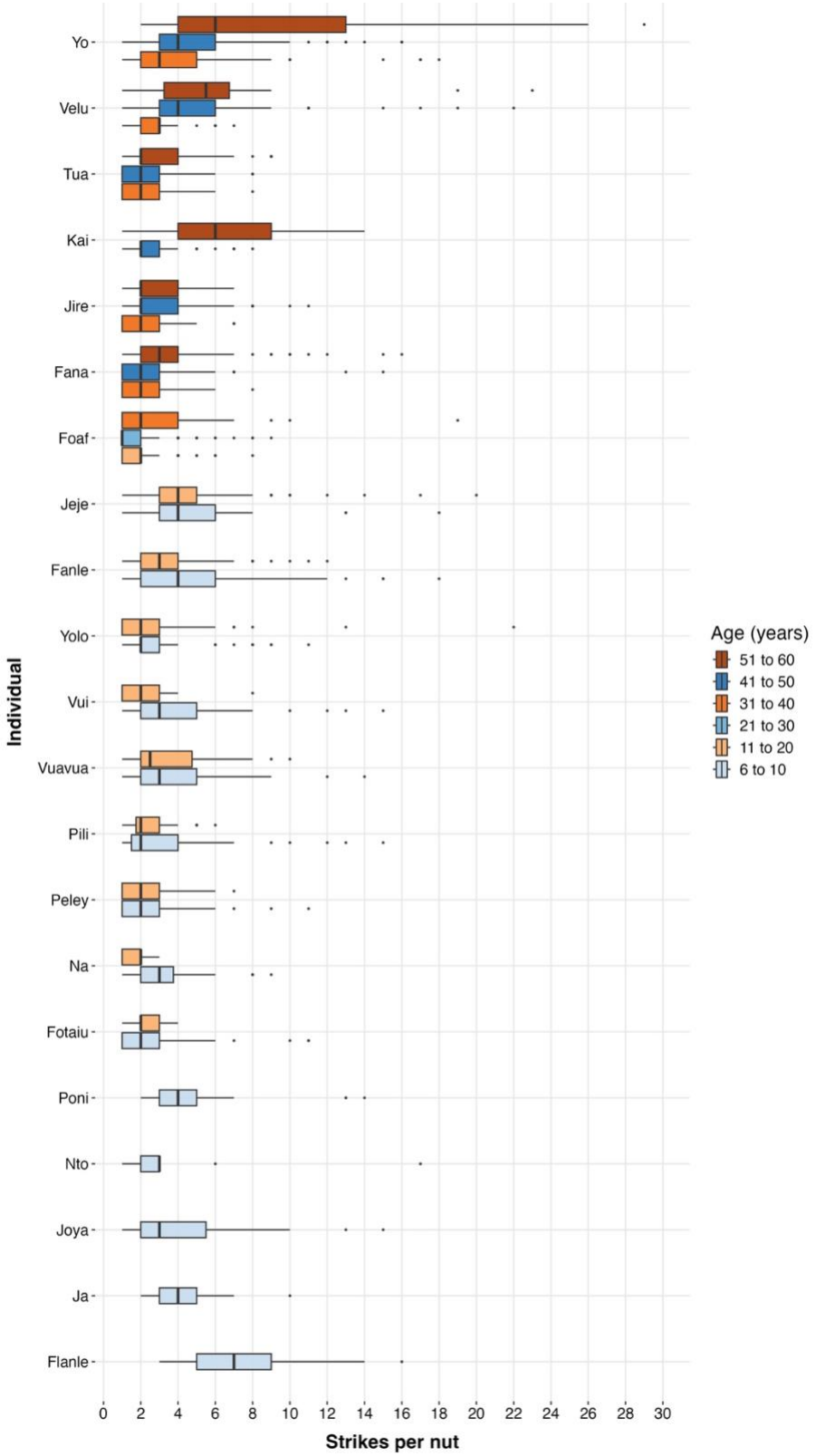


Figure S2. Stacked boxplots illustrating the intra-individual development of nut-cracking strikes per nut for each age class the chimpanzee is visible in the archive after their early learning period (aged 6 years and older). Where the chimpanzee was in the video archive over multiple age classes, older ages are stacked on top of younger age classes.
Note: Boxplots show the lower quartile, median, and upper quartile of values for each age class for each individual. The whiskers show the minimum and maximum values, and dots show the outliers.

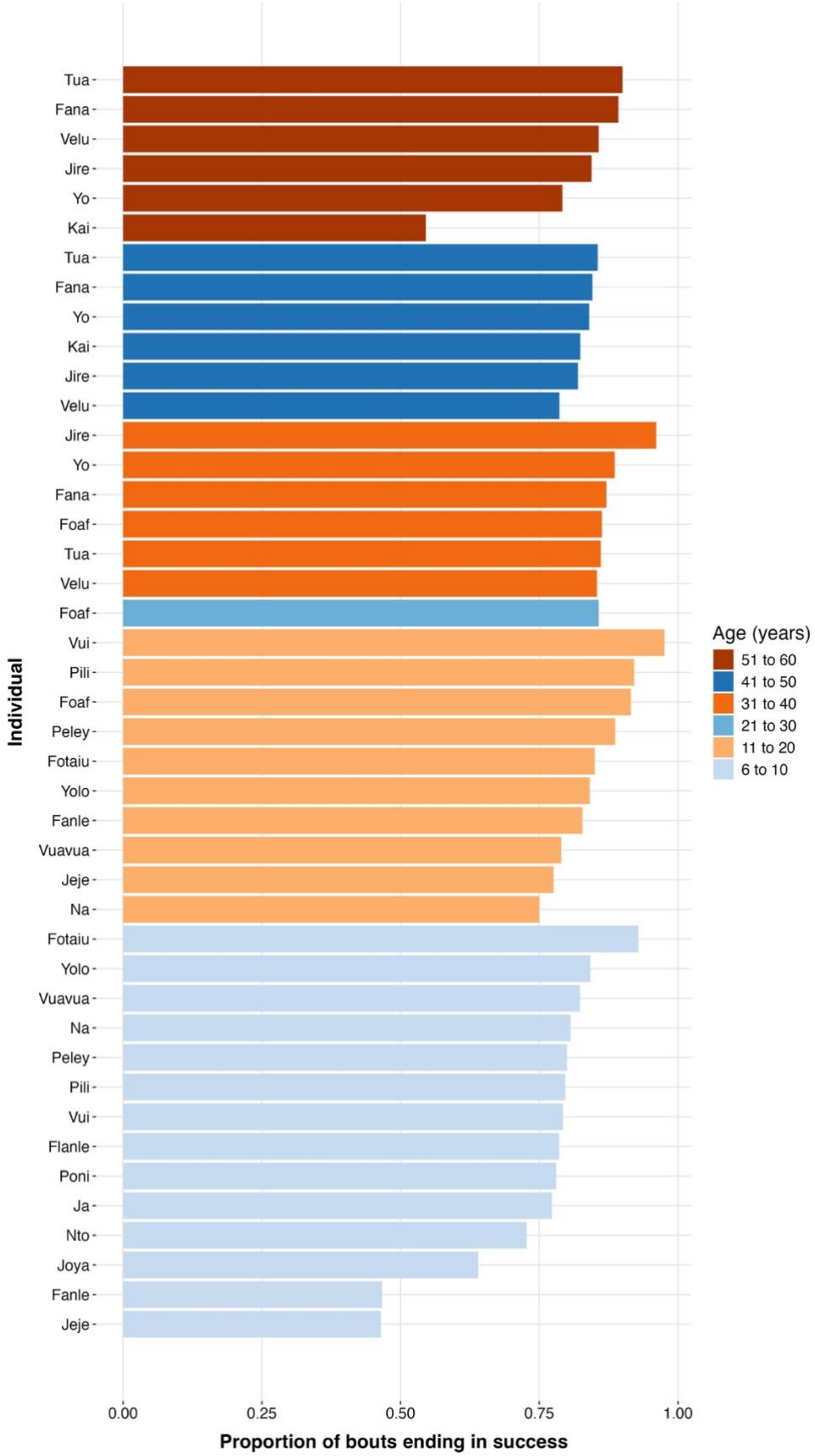


Figure S3. Bar chart illustrating the intra-individual development of successfully extracting the whole oil palm kernel for each age class (range in years) the chimpanzee was visible in the archive after their early learning period (aged 6 years and older).

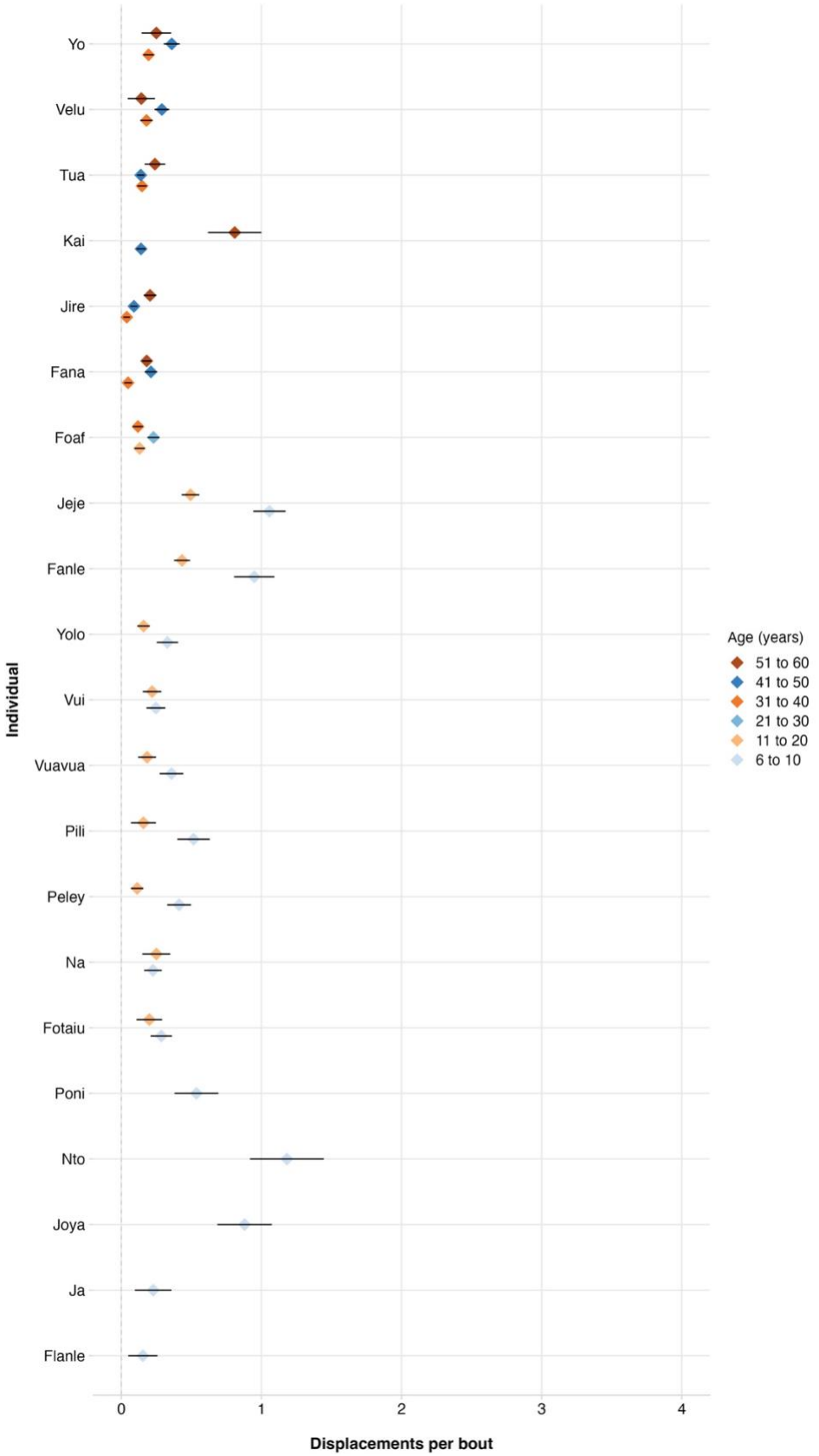


Figure S4. Stacked forest plot illustrating the intra-individual development of nut-cracking displacements per bout for each age class the chimpanzee is visible in the archive after their early learning period (aged 6 years and older). Where the chimpanzee was in the video archive over multiple age classes, older ages are stacked on top of younger age classes.
Note: The error bars represent the standard error of the mean.

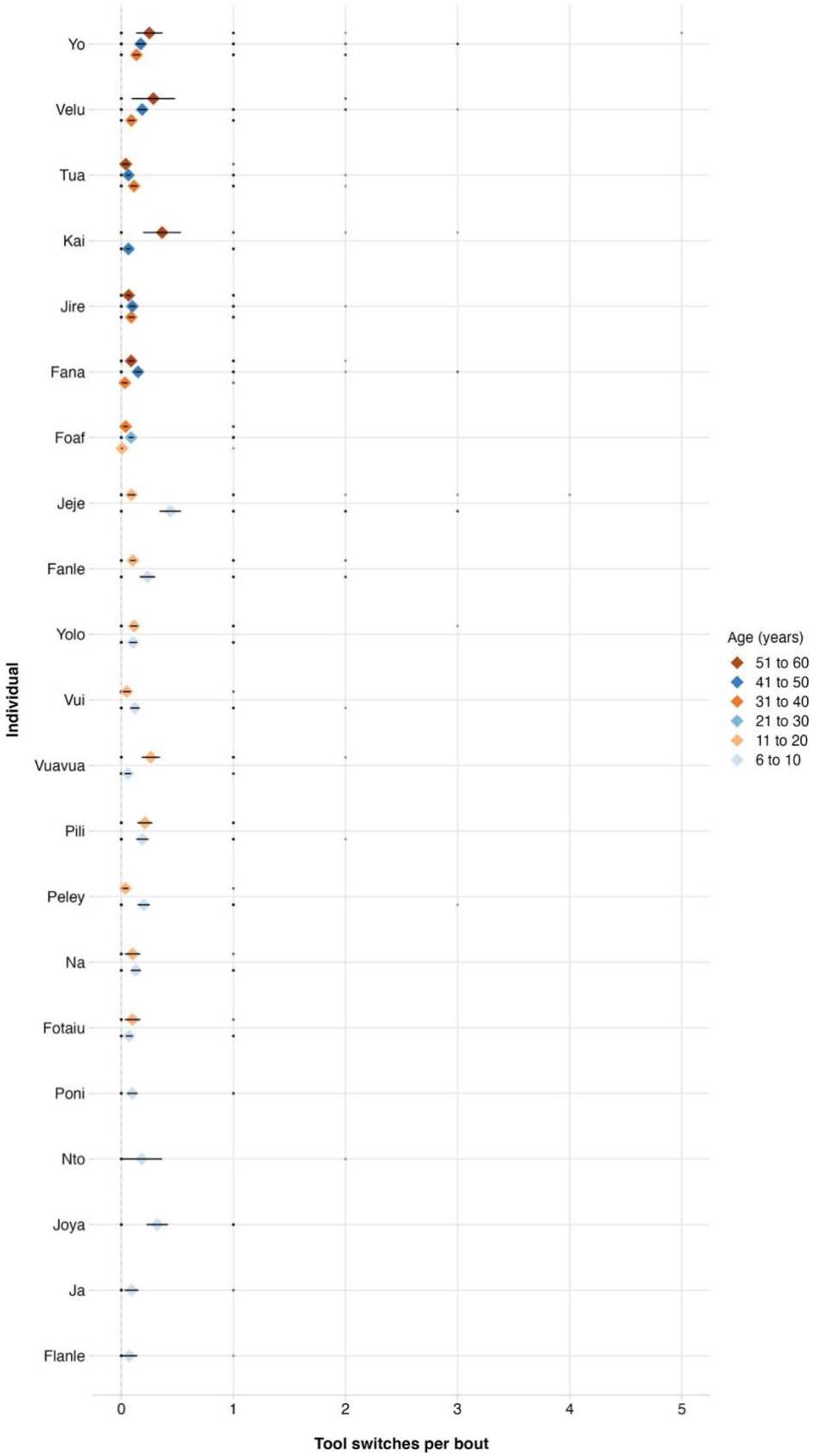


Figure S5. Stacked forest plot illustrating the intra-individual development of tool switch rate per bout for each age class the chimpanzee is visible in the archive after their early learning period (aged 6 years and older). Where the chimpanzee was in the video archive over multiple age classes, older ages are stacked on top of younger age classes.
Note: The error bars represent the standard error of the mean.

Stability of efficiency measures

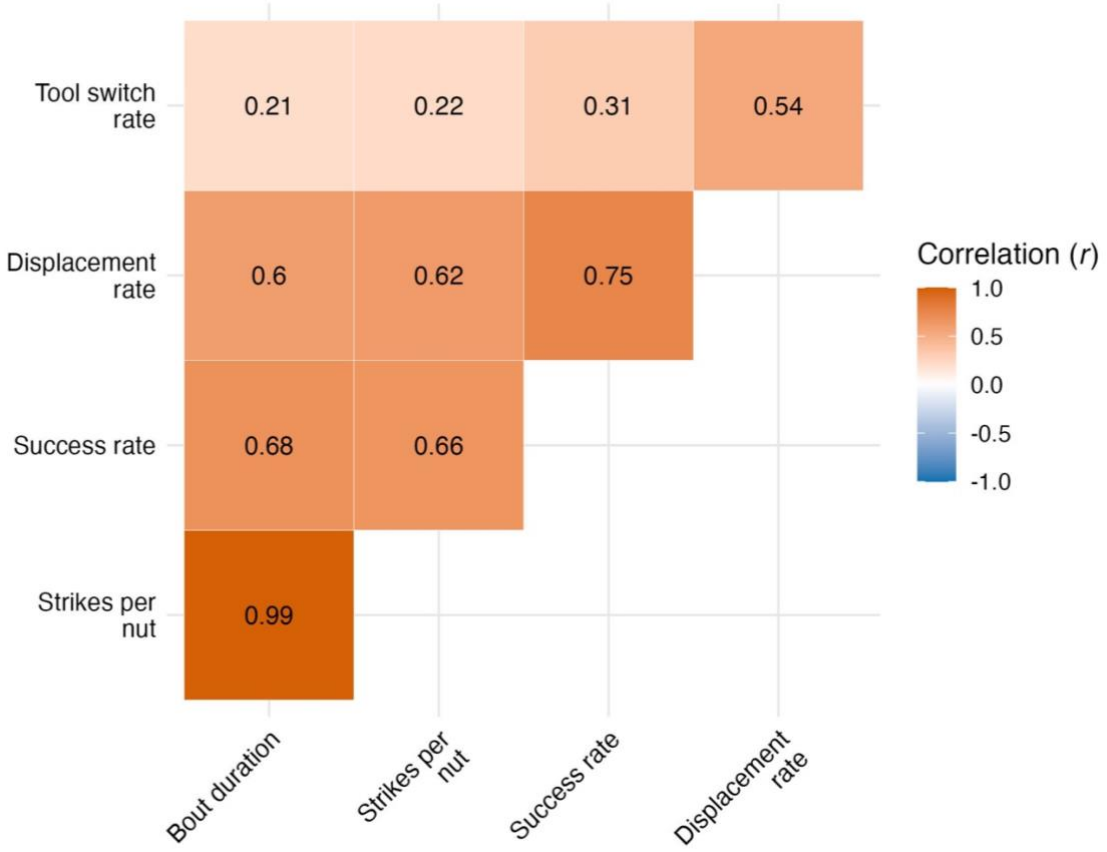


Figure S6. Correlation matrix for the Pearson's *r* correlation coefficient between the random intercept rankings for all pairs of nut-cracking efficiency measures.

Assumption checks

After fitting the models, the assumptions were checked to ensure inferences could be drawn from the findings. Multicollinearity between predictor variables for the *bout duration* model was checked using the *vif* function (variance inflation factor; VIF) in the *car* package[6]. The VIF was 1.13, indicating no issues of multicollinearity.

For the linear mixed-effects model (*bout duration*), the normality of the residuals was assessed visually using QQ-plots and homoscedasticity was checked by plotting the fitted values against the squared residuals[7]. For the cumulative link model (*success rate*), surrogate residuals[8] were obtained using the *sure* package[9]. We performed assumption checks on the single-level model (CLM) as the package does not currently support multilevel models (CLMM). We assumed this would be sufficient as only the intercepts were allowed to vary in the CLMM. The normality of the surrogate residuals was assessed visually using a QQ-plot and homoscedasticity was checked by plotting the fitted values against the surrogate residuals[10]. For all models, the normality of the random intercepts was assessed using QQ-plots and Shapiro-Wilk tests. Results indicated no significant deviations from normality.

We evaluated the multilevel models using influence diagnostics from the *influence.ME* package[11]. DFBETA values were calculated for each model to assess whether any individuals (i.e., the level two parameter) had an outsized influence on the results of the models. For *bout duration*, two individuals (Fana and Yo) had DFBETA values above the $2/\sqrt{n}$ cut-off[12], indicating that their data were influential. We re-ran the multilevel model (with individual as a random intercept, and age and sex as fixed effects) excluding their data and compared it to a simple linear model (without random effects). The random intercept model fit the data significantly better than the simple model ($\chi^2(1) = 203.75$, $p < 0.0001$), and as such we kept their data included in the model. We found no influential individuals in the *strikes per nut*, *displacement rate,* and *tool switch rate* models.

References

1. Allaire, J. J. *et al.* rmarkdown: dynamic documents for R. (2022).
2. Bateson, M. & Martin, P. *Measuring behaviour: an introductory guide*. (Cambridge University Press, 2021).
3. Landis, J. R. & Koch, G. G. The measurement of observer agreement for categorical data. *Biometrics* **33**, 159–174 (1977).
4. Koo, T. K. & Li, M. Y. A guideline of selecting and reporting intraclass correlation coefficients for reliability research. *J. Chiropr. Med.* **15**, 155–163 (2016).
5. Gamer, M., Lemon, J., Fellows, I. & Singh, P. irr: various coefficients of interrater reliability and agreement. (2019).
6. Fox, J. & Weisberg, S. *An R companion to applied regression*. (Sage, 2011).
7. Tkaczynski, P. *et al.* Long-term repeatability in social behaviour suggests stable social phenotypes in wild chimpanzees. *R. Soc. Open Sci.* **7**, 200454 (2020).
8. Liu, D. & Zhang, H. Residuals and diagnostics for ordinal regression models: a surrogate approach. *J. Am. Stat. Assoc.* **113**, 845–854 (2018).
9. Greenwell, B., McCarthy, A. & Boehmke, B. sure: surrogate residuals for ordinal and general regression models. (2017).
10. Greenwell, B., McCarthy, A., Boehmke, B. C. & Liu, D. Residuals and diagnostics for binary and ordinal regression models: an introduction to the sure package. *R J.* **10**, 381 (2018).
11. Nieuwenhuis, R., Te Grotenhuis, H. F. & Pelzer, B. J. Influence.ME: tools for detecting influential data in mixed effects models. *R J.* **4**, 38–47 (2012).
12. Belsley, D. D., Kuh, E. & Welsch, R. E. *Regression diagnostics: identifying influential data and sources of collinearity*. (Wiley, 1980).

6

THE ONTOGENY OF CHIMPANZEE TECHNOLOGICAL EFFICIENCY

In preparation for submission to *Proceedings of the National Academy of Sciences (PNAS)*

PNAS

Main Manuscript for

The ontogeny of chimpanzee technological efficiency

Sophie Berdugo*[1,2,3], Emma Cohen[1,2,4], Arran J. Davis[1,2,4], Tetsuro Matsuzawa[5,6,7], Susana Carvalho[2,3,8]

[1] Institute of Human Sciences, University of Oxford, Oxford, OX2 6NP, United Kingdom
[2] School of Anthropology and Museum Ethnography, University of Oxford, Oxford, OX2 6PE, United Kingdom
[3] ICArEHB, Interdisciplinary Center for Archaeology and Evolution of Human Behaviour FCHS, Universidade do Algarve, Faro 8005, Portugal
[4] Wadham College, University of Oxford, Oxford, OX1 3PN, United Kingdom
[5] Department of Pedagogy, Chubu Gakuin University, Gifu, 504-0837, Japan
[6] Division of the Humanities and Social Sciences, California Institute of Technology, Pasadena, CA 91125, United States
[7] College of Life Science, Northwest University, Xi'an 710069, China
[8] Department of Science, Gorongosa National Park, Sofala, Mozambique

*Corresponding author

Email: sophie.berdugo@anthro.ox.ac.uk

Author Contributions: **S.B.** conceived of the study, designed and coordinated the study, collected data, analysed and visualised the data, and wrote the manuscript. **E.C.** provided supervision, participated in the design of the study, and commented on the manuscript. **A.J.D.** analysed the data and commented on the manuscript. **T.M.** collected the original data set and commented on the manuscript. **S.C.** collected the original data set, provided supervision, participated in the design of the study, and commented on the manuscript.

Competing Interest Statement: The authors declare no conflict of interest.
Classification: Biological Sciences; Anthropology
Keywords: Social learning, development, chimpanzee, tool use, individual variation
This PDF file includes:

Main Text
Figures 1 to 3
Table 1

Abstract

Primate extractive foraging requires years of dedicated learning. Throughout this period, learners peer at conspecifics engaging in the behaviour ("models"), interacting with the model and their tools, and stealing the freshly extracted resource. This also corresponds to an extended period of tolerance from the models. Yet the long-term effect of variation in experiences during this period on the technological efficiency of individuals is unknown for primate tool use, and no research has assessed the role of both the learner and the model(s) in generating individual differences. Using over 680 hours of video spanning 25 years (1992–2017), we assessed whether divergent experiences during the stone tool use social learning period (the "early learning period"; ages 0–5) predicted the post-early learning period (ages 6+) technological efficiency in wild chimpanzees in Bossou, Guinea. We found that learners varied significantly in how frequently they peered at the models' whole nut-cracking bouts, how many learning opportunities their mothers presented, and the amount of tolerance and intolerance they experienced from all selected models. Learners who experienced more intolerance became less efficient tool users, whereas learners who were exposed to more social learning opportunities and more tolerance became more efficient. Peering at the whole nut-cracking bout decreased subsequent efficiency, hinting at learners acquiring less efficient cultural components of the behaviour. Our findings reiterate that social learning is fundamental to the acquisition of stone tool use, and opportunities to learn socially within a tolerant environment (with low active intolerance) are key in explaining the emergence and maintenance of more complex forms of primate technology.

Significance Statement

The capacity and inclination to learn from others, along with adequate social learning opportunities provided by tolerant groupmates, are thought to have enabled the evolution of technology in primates, including hominins. The influence of the skill early learning period on long-term individual variation in technological efficiency is currently unknown for non-human primates but has significant implications for our understanding of cultural transmission and evolution. We provide longitudinal support for the hypothesis that exposure to social learning opportunities during development predicts long-term technological efficiency. Moreover, we show that low amounts of *in*tolerance, not just general tolerance, is key in the ontogeny of technological efficiency. Finally, we illustrate that aspects of behavioural acquisition relate to accurate transmission of cultural traits rather than to learning to use tools efficiently.

Main Text

Introduction

Variation in tool use behaviour is found across wild primates, including in tufted capuchins (*Sapajus libidinosus*)[1], long-tailed macaques (*Macaca fascicularis*)[2,3], Sumatran orangutans (*Pongo pygmaeus abelii*)[4], and chimpanzees (*Pan troglodytes* spp.)[5]. Such variation is established at the community[6,7], age- and sex-class[1,8], and individual levels[9,10]. Variation in the efficiency ($\propto$ benefit/cost[11]), as opposed to simply the frequency, of extracting calorie-rich and nutrient-dense resources directly impacts energy expenditure[12], as well as being a driver in cultural and technological evolution[9,11,13].

Previous short-term studies on perishable tool use established that differences in behaviour stem from systematic variation in social learning experiences[4,5,14]—learning involving observing or interacting with another individual or their products[15]. However, the ontogenetic causes of individual differences are unknown for stone tools, and the long-term consequences of divergent learning experiences have never been explored in primate technology. Investigating how and why this variation in technological efficiency emerges will inform our understanding of processes with profound evolutionary consequences[9,16], including potential individual variation in social learning[13] and theories of the origins of tool use[17].

For culture to evolve, the trait and its variants must be inherited by the subsequent generation[18]. As such, cultural information transfer must be vertical (from older kin) or oblique (from older non-kin), with solely horizontal transmission (peer-to-peer) being inadequate[18]. Therefore, along with necessary ecological and manual dexterity prerequisites, exposure to suitable social learning opportunities enabled primates, including hominins, to evolve material culture[17]. Van Schaik and colleagues argued that opportunities to learn complex skills socially can only be exploited where the older competent conspecifics are also tolerant of the younger generation learning over prolonged periods[17]. A mathematical model on tool-using skills supported this hypothesis by

demonstrating that populations with sufficient social tolerance and opportunities for social learning are more likely to evolve complex skills, such as tool use[19].

Investigating the developmental drivers of individual variation in chimpanzee extractive-foraging techniques can also help advance our understanding of primate cognition and cognitive evolution. Carvajal & Schuppli argued that social learning opportunities are a central component of the evolution of complex cognition as they can dictate the ease and speed with which fitness-enhancing skills and information are obtained[20]. The propensity to learn faithfully from others—which enabled the intergenerational accumulation of knowledge—propelled hominins into the "cultural niche", which supported their ecological success[21]. Given that our knowledge of early hominin technology is currently constrained to non-perishable stone tools, it is important to establish the processes generating variation in primate stone tool use to better capture the scope of hominin cognitive capabilities[22].

West African chimpanzees (*P. t. verus*) use stone and wooden hammers to crack nuts[23,24], with the technique varying cross-culturally[6]. The chimpanzees of Bossou, Guinea, use a stone hammer-and-anvil composite to extract oil palm nut kernels (*Elaeis guineensis*)[25], with individuals varying in their technological efficiency[9]. The skill requires coordination of both hands whilst manoeuvring the three components (the hammer, anvil, and nut)[26], and is developed over a prolonged early learning period (hereafter, "ELP") proposed to last 3–5 years[8,27]. The successful sequencing of the fundamental nut-cracking actions (take nut, place nut, hold stone, hit nut, and eat kernel) becomes more formalised with age, with sequences consisting of four of the five actions only emerging from 3.5 years old[26]. This highlights the complexity of the behaviour and the importance of sustaining attention to observe the entire nut-cracking bout of knowledgeable models.

In fact, nut-cracking is acquired via a combination of individual and social learning[7] during an "education by master-apprenticeship" learning process, which necessitates a tolerant model (the "master," typically the mother) for the learner (the "apprentice"; see Figure 1)[28]. Two mothers in Bossou (Nina and Pama) could not crack nuts—they are thought to have

emigrated from a community without the behaviour—and yet all of their infants (Na, Nto, Pili, Poni, and Peley) learned the skill[23]. This illustrates the importance of non-maternal models acting as "masters" for the "apprentices".



Figure 1. Flanle, an infant male, peering at his mother, Fanle, as she cracks. He watches closely and rests his hand on Fanle's to learn the energy required to crack oil palm nuts (A). He then scrounges the extracted kernel (B). Image credit: Tetsuro Matsuzawa.

Nut-cracking with a stone hammer-and-anvil composite cannot be individually re-innovated in the wild—a competent conspecific is required to demonstrate the nut-cracking technique and motivate the learner to engage in the behaviour[29]. Allowing infants to scrounge (i.e., take the extracted kernel to eat themselves) helps to maintain motivation to learn the behaviour over the prolonged period[30–32], although it is thought that the main impetus to learn the skill is to engage in the same behaviours as groupmates[28]. However, individuals may vary in their reliance on social learning, and the mechanisms used may vary systematically across individuals due to an 'individual learning of social learning'[13,33] (p. 215). As such, variation in both learner and model behaviour during the nut-cracking ELP is likely to influence the post-early learning period (hereafter "post-ELP") tool use efficiency.

It is critical, therefore, to assess the combined influence of the learner and model(s) during the acquisition of complex skills at the individual level. Despite this, previous efforts have typically focused on establishing the source of sex differences, rather than of *individual* differences, in tool use, or have assessed the influence of singular components of the

developmental period, such as the amount of time peering (i.e., 'the attentive and sustained close-range watching of the activities of a conspecific'[34] (p. 5)) at the skill being performed. No prior research has assessed the role of both the learner and the model(s) in generating individual variation in technological behaviour.

Current hypotheses explaining the source of variation in technological behaviour are focused on explaining sex differences. Sex differences in tool-use are thought to emerge in infancy[35]. An investigation into sex differences in "preparation" behaviours (i.e., engagement with sticks and woody vegetation) for ant-dipping by chimpanzees in Kalinzu, Uganda, found that although males manipulated objects significantly more than females, this manipulation was predominantly play-based[36]. Conversely, females exhibited a more diverse array of early experiences with objects, such as breaking and plucking, which was more indicative of preparation for subsistence tool use. Thus, sex differences may arise from divergent experiences with objects during infancy. However, this finding does not explain the cause of variability in early object manipulation.

A 4-year longitudinal study on 14 infant-mother dyads in Gombe, Tanzania, assessed whether sex differences in the learning process precede the female bias in chimpanzee termite-fishing[5]. The researchers found that female infants spent more time termite-fishing, peered at their mothers more, and successfully fished significantly earlier (ca. 27 months) than male infants. The congruence between the termite-fishing technique of female offspring and their mothers was greater than between male offspring and their mothers, which was interpreted to indicate that females learn the skill more via imitation (process-focused learning) and males more via emulation (product-focused learning).

These results suggest that the female bias in termite-fishing stems in part from divergent motivations to learn the skill during the acquisition period. However, no studies have assessed factors that might contribute to this variation or whether differences in peering exists in other technological behaviours, such as in stone tool use contexts. In turn, there has been no assessment of whether variation in peering, and potential differences in social

learning mechanisms employed, produces variation in the long-term technological proficiency of individuals.

Because of the inherent role of model characteristics (in terms of, for example, tolerance) in the amount of time learners can peer, we argue that the proportion of complete nut-cracking sequences the learners peered at during their ELP is a more accurate measure to capture variation in learner peering than measuring total peering duration. Indeed, complete attention on the model performing the target behaviour is needed to ensure accurate observations[11]. As such, the present study assessed the proportion of learner's peering events that were directed at the entirety of the model's nut-cracking bout, defined as the period (in seconds) of using a stone hammer to crack one nut on a stone anvil.

Variation in model tolerance to peering and the number of learning opportunities provided (which impacts exposure to the behaviour) by the maternal model also greatly influence tool use proficiency[4]. Tolerant models also afford more learning opportunities as they allow the learner to be proximate whilst peering at the skill being modelled, interact with the model and their tools to learn about the mechanics of the skill, and scrounge the extracted resource so that the behaviour is positively reinforced[4,30,37]. Chimpanzee mothers in Gombe show the same amount of tolerance (defined as allowing their offspring to do whatever they were trying to do, such as peer or steal a tool) towards male and female infants learning to fish for termites[37]. This research also observed "negative" behaviours mothers showed towards their infants (i.e., shoving, moving, and avoiding infants at termite mounds), but it did not assess whether differential exposure to this intolerance affected the learners' behaviour. Given that intolerance is a form of punishment (thereby decreasing the likelihood of the behaviour being repeated[38]), it is a key variable to measure when assessing the ontogeny of technological efficiency.

Moreover, differences in social learning opportunities are thought to predict individual variation in tree-hole tool use in Sumatran orangutans[4]. Data gathered over 3 years of the Bossou chimpanzees found that mothers differ in the proportion of time spent ant-dipping

and hence provide varying degrees of learning opportunities for their infants[14]. Infants exposed to higher rates of ant-dipping peering opportunities (having mothers who spent > 0.2% of their total activity time ant-dipping) started to ant-dip significantly earlier, dipped for longer, and made fewer dipping errors than offspring of low opportunity mothers (< 0.2% of total activity time ant-dipping)[14]. For stone tool technology, the acquisition of nut-cracking in wild bearded capuchins is supported by tolerant models providing opportunities to observe (via stimulus enhancement) and practise the skill[39]. Although this research did not assess variation during the developmental period, it highlights the importance of model opportunity provision during the acquisition of lithic technology.

In chimpanzees, the influence of maternal behaviour on nut-cracking outcomes have previously been investigated in 11 immature chimpanzees (aged 2.4–8 years) in the Taï National Park, Côte d'Ivoire[40]. The 4-year study assessed "maternal scaffolding" (providing nut-cracking learning and practising opportunities for their offspring) and mother-initiated nut-sharing on: 1) the offspring's task understanding (defined as using all three nut-cracking components), 2) the proportion of successful cracking bouts, and 3) efficiency (nuts per minute). The researchers found that predicted maternal scaffolding did not significantly affect infant nut-cracking outcomes, and although using the mother's hammer did positively affect bout success and efficiency—likely by providing information on optimal hammer properties—offspring age had the largest influence on nut-cracking skills.

Although these findings appear to contradict the premise that opportunity provision and tolerance predict nut-cracking outcomes, the study did not encompass all the known elements of tolerant behaviour, such as allowing proximity and touch[30]. Likewise, the research only investigated mothers' "supportive behaviour" (scaffolding and nut-sharing) and did not assess *in*tolerance shown by the mothers (previously termed "negative" behaviours[37]). Intolerance is an important variable as it is an active model behaviour that directly affects the learner's ability to be proximate to the behaviour and to scrounge extracted food items—factors known to be important for maintaining motivation during

protracted learning periods[32]. Conversely, tolerance to infant scrounging, proximity, and interaction is typically passive. Both tolerance and intolerance should be studied to understand the full suite of interactions learners experience with their selected models. Also, the research was conducted on sub-adult chimpanzees over a short period and so could not assess the critical longer-term influence of maternal behaviour on offspring nut-cracking efficiency.

To date, research on the ontogeny of tool use in wild primates has relied on relatively short-term observations (over a maximum of 4 years) and has often used cross-sectional data. However, given chimpanzees' long lifespans and the protracted periods required to develop these skills[5,8,27], this data is insufficient for assessing the ontogeny of skill proficiency. The formation of video archives by long-term field sites are now offering insights that would not be possible based on data from relatively short-term studies. For example, research using 25-years of footage (1992–2017) of the Bossou chimpanzees established stable and reliable individual-level variation across four measures of nut-cracking efficiency in individuals aged 6+ (post-ELP)[9].

Here, we present a study aiming to establish the source of this variation by investigating the effect of experiences during the ELP (≤ 5 years old) on individuals' long-term nut-cracking efficiency (≥ 6 years old). Four key aspects of nut-cracking skill development were recorded: 1) how frequently the learner peered at the models' entire nut-cracking bout, 2) the amount of tolerance the models showed to the learner during peering, 3) the amount of *in*tolerance the models showed to the learner during peering, and 4) the social learning opportunities provided by the learner's mother (see Table 1). Using 25 years of longitudinal data (1992–2017), this research tested whether variation in the ELP predicted the four measures of post-ELP efficiency (time taken to crack one nut, number of strikes per nut, success rate, and number of times the nut was displaced from the anvil due to the hammer strike) of ten wild chimpanzees.

Table 1. Definitions of developmental measures.

Measure	Definition
Whole bout peering	Where the whole of the model's nut-cracking bout was peered at, the peering event was recorded as "whole bout". Where only a segment of the bout was peered at, the peering event was recorded as "not whole bout".
Opportunity provision	The total proportion of time that the maternal model provided opportunities for their infant/juvenile to learn to crack nuts. This was a measure of the total amount of time the focal subject's mother was cracking nuts in the outdoor laboratory with the focal present, over the continuous period of when the focal subject's mother was on camera in the outdoor laboratory whilst the focal is also present[14].
Model tolerance	Where the model permitted the peering learner to scrounge the extracted kernel, interact with the model (e.g., touching the model's arm or body) or the model's tools, or be proximate (≤ 1 m away) to the model during the nut-cracking bout[28,30].
Model intolerance	Where the model physically (e.g., shoving, hitting) or vocally (e.g., grunting, barking) rejected or resisted a peering learner's attempts to scrounge, interact with the model or the tools, or be proximate (≤ 1 m away) whilst they were engaged in a nut-cracking bout[37].

Results

***Variation in learning period experience*.** Learning period data were collected for 13 individuals (six female and seven male, ages 0–5). Results show significant variation around the average for each of the four developmental measures across these 13 infants (see Figure 2 for observed *t*-values). For the ten individuals (five female and five male, ages 6–20) that we have data on their post-ELP, there was one who peered at the whole nut-cracking sequence significantly less than average (n = 1), and four who peered at the whole nut-cracking sequence significantly more than average (n = 4). Also, one learner received significantly fewer learning opportunities from their mother than average (n = 1), and two received significantly more than average (n = 2). For *model tolerance to peering*, no learners experienced significantly more tolerance than average but two experienced significantly below average tolerance (n = 2). For *model intolerance to peering*, four learners experienced significantly less intolerance than average (n = 4), and two experienced significantly more than average (n = 2).

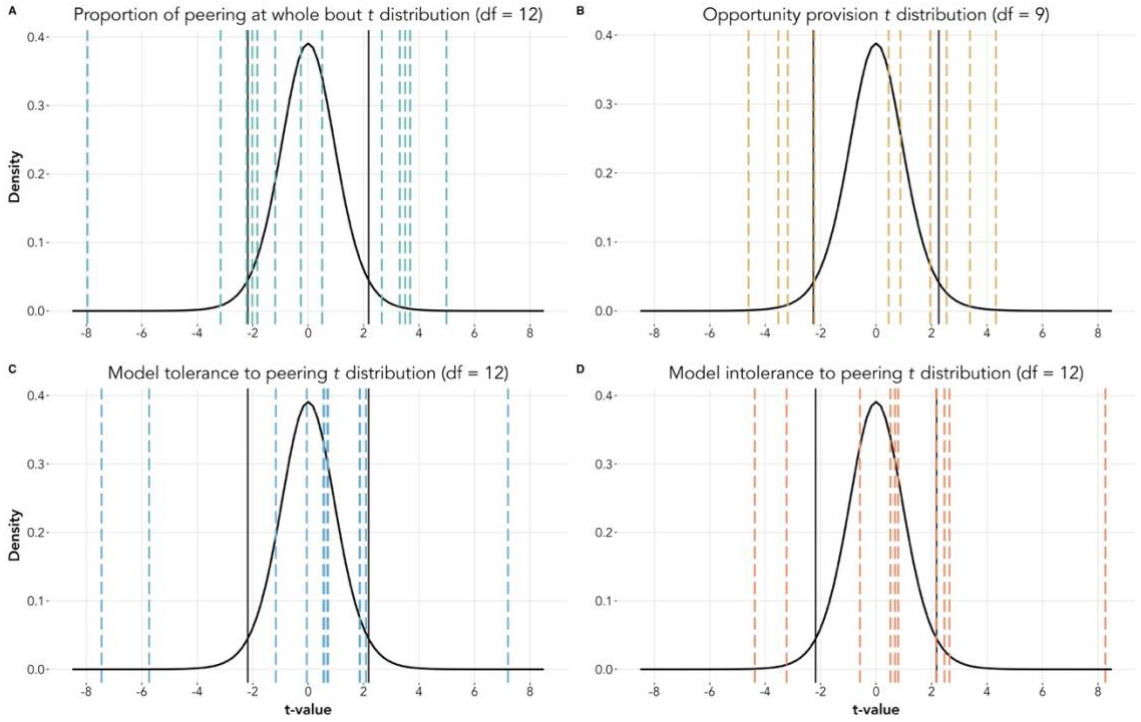


Figure 2. *t* distributions showing the variation in (A) proportion peering at the whole nut-cracking bout, (B) opportunity provision from the mother, (C) model tolerance to peering, and (D) model intolerance to peering during the development of nut-cracking.
Notes: The black vertical lines indicate the 95% two-tailed critical *t*-values. The dashed vertical lines indicate the observed *t*-values for the focal subjects. Two chimpanzees shared the same *t*-score (-1.16) for model tolerance to peering, which explains why only 12 dashed lines exist in plot C. Five chimpanzees shared the same *t*-score (three for -4.36 and two for -0.56) for model intolerance to peering, which explains why only ten dashed lines exist in plot D. Observed *t*-values that fall between the black vertical lines show average scoring individuals. Observed *t*-values that fall beyond the black vertical lines are significantly different to average.

***Influence of the models on post-ELP nut-cracking efficiency*.** Exposure to social learning opportunities from the mother had a significant negative effect on post-ELP *strikes per nut* (number of strikes to crack one nut; $z = -4.818$, $p < 0.001$) but no effect on log *bout duration* (time taken to crack one nut; $t = -1.946$ $p > 0.05$), *success rate* (proportion of bouts that end in the whole kernel, the partial kernel, and no kernel being extracted; $z = 1.453$, $p > 0.05$) or *displacement rate* (number of times the hammer strike displaces the nut from the anvil; $z = -0.907$, $p > 0.05$).

Mean model tolerance had a significant negative effect on log *bout duration* ($t = -2.395$, $p < 0.05$) and *strikes per nut* ($z = -2.978$, $p < 0.01$), but no effect on *success rate* ($z = -1.602$, $p > 0.05$) or *displacement rate* ($z = 0.505$, $p > 0.05$). Mean model intolerance had a significant

positive effect on log *bout duration* (t = 6.683, p < 0.001) and *strikes per nut* (z = 2.164, p < 0.05), but no significant effect on *success rate* (z = 0.229, p > 0.05) or *displacement rate* (z = 0.626, p > 0.05).

***Influence of the learner on post-ELP nut-cracking efficiency*.** The proportion of peering events where the whole nut-cracking bout was observed had a significant positive effect on *strikes per nut* (z = 2.995, p < 0.01), and *displacement rate* (z = 5.185, p < 0.001), and a significant negative effect on *success rate* (z = -4.180, p < 0.001). There was no significant effect on log *bout duration* (t = 1.912, p > 0.05).

The age of the post-ELP chimpanzee had a significant negative effect on log *bout duration* (t = -4.514, p < 0.001), *strikes per nut* (z = -2.492, p < 0.05), and *displacement rate* (z = -6.537, p < 0.001), and a significant positive effect on *success rate* (z = 6.395, p < 0.001). There was also a significant effect of sex, with being male having a positive effect on *strikes per nut* (z = 2.985, p < 0.01), a significant negative effect on *success rate* (z = -2.420, p < 0.05), and no effect on *displacement rate* (z = 1.314, p > 0.05). Model coefficient estimates are shown in Figure 3.

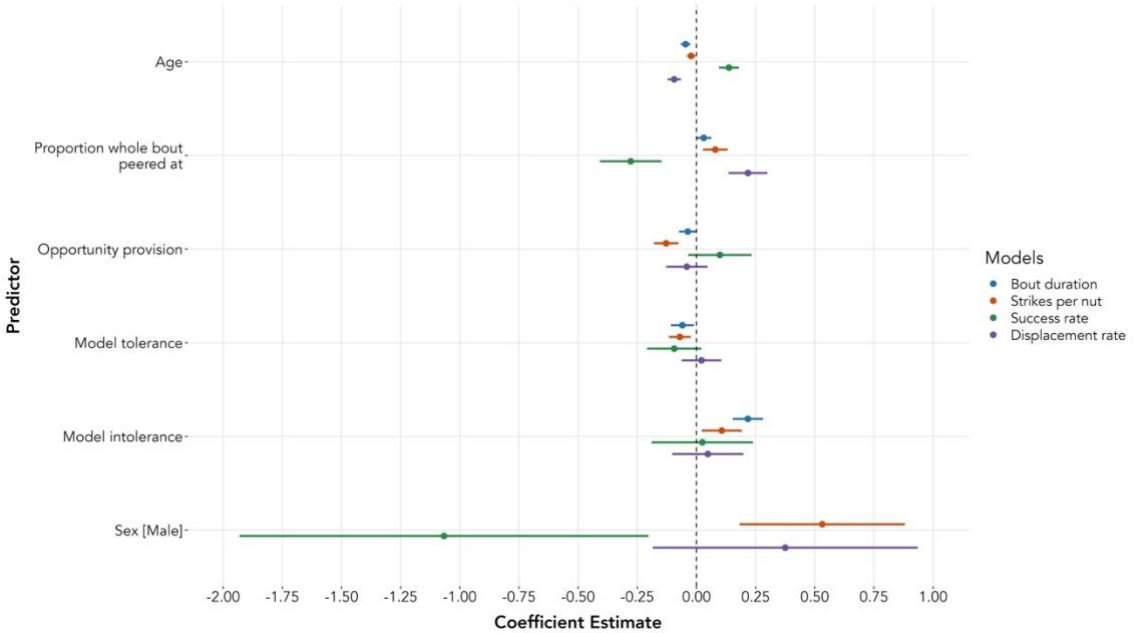


Figure 3. Coefficient estimates for each predictor variable from the model outputs of the four efficiency models. Dots indicate the estimate, and whiskers show the 95% confidence interval. The dashed vertical line at zero indicates no effect of the predictor on the outcome.

Discussion

Understanding the factors driving variation in chimpanzee tool use is critical for understanding the selective pressures on primate and early hominin cognitive and technological evolution. This longitudinal study shows that divergent experiences during the development of tool use predict variation in the subsequent technological efficiency of wild primates. Specifically, we show that variation in the opportunities to learn socially, as well as the amount of tolerance and intolerance experienced whilst attempting to peer at nut-cracking models during the learning period, affect the individual's post-ELP nut-cracking efficiency[9]. This has implications for theories of the origins of tool use[17], particularly as we found that model *in*tolerance was a stronger predictor than model tolerance for subsequent skill efficiency (in terms of bout duration).

Our results offer longitudinal support for the hypothesis that the number of social learning opportunities and the amount of tolerance to peering (i.e., being allowed to scrounge, interact with, and be in close proximity to nut-cracking models) provided during development predicts future technological proficiency[4]. Individuals exposed to more social learning opportunities from their mother and those who experienced more tolerance when attempting to peer subsequently required fewer strikes to extract the kernels (which reflects energy spent relative to energy gained[9]). Additionally, learners who were exposed to more tolerance from models subsequently had shorter nut-cracking bouts—an indicator of energy intake rate[9]. Being exposed to social learning opportunities by tolerant models (including local and stimulus enhancement and observational learning) is considered to be a form of niche construction[32], which is facilitated by the enduring nature of stone tools[41]. The distinctive sound of the nut-cracking percussion[42] along with the capacity for young learners to reuse adults' tools provides both the physical affordance to use the tool composite and the motivation to do so[41].

Conversely, exposure to social learning opportunities presented by mothers and model tolerance to peering did not predict subsequent success rate or displacement rate, which

are indicators of strike and kinetic energy accuracy[9,43,44]. Similarly, the maternal opportunity provision did not predict subsequent log bout duration. This may suggest that these components of nut-cracking efficiency are honed and impacted by different developmental processes, such as learning by trial-and-error. Alternatively, the results may reflect the fact that our research only focussed on the social learning opportunities provided by mothers, meaning that all learning opportunities available to the chimpanzees during the development of nut-cracking were not captured. Nonetheless, our results provide an important step in highlighting the long-term consequences of differential exposure to learning opportunities on skill efficiency.

Our findings that learners who experience more intolerance (e.g., being shoved away or not being allowed to scrounge) whilst attempting to peer at nut-cracking models were less efficient (in terms of bout duration and strikes per nut) later in life advances van Schaik and colleagues' theory of the ontogeny of primate technological behaviour[4]. Intolerant behaviour punishes the learners for trying to observe the skill, meaning that they are unable to watch the behaviour at close range to learn the technique or gain motivating positive reinforcement from scrounging. Again, the future success rate and displacement rate of the individual was not impacted by intolerance to peering, further suggesting that these aspects of efficiency develop via different learning processes.

This supports the idea that individual variation can arise from "individual learning of social learning", whereby the rate of learning and the learning strategies used are phenotypically plastic, contingent upon previous social learning interactions[13]. Experiencing high degrees of intolerance whilst attempting to learn by observation (i.e., peering) may force learners to rely upon other forms of learning (whether social or asocial). These learning mechanisms may be suboptimal for acquiring complex extractive foraging skills and becoming technologically efficient, hence the resultant reduction in relative efficiency post-ELP for these individuals. Future research investigating whether the rate of individual and social

learning of the skill varies depending on the amount of intolerance individuals experience from models would shed further light on this process.

Regarding the influence of the learner's behaviour on nut-cracking efficiency, we found that, counter to predictions, learners who peered at a higher proportion of whole nut-cracking bouts subsequently became *less* efficient nutcrackers (in terms of fewer strikes per nut, reduced success rate, and more nut displacements). Although not statistically significant, these learners also tended to have longer nut-cracking bouts. It is possible that the "whole-bout-peerers" could have peered less overall, meaning that although they observed a larger proportion of whole bouts, they also observed fewer bouts overall relative to their conspecifics. However, there was only a weak correlation (r = 0.26) between number of peering events and proportion of whole bout peering. Alternatively, the finding that "whole-bout-peerers" became less efficient nutcrackers may be an artefact of the binary nature of the "whole bout peered at" measure used in this research, with a peering event being coded as either a "whole bout" or "not the whole bout". Notwithstanding this possibility, the fact that the proportion of whole nut-cracking bouts peered at during the learning period predicted three of the four measures of efficiency highlights the importance of this variable in the ontogeny of chimpanzee technological efficiency.

We tentatively suggest that these results may reflect the process of cultural transmission: peering at the whole bout is not to learn how to perform the behaviour efficiently, but rather to learn 'the way we do things' as a cultural group[45] (p. 433). Peering at the whole nut-cracking sequence of models increases the likelihood of the cultural behaviour being maintained, as the technique can be more faithfully transmitted. We found that the majority of all 436 peering events (60.55%) involved the learner peering at the whole of the model's nut-cracking bout, with the proportion increasing as infants aged (see Figure S1). Although the increase in the proportion of whole bout peering over the course of the ELP is likely to reflect, at least in part, developmental changes in the ability to sustain attention, it may also illustrate this process of cultural transmission and maintenance. Research is now needed to

determine the degree of congruence between the technique of the models whose whole bouts were peered at, and the learners' subsequent nut-cracking techniques (as was previously done in termite-fishing in Gombe[5]). This will shed light on whether learners who peer at the whole nut-cracking bout more are imitating the model's behaviour, rather than emulating the sequence to achieve the same outcome, thereby advancing understandings of the social learning mechanisms employed by wild chimpanzees[46,47]. At the very least, the finding reiterates the need to test assumptions of the social learning capabilities of chimpanzees in wild populations learning naturally occurring skills, rather than in artificial tasks in captive individuals[48].

This research assessed the combined influence of the learner and model on the long-term technological efficiency of primates. We show the importance of both the learners' and the models' (maternal and non-maternal) behaviour on subsequent nut-cracking efficiency. Although our sample is limited to the relatively small size of the Bossou community (which is in the lower end of the normal range for chimpanzee populations[49]), this population, currently very close to extinction, is the only one where long-term stone tool use has been recorded yearly using a systematic video recording approach. It thus offers a unique and unrepeatable opportunity to disentangle the relative contribution of both the "master" and the "apprentice" during the learning period. Observational learning plays an integral role in the acquisition of nut-cracking by wild chimpanzees. Follow up research will ascertain whether any model-based social learning strategies[50] are involved in non-maternal model choice, such as kin or proficiency biases[51,52].

Age had a significant effect on all post-ELP efficiency measures. As chimpanzees got older, their bout durations decreased, they required fewer strikes to extract the kernel, their success rate increased (i.e., their bouts were more likely to end with the whole kernel being extracted), and they made fewer displacements per nut. We also found a significant effect of sex for two measures of efficiency, with male chimpanzees requiring more strikes per nut and having a lower success rate than females. However, these results should be viewed with

caution as previous research found there was no effect of sex in chimpanzee nut-cracking efficiency across a larger sample and dataset[9]. Results may be a function of the sample size, as data on the learning and post-ELP across the 25-year period sampled existed for ten chimpanzees, compared to the 21 individuals in the previous research[9].

This research has two limitations. First, as mentioned, the binary measure for whether the individual peered at the whole nut-cracking bout or not may have been too coarse to sufficiently capture variation in the learners' peering behaviour, and its effect on subsequent efficiency. Future research should investigate the exact proportions of the models' bouts the learners peered at, and the reasons for looking away (e.g., to manipulate objects, because of a loud noise, to engage in a social interaction, etc.) to better understand the role of peering at the entire behavioural sequence on the acquisition of the skill.

Second, the research was inherently constrained by using pre-collected and historic data. At times, events of interest (particularly peering) were happening on camera but the camera angle or video quality hindered data being collected. While we doubt that this biased our results, it did reduce the size of the overall data set. Moreover, the observational nature of the research limits our ability to establish a causal link between experiences during the ELP and subsequent efficiency. However, these constraints are outweighed by the advantages of using long-term video records, which allow tests of questions which cannot be answered using short-term field research alone[53].

We provide critical longitudinal data strongly suggesting that observational social learning processes are fundamental to the acquisition of nut-cracking. This has important implications for the use of animal culture in conservation. Nut-cracking by West African chimpanzees is protected by the United Nations' Convention on the Conservation of Migratory Species of Wild Animals and is recognised as being vital for the conservation of the subspecies[54]. Our data reiterate the warnings of the disturbance hypothesis: where the core components of social transmission are impacted by human pressures, such as hunting and habitat degradation and fragmentation, behavioural repertoires and fitness-enhancing

skills and knowledge will be severely disrupted[55]. Long-term data, such as those presented here, can contribute significantly to understanding whether culture can and should be used in conservation policy. It is clear that if nut-cracking is to be protected, the social learning processes through which the behaviour is acquired must be too.

Materials and Methods

Subjects and Data Acquisition

***Study site*.** The wild chimpanzees neighbouring Bossou village in the tropical wet seasonal climate of south-eastern Guinea (7°38'71.7'N, 8°29'38.9'W) have a home range of 15km^2 and a core area of 7km^2 within primary and secondary forest[56]. The community has been under investigation since 1976, with the population size always being relatively small (9–21 individuals during the research period of 1992–2017)[57,58].

Study materials. The nut-cracking behaviour of the Bossou chimpanzees has been recorded in every dry season (December–February) since 1988, with videos taken from behind a grass screen from at least two standardised positions[59]. This has produced a long-term video archive from within the so-called "outdoor laboratory": a 7m x 12m site on Mont Gban (7°38'41.5'' N, 8°29'50.0'' W) where locally sourced stones and nuts are experimentally provisioned[8,58]. This study used the 1992–2017 footage, excluding 2001 and 2011 as footage was not taken in these years. The 2009 footage was also excluded, as only experimentally introduced *Coula edulis* nut-cracking bouts were peered at that year.

Measures. This study assessed four developmental measures (see Table 1): proportion of peering at the full length of the models' nut-cracking bouts, exposure to social learning opportunities by the mother, tolerance experienced from all models whilst peering, and intolerance experienced from all models whilst attempting to peer. Peering is 'the attentive and sustained close-range watching of the activities of a conspecific'[34] (p. 5). Here, a peering event was defined as the period (in seconds) where the learner's gaze was directly oriented towards a model's hand, arm, nut, or stone tool composite during a nut-cracking bout[8]. A

nut-cracking bout was defined as the length of time between the chimpanzee lifting the hammer for the first strike and the hammer making contact for the final time[9,24]. Each peering event occurred at the bout-level, meaning that a new peering event was recorded for each new oil palm nut the model cracked. The name of the model and their relation to the learner was recorded for each peering event. Whether or not the learner peered at the whole bout was recorded. Whether the model permitted learner scrounging, proximity, or interaction whilst peering (tolerance), or expressed physical or vocal intolerance towards the learner attempting to peer, was also recorded for every peering event.

The four separate (but stable and reliable) measures of post-ELP efficiency were used: the amount of time taken in seconds to crack one nut ("bout duration"), the number of strikes required to crack one nut ("strikes per nut"), the "success rate" of the individual, and the number of times the nut was displaced from the anvil due to the hammer strike ("displacement rate")[9].

Data collection. Data for the four developmental measures were collected using *Behavioural Observation Research Interactive Software* (BORIS; v. 7.13.9)[60]. Data on post-ELP efficiency were collected as part of previous research[9]. All-occurrence sampling was employed to gather data from all visible peering events during the video archive for each focal individual for every available year of their learning period (six years per individual from 0–5 years old, inclusive). Visible peering events were those where the focal was facing the camera or where they were not directly facing the camera, but their gaze was observable. For model tolerance to peering and model intolerance to peering, data were gathered from all peering events using the "modifier" function in BORIS. All instances of tolerance and intolerance the model showed to the learner during a peering (or attempted peering) event were recorded. The ethogram and modifiers used during data collection can be found in Tables S1 and S2.

For opportunity provision, all-occurrence sampling was used to gather data on the proportion of the total observation time that the learners' mothers were nut-cracking in the

outdoor laboratory. Data were not obtained from 1994 or 1995, as rapid and shaky camera movements hindered the ability to accurately measure the length of nut-cracking.

Since 1976, there have been 28 mother-infant dyads[61] (see Table S3), but footage of the full nut-cracking learning period is only available for 19 of these infants. Of these 19 chimpanzees, one was born after the study period, and one's learning period commenced prior to 1992 and so they were excluded from the study. Four chimpanzees died before age three, and so not enough footage existed for them to be included. A further three chimpanzees either died before age six or reached age six after 2017, and so there is no data on their post-ELP efficiency. As such, developmental data were collected from 13 infants, and the role of the developmental period on post-ELP efficiency was assessed in ten of these individuals. Three of these infants (Nto, Poni, and Peley) had mothers who did not crack nuts, and post-ELP data exist for all three.

Details on the data collection protocol for the post-ELP efficiency of the Bossou chimpanzees has been previously published[9]. In short, data were gathered from at least 20 bouts (where possible) for each year the ten focal subjects (aged 6+) were visibly cracking oil palm nuts in the footage from 1998–2017.

For the developmental period, a total of 436 peering events, 466 instances of model tolerance, and 52 instances of model intolerance were recorded across 13 chimpanzees (six female and seven male, ages 0–5) from over 680 hours of footage from 1992–2017 (see Table S4). Of the 436 peering events, 264 (60.55%) involved the learner peering at the model's entire nut-cracking bout. For the post-ELP efficiency measures, a total of 1098 nut-cracking bouts were recorded across the ten focal chimpanzees (five female and five male, ages 6–20) from 1998–2017[9].

Ethics. During the 1992–2017 research period, research authorisation and ethical approval were collectively given to TM, the leader of the Bossou Project of Kyoto University, from Guinean authorities (Direction Générale de la Recherche Scientifique et de l'Innovation Technologique, DGERSIT, and the Institut de Recherche Environnementale de Bossou,

IREB) based on the Memorandum of Understanding. Since data collected were all archival and required no human participants, no further ethical approval was required by the School of Anthropology and Museum Ethnography, University of Oxford, or the Social Science Division, University of Oxford.

Statistical analysis

All analyses were performed using R (v. 4.3.2)[62] and RStudio (v. 2023.09.1+494)[63] for MacOS. Given the small sample size, variation in the four developmental measures was assessed by comparing observed *t*-values to critical *t*-values ($p < 0.05$, two-tailed). All observed *t*-values less than the lower critical *t*-value threshold were significantly below average (e.g., significantly fewer learning opportunities provided by their mother, etc.), and all observed *t*-values greater than the upper critical *t*-value threshold were significantly above average (e.g., significantly more learning opportunities provided by their mother). These *t*-values were then used as predictors in the regression models. As *t*-scores use the average of the data points for each case, this approach resolves the issue of the data often being sequential, which leads to non-independence due to temporal autocorrelation[64].

For bout duration and strikes per nut efficiency measures, all "failed" bouts ($n = 146$) were removed to ensure the analyses assessed the amount of time and energy exerted to retrieve the energetic reward[9]. This left 952 post-ELP bouts for analysis. All bouts ($n = 1,098$) were analysed for success rate and displacement rate.

Mixed-effect models (with subject and mother as random intercepts) were constructed for each of the four efficiency outcome variables, with age, sex, whole bout peering proportion *t*-score, opportunity provision *t*-score, model tolerance *t*-score, and model intolerance *t*-score as predictors.

The bout duration data were log transformed to normalise the positively skewed distribution. The linear mixed-effects model for log bout duration was fitted using the *lme4* package[65]. The sex predictor had an issue of multicollinearity (VIF = 7.07), and so was removed from the model. A zero-truncated Poisson generalised linear mixed model (GLMM)

was fitted for strikes per nut using the *glmmTMB* package[66]. Overdispersion was detected, so a zero-truncated negative binomial GLMM with quadratic parameterisation was fitted to counteract this issue. For success rate, a cumulative link mixed model was fitted using the *ordinal* package[68] as the outcome variable data were ordered in order of increasing efficiency (Failed, Smash, Successful)[43]. Given the substantial number of zeros in the displacement rate data (n = 754), a zero-inflated (zi ~ 1) Poisson GLMM was fitted using the *glmmTMB* package. This model was over-dispersed, so a zero-inflated (zi ~ 1) negative binomial GLMM was fitted to the data. However, there was a model convergence problem, likely due to over-parameterisation with a small sample size. Removing the random intercepts for subject and mother fixed this issue; the final model thus did not contain random intercepts for subject and mother.

Allowing the intercept to vary by subject did not significantly improve the model fit for any of the models, as indicated by larger AIC scores. The assumptions of all models were checked *post hoc* (see Supporting Information).

Independent, hypothesis-blind coders reviewed 14.5 hours of footage for inter-coder reliability analyses, which totalled 81 peering events. Unweighted Cohen's κ indicated substantial agreement between coders for model tolerance ($\kappa = 0.797$, $z = 10.7$, $p < 0.001$), model intolerance ($\kappa = 0.741$, $z = 6.7$, $p < 0.001$), and whether the whole bout was peered at or not ($\kappa = 0.833$, $z = 7.51$, $p < 0.001$). For opportunity provision, two-way, single-rating random-effects intraclass correlation (ICC) analyses were performed using the *irr* package[69]. Results indicated excellent consistency between coders for both the start ($ICC(C,1) = 1$, $F(26,26) = 29775$, $1 < ICC < 1$, $p < 0.001$) and stop ($ICC(C,1) = 1$, $F(26,26) = 5403$, $0.999 < ICC < 1$, $p < 0.001$) time of maternal opportunity provision.

Acknowledgements

We thank the Direction Générale de la Recherche Scientifique et de l'Innovation Technologique and the Institut de Recherche Environnementale de Bossou in Guinea for research authorisation. The video data for this research was provided by the Bossou video archive team led by TM. The team consists of Tetsuro Matsuzawa, Dora Biro (University of Rochester), Misato Hayashi (Chubu Gakuin University), Susana Carvalho, and Catherine Hobaiter (University of St. Andrews). The original video archive was digitised, organised, and systematised by Daniel Schofield (University of Oxford), and catalogued by Alexander Mielke (Queen Mary University of London) and Sophie Berdugo. Special thanks to all the field assistants and researchers at Bossou, specifically Henry Didier Camara, Cé Vincent Mami, Gouanou Zogbila, Boniface Zogbila, Jules Doré, Gouanou Goumy, Tino Camara, Pascal Goumy, Paquílé Cherif, Jiles Gondo Doré, and Marcel Doré. Thank you to Alexander Mielke for early discussions about this research. Thank you to Rebecca Funnell and Carolyn Gover for research assistance with hypothesis-blind coding for the inter-rater reliability analyses.

Funding sources

This research was financially supported by the Clarendon Fund, the Keble College Sloane-Robinson Clarendon Scholarship, and the Boise Trust Fund (University of Oxford, UK) to **S.B.**, and by the Ministry of Education, Culture, Sports, Science, and Technology (MEXT), Japan, (grant numbers 07102010, 12002009, 16002001, 20002001, 24000001, and 16H06283) to **T.M.**.

References

1. Falótico, T., Bueno, C. Q. & Ottoni, E. B. Ontogeny and sex differences in object manipulation and probe tool use by wild tufted capuchin monkeys (*Sapajus libidinosus*). *Am. J. Primatol.* **83**, (2021).
2. Tan, A., Tan, S. H., Vyas, D., Malaivijitnond, S. & Gumert, M. D. There is more than one way to crack an oyster: identifying variation in Burmese long-tailed macaque (*Macaca fascicularis aurea*) stone-tool use. *PLoS One* **10**, e0124733 (2015).
3. Gumert, M. D., Kuan Hoong, L. & Malaivijitnond, S. Sex differences in the stone tool-use behaviour of a wild population of Burmese long-tailed macaques (*Macaca fascicularis aurea*). *Am. J. Primatol.* **73**, 1239–1249 (2011).
4. van Schaik, C. P., Fox, E. A. & Fechtman, L. T. Individual variation in the rate of use of tree-hole tools among wild orang-utans: implications for hominin evolution. *J. Hum. Evol.* **44**, 11–23 (2003).
5. Lonsdorf, E. V. Sex differences in the development of termite-fishing skills in the wild chimpanzees, *Pan troglodytes schweinfurthii*, of Gombe National Park, Tanzania. *Anim. Behav.* **70**, 673–683 (2005).
6. Luncz, L. V, Sirianni, G., Mundry, R. & Boesch, C. Costly culture: differences in nut-cracking efficiency between wild chimpanzee groups. *Anim. Behav.* **137**, 63–73 (2018).
7. Pascual-Garrido, A. Cultural variation between neighbouring communities of chimpanzees at Gombe, Tanzania. *Sci. Rep.* **9**, (2019).
8. Biro, D. *et al.* Cultural innovation and transmission of tool use in wild chimpanzees: evidence from field experiments. *Anim. Cogn.* **6**, 213–223 (2003).
9. Berdugo, S., Cohen, E., Davis, A. J., Matsuzawa, T. & Carvalho, S. Stable long-term individual variation in chimpanzee technological efficiency. *bioRxiv* 2023.11.21.568000 (2023).
10. Estienne, V., Stephens, C. & Boesch, C. Extraction of honey from underground bee nests by central African chimpanzees (*Pan troglodytes troglodytes*) in Loango National Park, Gabon: techniques and individual differences. *Am. J. Primatol.* **79**, e22672 (2017).
11. Gruber, T., Chimento, M., Aplin, L. M. & Biro, D. Efficiency fosters cumulative culture across species. *Philos. Trans. R. Soc. B Biol. Sci.* **377**, 20200308 (2021).
12. Pontzer, H. *et al.* Primate energy expenditure and life history. *Proc. Natl. Acad. Sci.* **111**, 1433–1437 (2014).
13. Mesoudi, A., Chang, L., Dall, S. R. X. & Thornton, A. The evolution of individual and cultural variation in social learning. *Trends Ecol. Evol.* **31**, 215–225 (2016).

14. Humle, T., Snowdon, C. T. & Matsuzawa, T. Social influences on ant-dipping acquisition in the wild chimpanzees (*Pan troglodytes verus*) of Bossou, Guinea, West Africa. *Anim. Cogn.* **12**, S37–S48 (2009).
15. Heyes, C. Social learning in animals: categories and mechanisms. *Biol. Rev.* **69**, 207–231 (1994).
16. Fröhlich, M., van Schaik, C. P., Van Noordwijk, M. A. & Knief, U. Individual variation and plasticity in the infant-directed communication of orang-utan mothers. *Proc. R. Soc. B Biol. Sci.* **289**, (2022).
17. van Schaik, C. P., Deaner, R. O. & Merrill, M. Y. The conditions for tool use in primates: implications for the evolution of material culture. *J. Hum. Evol.* **36**, 719–741 (1999).
18. Danchin, É. *et al.* Beyond DNA: integrating inclusive inheritance into an extended theory of evolution. *Nat. Rev. Genet.* **12**, 475–486 (2011).
19. van Schaik, C. P. & Pradhan, G. R. A model for tool-use traditions in primates: implications for the coevolution of culture and cognition. *J. Hum. Evol.* **44**, 645–664 (2003).
20. Carvajal, L. & Schuppli, C. Learning and skill development in wild primates: toward a better understanding of cognitive evolution. *Curr. Opin. Behav. Sci.* **46**, 101155 (2022).
21. Boyd, R., Richerson, P. J. & Henrich, J. The cultural niche: why social learning is essential for human adaptation. *Proc. Natl. Acad. Sci.* **108**, 10918–10925 (2011).
22. Harmand, S. & Arroyo, A. Linking primatology and archaeology: the transversality of stone percussive behaviors. *J. Hum. Evol.* **181**, (2023).
23. Matsuzawa, T. Stone tools for nut-cracking. in *The Chimpanzees of Bossou and Nimba* (eds. Matsuzawa, T., Humle, T. & Sugiyama, Y.) 73–84 (Springer, 2011).
24. Boesch, C. & Boesch, H. Sex differences in the use of natural hammers by wild chimpanzees: a preliminary report. *J. Hum. Evol.* **10**, 585–593 (1981).
25. Sugiyama, Y. & Koman, J. Tool-using and -making behaviour in wild chimpanzees at Bossou, Guinea. *Primates* **20**, 513–524 (1979).
26. Sugiyama, Y., Fushimi, T., Sakura, O. & Matsuzawa, T. Hand preference and tool use in wild chimpanzees. *Primates* **34**, 151–159 (1993).
27. Inoue-Nakamura, N. & Matsuzawa, T. Development of stone tool use by wild chimpanzees (*Pan troglodytes*). *J. Comp. Psychol.* **111**, 159–173 (1997).
28. Matsuzawa, T. *et al.* Emergence of culture in wild chimpanzees: education by master-apprenticeship. in *Primate origins of human cognition and behavior* (ed. Matsuzawa, T.) 557–574 (Springer, 2001).

29. Koops, K., Gaspard Soumah, A., van Leeuwen, K. L., Didier Camara, H. & Matsuzawa, T. Field experiments find no evidence that chimpanzee nut cracking can be independently innovated. *Nat. Hum. Behav.* **6**, 487–494 (2022).
30. Biro, D., Sousa, C. & Matsuzawa, T. Ontogeny and cultural propagation of tool use by wild chimpanzees at Bossou, Guinea: case studies in nut cracking and leaf folding. in *Cognitive development in chimpanzees* (eds. Matsuzawa, T., Tomonaga, M. & Tanaka, M.) 476–506 (Springer, 2006).
31. Fröhlich, M., Müller, G., Zeiträg, C., Wittig, R. M. & Pika, S. Begging and social tolerance: food solicitation tactics in young chimpanzees (*Pan troglodytes*) in the wild. *Evol. Hum. Behav.* **41**, 126–135 (2020).
32. Ottoni, E. B. The lasting and the passing: behavioural traditions and opportunities for social learning in wild tufted capuchin monkeys. in *Comparative cognition: commonalities and diversity* (eds. Anderson, J. R. & Kuroshima, H.) 153–169 (Springer Singapore, 2021).
33. Miu, E., Gulley, N., Laland, K. N. & Rendell, L. Flexible learning, rather than inveterate innovation or copying, drives cumulative knowledge gain. *Sci. Adv.* **6**, eaaz0286 (2020).
34. Schuppli, C. & van Schaik, C. P. Animal cultures: how we've only seen the tip of the iceberg. *Evol. Hum. Sci.* **1**, 1–13 (2019).
35. Lonsdorf, E. V, Eberly, L. E. & Pusey, A. E. Sex differences in learning in chimpanzees. *Nat. Br. Commun.* **428**, 715–716 (2004).
36. Koops, K., Furuichi, T., Hashimoto, C. & van Schaik, C. P. Sex differences in object manipulation in wild immature chimpanzees (*Pan troglodytes schweinfurthii*) and bonobos (*Pan paniscus*): preparation for tool use? *PLoS One* **10**, e0139909 (2015).
37. Lonsdorf, E. V. What is the role of mothers in the acquisition of termite-fishing behaviors in wild chimpanzees (*Pan troglodytes schweinfurthii*)? *Anim. Cogn.* **9**, 36–46 (2006).
38. Crosbie, J. Negative reinforcement and punishment. in *Handbook of research methods in human operant behavior* (eds. Lattal, K. A. & Perone, M.) 163–189 (Springer US, 1998).
39. Eshchar, Y., Izar, P., Visalberghi, E., Resende, B. D. & Fragaszy, D. M. When and where to practice: social influences on the development of nut-cracking in bearded capuchins (*Sapajus libidinosus*). *Anim. Cogn.* **19**, 605–618 (2016).
40. Estienne, V., Cohen, H., Wittig, R. M. & Boesch, C. Maternal influence on the development of nut-cracking skills in the chimpanzees of the Taï forest, Côte d'Ivoire (*Pan troglodytes verus*). *Am. J. Primatol.* **e23022**, (2019).

41. Fragaszy, D. M. *et al.* The fourth dimension of tool use: temporally enduring artefacts aid primates learning to use tools. *Philos. Trans. R. Soc. B* **368**, (2013).
42. Bain, M. *et al.* Automated audiovisual behavior recognition in wild primates. *Sci. Adv.* **7**, eabi4883 (2021).
43. Tan, A. From play to proficiency: the ontogeny of stone-tool use in coastal-foraging long-tailed macaques (*Macaca fascicularis*) from a comparative perception-action perspective. *J. Comp. Psychol.* **131**, 89–114 (2017).
44. Sirianni, G., Luncz, L. V & Gratton, P. An energetic model of foraging optimization: wild chimpanzee hammer selection for nut-cracking. in *The chimpanzees of the Taï forest: 40 years of research* (eds. Boesch, C. & Wittig, R.) 104–124 (Cambridge University Press, 2019).
45. McGrew, W. C. Ten dispatches from the chimpanzee culture wars. in *Animal aocial complexity: intelligence, culture, and individualized societies* (eds. de Waal, F. B. M. & Tyack, P. L.) 419–439 (Harvard University Press, 2003).
46. Whiten, A. Blind alleys and fruitful pathways in the comparative study of cultural cognition. *Phys. Life Rev.* **43**, 211–238 (2022).
47. Tennie, C., Call, J. & Tomasello, M. Ratcheting up the ratchet: on the evolution of cumulative culture. *Philos. Trans. R. Soc. B* **364**, 2405–2415 (2009).
48. Gruber, T. & Biro, D. Escaping a blind alley: the ZLS as a 'cultural crucible'?: Comment on "Blind alleys and fruitful pathways in the comparative study of cultural cognition" by Andrew Whiten. *Phys. Life Rev.* **44**, 86–88 (2023).
49. Wittig, R. M. & Boesch, C. Demography and life history of five chimpanzee communities in Taï National Park. in *The chimpanzees of the Taï forest: 40 years of research* (eds. Boesch, C. & Wittig, R. M.) 125–140 (Cambridge University Press, 2019).
50. Laland, K. N. Social learning strategies. *Learn. Behav.* **32**, 4–14 (2004).
51. Horner, V., Proctor, D., Bonnie, K. E., Whiten, A. & de Waal, F. B. M. Prestige affects cultural learning in chimpanzees. *PLoS One* **5**, e10625 (2010).
52. Kendal, R. L. *et al.* Chimpanzees copy dominant and knowledgeable individuals: implications for cultural diversity. *Evol. Hum. Behav.* **36**, 65–72 (2015).
53. Hayes, L. D. & Schradin, C. Long-term field studies of mammals: what the short-term study cannot tell us. *J. Mammal.* **98**, 600–602 (2017).
54. Expert Working Group on Animal Culture and Social Complexity. *Reports of the Concerted Action Sub-Groups: Chimpanzees*. https://www.cms.int/sharks/en/document/reports-concerted-action-sub-groups-chimpanzees (2023).

55. van Schaik, C. P. Fragility of traditions: the disturbance hypothesis for the loss of local traditions in orangutans. *Int. J. Primatol.* **23**, 527–538 (2002).
56. Humle, T. Location and ecology. in *The chimpanzees of Bossou and Nimba* (eds. Matsuzawa, T., Humle, T. & Sugiyama, Y.) 13–21 (Springer, 2011).
57. Matsuzawa, T. & Humle, T. Bossou: 33 years. in *The chimpanzees of Bossou and Nimba* (eds. Matsuzawa, T., Humle, T. & Sugiyama, Y.) 3–10 (Springer, 2011).
58. Sugiyama, Y. & Koman, J. Social structure and dynamics of wild chimpanzees at Bossou, Guinea. *Primates* **20**, 323–339 (1979).
59. Matsuzawa, T. Field experiments on use of stone tools by chimpanzees in the wild. in *Chimpanzee cultures* (eds. Wrangham, R. W., McGrew, W. C., De Waal, F. B. M. & Heltne, P. G.) 351–370 (Harvard University Press, 1994).
60. Friard, O. & Gamba, M. BORIS: a free, versatile open-source event-logging software for video/audio coding and live observations. *Methods Ecol. Evol.* **7**, 1325–1330 (2016).
61. *The chimpanzees of Bossou and Nimba*. (Springer, 2011).
62. R Core Team. R: a language and environment for statistical computing. (2023).
63. Posit team. RStudio: integrated development environment for r. (2023).
64. Setchell, J. M. *Studying primates: how to design, conduct and report primatological research*. (Cambridge University Press, 2019).
65. Bates, D., Maechler, M., Bolker, B. & Walker, S. Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* **67**, 1–48 (2015).
66. Brooks, M. E. *et al.* glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *R J.* **9**, 378–400 (2017).
67. Lüdecke, D., Ben-Shachar, M. S., Patil, I. & Makowski, D. performance: an R package for assessment, comparison and testing of statistical models. *J. Open Source Softw.* **6**, 3139 (2021).
68. Christensen, R. H. B. ordinal - regression models for ordinal data. (2019).
69. Gamer, M., Lemon, J., Fellows, I. & Singh, P. irr: various coefficients of interrater reliability and agreement. (2019).

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Supporting Information for

The ontogeny of chimpanzee technological efficiency

Sophie Berdugo*[1,2,3], Emma Cohen[1,2,4], Arran J. Davis[1,2,4], Tetsuro Matsuzawa[5,6,7], Susana Carvalho[2,3,8]

[1] Institute of Human Sciences, University of Oxford, Oxford, OX2 6NP, United Kingdom
[2] School of Anthropology and Museum Ethnography, University of Oxford, Oxford, OX2 6PE, United Kingdom
[3] ICArEHB, Interdisciplinary Center for Archaeology and Evolution of Human Behaviour FCHS, Universidade do Algarve, Faro 8005, Portugal
[4] Wadham College, University of Oxford, Oxford, OX1 3PN, United Kingdom
[5] Department of Pedagogy, Chubu Gakuin University, Gifu, 504-0837, Japan
[6] Division of the Humanities and Social Sciences, California Institute of Technology, Pasadena, CA 91125, United States
[7] College of Life Science, Northwest University, Xi'an 710069, China
[8] Department of Science, Gorongosa National Park, Sofala, Mozambique

*Corresponding author

Email: sophie.berdugo@anthro.ox.ac.uk

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Statistical Analysis

Assumption checks. *Post hoc* analyses were run to check the model assumptions. For the *bout duration* linear model, multicollinearity between the predictor variables was checked using the *vif* function from the *car* package[1]. The VIFs did not exceed 3.34, indicating no issues with multicollinearity[2]. The normality of the residuals was checked visually using a histogram and QQ-plot and homoscedasticity was assessed with a plot of fitted values against squared residuals. Influential observations were identified using the *cooks.distance* function from the *car* package. The linear model was rerun without the 65 observations that exceeded three times the mean of the Cooks Distance. All results remained unchanged, but the effect of one predictor—social learning opportunities provided by the maternal model—became significant (t = -3.263, $p < 0.01$).

For the *success rate* cumulative link model, the normality of the surrogate residuals[3] was checked using a QQ-plot and the homoscedasticity was checked with a plot of fitted values against surrogate residuals[4] using the *sure* package[5]. For the *strikes per nut* and *displacement rate* glmmTMB models, the normality of the simulated residuals and homoscedasticity were checked using the *DHARMa* package[6]. No significant problems of homoscedasticity were detected for either model when the model residuals were plotted against the predicted values. The QQ-plot of expected *versus* observed residuals indicated the simulated residuals did not deviate from normality for *displacement rate*. However, the simulated residuals deviated from normality for *strikes per nut*, likely due to the presence of nine outliers (indicated by a two-sided DHARMa bootstrapped outlier test, $p < 0.05$). The *strikes per nut* zero-truncated negative binomial model was rerun with these nine outlying observations removed, which resolved the issue of the normality of the residuals. Results of the *strikes per nut* model were unchanged, suggesting the results are robust to outliers.

Table S1. Ethogram of behaviours coded in BORIS.

Behavioural Category	**Type**	**Definition**
Start Peering	Point event	The start of the period when the focal subject's gaze is directly oriented towards a model's hand, arm, nut, or stone tool composite during a nut-cracking bout.
End Peering	Point event	When the focal subject's gaze is no longer oriented towards the model's hand or arm or towards the nut and stone tool composite.
Start Opportunity	Point event	When the focal's mother commences nut-cracking whilst the focal subject is in the outdoor laboratory.
End Opportunity	Point event	The focal's mother ceases to crack nuts whilst the focal subject is in the outdoor laboratory.
Total Visibility	State event	The continuous period of when the focal subject's mother is on camera whilst the focal subject is in the outdoor laboratory.

Table S2. Modifiers applied to the ethogram in BORIS.

Behaviour	Modifier	Definition
Start Peering	Model name	The name of the individual the focal subject was peering at during their nut-cracking bout.
	Maternal model	Whether the model was the learner's mother or not.
End Peering	Complete peering event	Whether or not the full peering event was able to be recorded because of the video footage itself.
	Whole bout	Whether or not the learner was peering for the whole nut-cracking bout.
	Model name	The name of the individual the focal subject was peering at during their nut-cracking bout.
	Maternal model	Whether or not the model was the learner's mother.
	Model tolerance	Whether the model permitted any of the following learner behaviours: scrounge, tool interaction, model interaction, proximity.
	Model intolerance	Whether the model expressed physical or vocal intolerance towards the learner.
End Opportunity	Complete opportunity	Whether or not the full opportunity was able to be recorded because of the video footage itself.
	Learner behaviour	Which behaviour(s) the infant was engaged in when their mother was cracking nuts: solitary play, social play, object play, behavioural episode, bout, feeding, drinking, resting, peering, clinging, unknown.
	Scrounge events	How many times the focal subject took the kernel extracted by the maternal model to eat themselves. Only record these scrounge events where the focal subject took the kernel but did not peer at the nut-cracking bout.

Table S3. Genealogy of the Bossou chimpanzees since the formation of the field site in 1976.

Mother	Born	Disappeared	Offspring	Offspring sex	Born	Disappeared
Jire	~1958	Present	Ja	Female	1983	Feb 1993
			Jokuro	Female	1989	Jan 1992
			Juru	Female	1993	Dec 2001
			Jeje	Male	1997	Present
			Jimato	Male	2002	Dec 2003
			Joya	Female	2004	2013
			Jodoamon	Female	2009	2010
Yo	~1961	2022	Yunro	Female	1984	Feb 1993
			Yolo	Male	1991	Nov 2009
Fana	~1956	Sept 2022	Foaf	Male	1980	2023
			Fotaiu	Female	1991	Nov 2004
			Fanle	Female	1997	Feb 2024
Fanle	1997	Feb 2024	Flanle	Male	2007	Aug 2016*
			Fanwa	Male	2012	Present
			Fangasi	Female	2020	2021
Fotaiu	1991	Nov 2004	Fokaiye	Male	2001	Nov 2004
Pama†	~1967	Sept 2013*	Pili	Female	1987	May 2001
			Poni	Male	1993	Dec 2003
			Peley	Male	1998	Sept 2013*
Pili	1987	May 2001	Pokuru	Male	1996	May 2001
Velu	~1959	Mar 2017*	Vube	Female	1982	Mar 1990
			Vui	Male	1986	Jul 1999
			Vuavua	Female	1991	Mar 2004
Vuavua	1991	Mar 2004	Veve	Female	2001	Dec 2003
Nina†	~1954	Nov 2003	Na	Male	1985	May 1996
			Nto	Female	1993	Dec 2001
Kai	1950	Dec 2003	Kie	Female	1976	Dec 2003
Kie	1976	Dec 2003	Kakuru	Female	1986	Mar 1991

Notes: Data from "*The Chimpanzees of Bossou and Nimba,*" eds. T., Matsuzawa, T., Humle, & Y., Sugiyama, 2011, Appendix A, p. 404–5. * = Data from "*The chimpanzees in Bossou,*" https://www.greencorridor.info/en/chimp/profile/relationship.html. † = Could not crack nuts.

Table S4. Focal subject information and data summary.

Subject	Sex	Learning period	Post-learning period	Nut-cracking mother	Age range	Proportion peering whole bout	Opportunity provision	Mean tolerance	Mean intolerance	Post-learning period bouts
Fotaiu	F	1992–1997	1998–2003	Yes	0–11	0.606	0.675	0.758	0.030	90
Vuavua	F	1992–1997	1998–2004	Yes	0–12	0.500	0.403	1.100	0.100	106
Yolo	M	1992–1997	1998–2009	Yes	0–17	0.440	0.593	1.160	0.100	208
Juru†	F	1994–1999	-	Yes	0–5	0.750	0.613	1.090	0.136	-
Nto	F	1994–1999	2000	No	0–6	0.529	-	1.060	0.000	11
Poni	M	1994–1999	2000–2002	No	0–9	0.571	-	1.000	0.000	41
Pokuru*	M	1997–2000	-	Yes	0–4	0.222	0.366	1.440	0.333	-
Fanle	F	1998–2003	2004–2017	Yes	0–20	0.742	0.541	1.160	0.129	234
Jeje	M	1998–2003	2004–2017	Yes	0–20	0.704	0.642	1.090	0.185	236
Peley	M	1999–2004	2005–2012	No	0–14	0.733	-	1.000	0.133	133
Joya	F	2004–2010	2010–2012	Yes	0–8	0.810	0.556	0.667	0.000	25
Flanle	M	2008–2013	2014	Yes	0–6	0.492	0.448	1.010	0.129	14
Fanwa†	M	2012–2017	-	Yes	0–5	0.483	0.415	1.170	0.172	-

Notes: * = Died before the end of their learning period. † = No data on post-learning period nut-cracking efficiency.

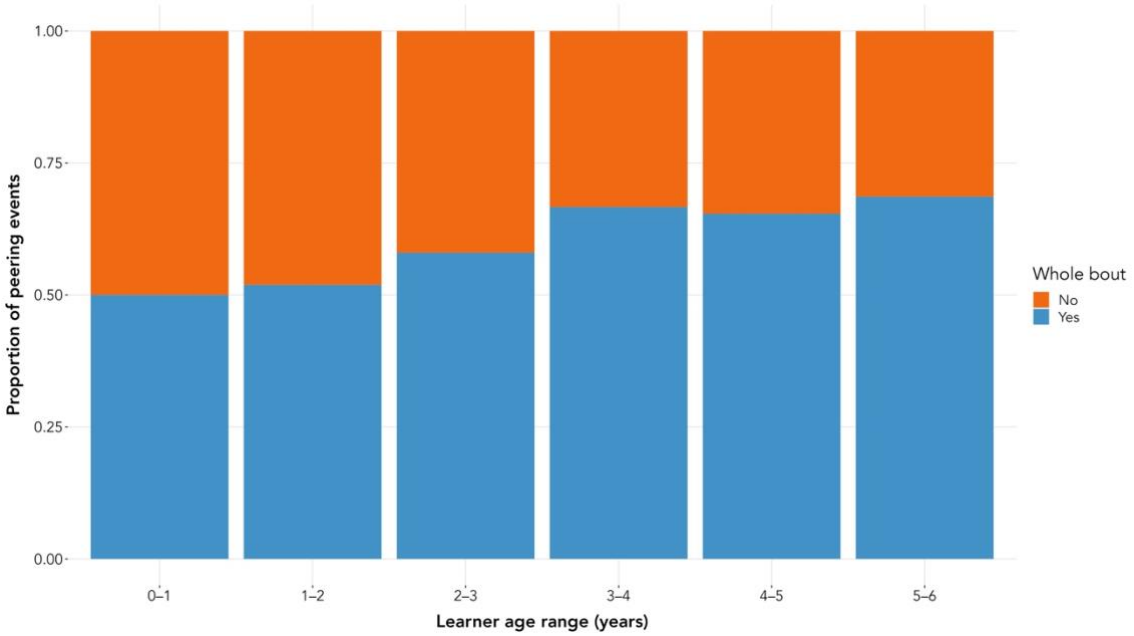


Figure S1. Proportion of peering at the whole nut-cracking bout according to the learner's age.
Note: The age range for each bar is inclusive of the lower value and exclusive of the upper value (e.g., $0 \leq x < 1$).

SI References

1. Fox, J. & Weisberg, S. *An R companion to applied regression*. (Sage, 2019).
2. Field, A., Miles, J. & Field, Z. *Discovering statistics using R*. (SAGE Publications, 2012).
3. Liu, D. & Zhang, H. residuals and diagnostics for ordinal regression models: a surrogate approach. *J. Am. Stat. Assoc.* **113**, 845–854 (2018).
4. Greenwell, B., McCarthy, A., Boehmke, B. C. & Liu, D. Residuals and diagnostics for binary and ordinal regression models: an introduction to the sure package. *R J.* **10**, 381 (2018).
5. Greenwell, B., McCarthy, A. & Boehmke, B. sure: surrogate residuals for ordinal and general regression models. (2017).
6. Hartig, F. & Lohse, L. DHARMa: residual diagnostics for hierarchical (multi-level/mixed) regression models (2022).

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THE ROLE OF NON-KIN IN THE TRANSMISSION OF A PREHISTORIC APE CULTURE

In preparation for submission to *Nature Human Behaviour*

The role of non-kin in the transmission of a prehistoric ape culture

Berdugo, S.[1,2,3], Cohen, E.[1,2,4], Davis, A. J.[1,2,4], Matsuzawa, T.[5,6,7], Schofield, D. P. [2,8] & Carvalho, S. [2,3,9]

[1] Institute of Human Sciences, University of Oxford, Oxford, OX2 6NP, United Kingdom

[2] School of Anthropology and Museum Ethnography, University of Oxford, Oxford, OX2 6PE, United Kingdom

[3] ICArEHB, Interdisciplinary Center for Archaeology and Evolution of Human Behaviour FCHS, Universidade do Algarve, Faro 8005, Portugal

[4] Wadham College, University of Oxford, Oxford, OX1 3PN, United Kingdom

[5] Department of Pedagogy, Chubu Gakuin University, Gifu, 504-0837, Japan

[6] Division of the Humanities and Social Sciences, California Institute of Technology, Pasadena, CA 91125, United States

[7] College of Life Science, Northwest University, Xi'an 710069, China

[8] Department of Engineering Science, University of Oxford, Oxford, OX1 3PJ, United Kingdom

[9] Department of Science, Gorongosa National Park, Sofala, Mozambique

Corresponding author

Sophie Berdugo, Institute of Human Sciences,

School of Anthropology and Museum Ethnography, University of Oxford,

Oxford, OX2 6PE, United Kingdom,

sophie.berdugo@anthro.ox.ac.uk

Abstract

Mothers are typically regarded to be the most important social learning model for skill and cultural behaviour acquisition during early primate development. However, in humans, unrelated individuals are also known to be central to knowledge sharing. Given the trade-off between information accuracy and time-investment in social learning, it pays to be selective in whom to learn from. Yet, despite the implications for cultural transmission in hominins, no research has investigated the use of these social learning strategies by wild chimpanzee infants learning pre-established material culture. Here, we present results from data collected over a 25-year period, during which young wild chimpanzees (0–5 years old) routinely peered at models to learn how to use stone tools to crack nuts. Though mothers were the primary models during the critical period of dependency prior to weaning (0–4 years), when learners reached age 5, non-kin became the main models. Throughout the whole 5-year learning period, 40% of peering events involved the learner observing a non-maternal model. When multiple potential models were cracking at the same time and the learners peered at non-maternal models, the age and sex of the model did not affect the likelihood of being peered at, but models with lower rates of displacing the nut and longer bouts were more likely to be observed. Non-kin were the predominant model choice. As such, non-kin support the transmission of a complex chimpanzee technology that is known to be at least 4,300 years old.

Main

Learning complex skills and information socially—that is, via other individuals or their products[1]—allows for faster acquisition relative to solely relying on asocial learning (i.e., through trial-and-error). Because of the inherent trade-off between time-investment and information accuracy in social learning[2], individuals benefit from being selective in whom they choose to learn from. There is evidence that social learning across taxa is not indiscriminate, but supported by strategies that guide *who* is copied, and *when*[3]. These social learning strategies, such as copying prestigious individuals[4,5], are well established in humans[6,7], and have also been found in insects[8,9], fish[10], birds[11–14], and primates[15–18].

Model-based ("who") selection strategies guide the evolutionary trajectory of cultural traits within groups, with the inheritance of cultural traits by younger generations being contingent upon the variant used by the most frequently copied models. However, there has been limited research investigating strategies based on model-specific characteristics during the acquisition of material culture in wild chimpanzees, and no research has assessed how skill efficiency affects the likelihood of a model being observed. Here, we establish apparent "who" social learning strategies in the development of a wild chimpanzee cultural technological behaviour over a 25-year period.

The social learning capabilities of humans and (captive) chimpanzees have frequently been compared[19–22]. Such research often seeks to establish the unique human skill that enabled the expansion into the so-called "cultural niche"[23]. Indeed, the human propensity to learn faithfully from other individuals is considered an essential adaptation, supporting unprecedented geographical expansion and the accumulation of a vast amount of cultural knowledge[23]. Moreover, an emergent property of the way human societies are structured is that transmission appears to be maximised. For example, the organisation of Agta (Philippines) and BaYaka (Republic of the Congo) social networks support efficient cultural transmission among these hunter-gatherer populations, with a few strong connections between non-kin being essential for knowledge sharing between individuals[24]. Migliano and

colleagues found that knowledge sharing about plants between mother and child is lower than that between non-kin (odds of shared knowledge were 1.48 and 1.82, respectively), demonstrating the key role of "friendships" in the transmission of information. The authors referenced previous findings that hunter-gatherers interact with over 10 times the number of individuals over the course of their lives than do chimpanzees[25], which they argue promotes the formation of these "friendships" in humans.

Although chimpanzees may encounter fewer individuals over their lifetime, they possess a range of cultural behaviours which are reliant upon learning from conspecifics[26,27]. Chimpanzees are typically male philopatric and live in multimale/multifemale groups which exhibit fission-fusion dynamics[28]. As such, their group composition allows access to both kin and non-kin as potential models from whom to learn. This offers an opportunity to study the extent to which learning takes place between non-kin, as in humans. If non-kin are found to be similarly important to knowledge transfer in chimpanzees as in humans, this would suggest that the relatively fewer interactions with non-kin over a lifetime in chimpanzees does not preclude their importance for cultural transmission. If non-kin social learning strategies are not identified in chimpanzees, this may highlight a qualitative difference between human and chimpanzee social and cultural learning. Either way, to draw inferences about early hominin cultural transmission, such as of lithic technology, it is essential to study the social learning strategies employed by wild chimpanzees during behavioural acquisition and cultural maintenance[29].

Chimpanzees in Bossou, Guinea, use stone hammers and anvils to crack oil palm nuts (*Elaeis guineensis*). Nut-cracking using stone tools is a prehistoric West African chimpanzee behaviour, persisting for at least the last 4,300 years[30]. It takes Bossou infants approximately 3–5 years[31] to develop this complex skill via an "education by master-apprenticeship" learning process[32], where tolerant, competent conspecifics ("masters") act as models of the behaviour for the infants ("apprentices") to peer at (defined as close and focused watching of a conspecific's behaviour, adapted from Schuppli et al., 2016[33]).

Learners will sometimes scrounge (i.e., steal) the extracted kernel, which provides them with important positive reinforcement[34]. Although infants use a mixture of individual and social learning to acquire the skill[31], the behaviour is not readily independently re-innovated by naïve wild chimpanzees[27]. There are significant individual differences in technological efficiency once the behaviour has been learned[35], which would provide learners with sufficient variation upon which to select models if a *copy successful individuals* social learning strategy is used in the community.

Previous studies indicate the importance of maternal models for the acquisition of this prehistoric skill in early infancy, and the increasing role non-maternal models play for older infants and juveniles. For example, research on three Bossou chimpanzees over four years found that the proportion of peering directed towards the learner's mother significantly decreases as a function of age, with mothers being observed 100%, 71%, 42%, and 14% of the time at 0.5, 1.5, 2.5, and 3.5 years old, respectively[36]. Where their mother was not the model, infants peered at adult females (64%), juveniles (21%), an alpha male (9%), and siblings (7%). However, this research is constrained by a limited sample size, and there have been no replications of the assessment of the changing importance of matrilineal kin and non-kin during the acquisition of nut-cracking.

It should be noted that, although preliminary, these results are not isolated: similar patterns have been observed in Sumatran (*Pongo abelii*) and Bornean orangutans (*P. pygmaeus wurmbii*), with infants increasingly peering at non-maternal models as they age[33]. Collectively, these findings support the two-phase model of primate social learning within natal groups: mothers are the first primary focus of social learning, with the focus widening beyond the mother to the broader group as learners age[37]. Whiten and van de Waal explained that this wider pool of models later in development is constrained to the groupmates who tolerate close-range learning[37].

Subsequent research over two field seasons (2000 and 2002) reported that the Bossou chimpanzees preferentially peered at conspecifics who were either the same age or older

than themselves (but never younger), and that infants peered at relatives (including their mother) significantly more than juveniles did[31]. However, of the 203 episodes of observational learning assessed in this research, the majority were directed at individuals cracking non-native nut species (*Coula edulis* and *Panda oleosa*) which had been experimentally introduced to Bossou, with only the minority of peering being towards the natural oil palm nut-cracking behaviour. This is important, as although this research provides a critical insight into how behavioural modifications may spread through a population, we cannot be sure how this affects the dynamics of information learning and transmission and so it may not speak to the strategies that maintain pre-existing cultural traits intergenerationally. Moreover, to date, no research has established whether the extra-maternal model selection is determined by the characteristics of the conspecific.

Previous studies have demonstrated that primates consider dominance when selecting an individual from whom to learn. Wild vervet monkeys (*Chlorocebus pygerythrus*) preferentially learned how to open a box (which could be opened in two ways) from high-ranking individuals, but exhibited no kin-, sex-, or age-based transmission biases[38]. Similarly, wild vervets directed their learning of a food processing technique for a novel resource (peanuts; *Arachis hypogaea*) towards high-ranking conspecifics but showed no sex or kin biases[39]. Semi-wild chimpanzees (*P. t. schweinfurthii*) from the Chimfunshi Wildlife Orphanage Trust, Zambia, were most influenced by older and higher-ranking conspecifics when engaging in the grooming handclasp social custom[40]. Non-kin were just as likely to influence learners' behaviour as mothers, highlighting the central role of oblique (via older non-kin) as well as vertical transmission (via older kin) in social learning. Moreover, experimental research on captive chimpanzees found that no one learned from the lowest ranking female after she discovered an alternative solution to a seeded behaviour, which is consistent with a rank-based social learning strategy[41].

There is also evidence of a proficiency bias when primates are selecting models. When presented with increasingly challenging foraging tasks, semi-free ranging Barbary

macaques (*Macaca sylvanus*) relied on social learning for the most challenging task (a *copy when uncertain* strategy) and copied the most successful model[17]. Wild tufted capuchins (*Sapajus* spp.) not only selected older and higher-ranking models, but also actively chose more proficient conspecifics when learning to use stone tools to crack queen palm nuts (*Syagrus romanzoffiana*)[15]. Semi-free-ranging brown capuchins (*Cebus apella*) preferred more proficient nut-cracking models, indicating that they incorporate knowledge of conspecifics' relative tool using skills into their model selection process[42]. Moreover, research undertaken over the course of a year found that infant long-tailed macaques (*M. fascicularis*) learning to use stone tools to open sessile oysters preferentially selected older and more efficient models (those requiring fewer hammer strikes to extract the resource)[18]. Captive chimpanzees also employ "who" social learning strategies. When given the choice, chimpanzees copied the behaviour of the highest ranking and more experienced model significantly more frequently than of the less prestigious and experienced model when learning to solve token tasks[43]. Similarly, when presented with a novel extractive foraging task, chimpanzees employed *copy higher ranking individuals* and *copy knowledgeable individuals* biases[16]. Wild female chimpanzees in Taï National Park, Côte d'Ivoire, conformed to the nut-cracking technique of their post-migration community, even when their original technique was more efficient[44]. Also, the novel moss-sponging behaviour that arose in the Sonso chimpanzee community in Budongo National Park, Uganda, in 2011 spread via matrilines three years later[45]. However, to date, there has been no research investigating whether wild chimpanzee infants and juveniles employ social learning strategies when selecting which model(s) from whom to learn pre-established extractive foraging skills.

The use of captive primates or artificial apparatuses in social learning research lacks ecological validity and generalisability to wild populations. Although these approaches allow for experimental control when assessing the spread of a behaviour through a group, it cannot speak to what primates do in their natural environments. Moreover, this research, and other previous research in this area more generally, is limited by the lack of long-term

data. Using long-term data on wild primate behaviour enables the effects of development to be tested, as well as the potential phenotypic plasticity of traits to be identified[46]. Therefore, tracking social learning strategies across the course of the development of the skill in the wild is crucial for understanding cultural transmission in primates.

This study assessed whether model-based social learning strategies exist during the transmission of stone tool-use to crack oil palm nuts in a 25-year (1992–2017) video archive of the wild Bossou chimpanzee population. Data were collected from each year of the early learning period (hereafter, "ELP"; ages 0–5) for all 13 learners present in the archive (see Table S1). We first investigated the changing role of the mother, matrilineal kin (maternal grandmothers and siblings), and non-kin during the course of the education by master-apprenticeship learning process. Next, we assessed whether the efficiency, kin, age, and sex of the non-maternal nut-cracking models affected their likelihood of being peered at (see Figure 1).



Figure 1. Infant and juvenile chimpanzees peering at conspecifics cracking nuts. Learners peer at non-maternal models whilst their mothers are also nut-cracking (A and B), and at matrilineal kin, such as their grandmother (C) or non-kin (D) when their mother is not cracking nuts. Image credit: Tetsuro Matsuzawa.

Results

Peering events. Peering events were defined as the period during which a learner was watching a nut-cracking model's hand, arm, nut, or hammer-and-anvil composite whilst they were cracking an oil palm nut. A total of 439 peering events were recorded across 13 learners (six females, seven males; ages 0–5) peering at 18 models (ten females, eight males; ages 6–58) from 1992–2017 (see Table S2). A similar number of peering events were obtained for female learners (204; 46.47%) and male learners (235; 53.53%). For the ten learners (five females, five males) with a mother who cracked nuts, 257 (68.35%) peering events were directed at their mother, 25 (6.65%) were towards matrilineal kin such as their maternal grandmother or sibling, and 94 (25%) involved non-kin. For the three learners (one female, two males) with no maternal model available, 10 (15.87%) were towards matrilineal kin, and 53 (84.13%) involved non-kin. Of all 147 peering events directed at non-kin, five were directed towards individuals aged 5 or younger and still learning the skill (two the same age as the learner, and three just two years older than the learner). As no efficiency data were available for these models[34], these peering events were excluded from the analyses.

Learners scrounged the extracted kernel in 18.45% of peering events. Scrounging was predominantly from their mother (80.25%) and was higher in older infants/juveniles (3–5 years old; 70.37%) than in younger infants (0–2 years old; 29.63%). Moreover, learners were more likely to scrounge from female than male non-maternal models (68.75% *versus* 31.25%, respectively).

Age-related changes in model selection. The proportion of peering events directed towards mothers, matrilineal kin, and non-kin varied throughout the nut-cracking learning period of the ten learners with nut-cracking mothers (see Figure 2). From ages 0 to 4, mothers were the most peered at models, with a downward trend in the proportion of peering events directed towards the mother from ages 3 and 4. At age 5, mothers dropped to being less than 50% of all peering events.

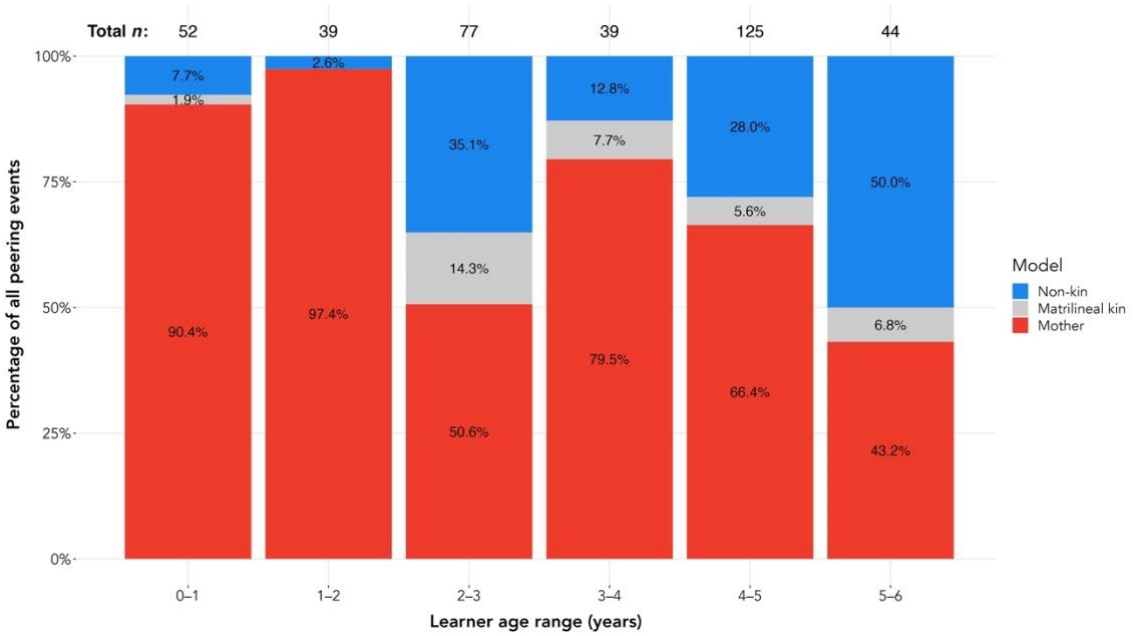


***Figure 2*.** Percentage of peering events directed towards maternal and non-maternal models throughout the nut-cracking early learning period for the ten learners whose mothers could crack nuts.
Notes: The total number of peering events for each learner age range is shown above. The age range for each bar is inclusive of the lower value and exclusive of the upper value (e.g., $0 \leq x < 1$).

Peering at non-maternal models. A binomial logistic regression was performed to assess the likelihood of a non-maternal model (n = 17) being peered at (1) or not (0) by a learner (n = 10), across all 116 peering events where the model was not the learners' mother. The regression included learner age, model age, model sex, kinship, and model nut-cracking efficiency (bout duration rank, strikes per nut rank, success rate rank, and displacement rate rank) as fixed effects, and nut-cracking model ID was included as a random intercept. Efficiency ranks ranged from 1–13, with 1 indicating the relatively most efficient individual, and 13 the relatively least efficient individual. As the full model failed to converge, a reduced model was fitted with kinship, model sex, bout duration rank, and displacement rate rank as fixed effects, and nut-cracking model ID included as a random intercept.

There were no significant effects of model sex (z = 0.586, p > 0.05) on the likelihood of being peered at. Model sex was thus removed from the reduced model to improve model fit (smaller Akaike Information Criterion). Results of this reduced model (see Table S3) revealed that being kin *reduced* the likelihood of a nut-cracking individual being peered at

by a learner (z = -3.912, p < 0.001); the odds of being peered at were 95% lower for kin than for non-kin. Displacement rate ranking had a significant negative effect on the likelihood of being peered at (i.e., relatively more efficient models were more likely to be peered at; z = -3.890, p < 0.001), whereas bout duration rank had a significant positive effect of on the likelihood of being peered at (i.e., relatively less efficient models were more likely to be peered at; z = 2.399, p < 0.05). The relationship between kinship, bout duration rank, displacement rank, and the likelihood of being peered at showed significant variance in intercepts across nut-cracking models (z = 2.752, p < 0.001).

"Who" social learning strategies. Next, we assessed the 79 peering events where all learners (n = 13) peered at a model other than their mother and had options for which model to peer at (i.e., there were at least two individuals cracking at the same time). The binomial logistic regression included learner age, model age, model sex, kinship, and model nut-cracking efficiency (bout duration rank, strikes per nut rank, success rate rank, and displacement rate rank) as fixed effects, and nut-cracking model ID (n = 17) as a random intercept.

The *drop1* function was used to find the best fitting model (smallest AIC, see Table S3). Results revealed that there was a significant effect of kinship, with individuals being more likely to be peered at when they were not related to the learner (z = -2.105, p < 0.05). The efficiency of the model also had a significant effect on the likelihood of being peered at. Displacement rate ranking had a significant negative effect on the likelihood of being peered at (z = -2.522, p < 0.05), whereas bout duration rank (z = 2.174, p < 0.05) and success rate rank (z = 2.103 p < 0.05) had a significant positive effect of on the likelihood of being peered at. The relationship between kinship, bout duration rank, success rate rank, displacement rank, and the likelihood of being peered at showed no significant variance in intercepts across nut-cracking models (z = -1.371, p > 0.05).

To assess whether the higher rate of peering towards non-kin was due to differences in availability of kin and non-kin models, we identified 37 peering events where both kin and

non-kin were available options to peer at. Of these 37 peering events, there were equal numbers of kin and non-kin cracking in 26 cases (i.e., 50% of crackers were kin, 50% were non-kin). Of the remaining 11 peering events, six had a higher proportion of non-kin cracking, and five had a higher proportion of kin cracking. We asked: what factors affect the likelihood that a nut-cracking individual is peered at when there are both kin and non-kin models available to the learner?

In these 37 cases, 81.08% involved the non-kin being peered at, and 18.82% involved kin being peered at. Results of the best fitting binomial logistic regression revealed that being kin was associated with significantly less peering (z = -4.014, p < 0.001); the odds of being peered at were 90% lower when the individual was related to the learner. There was a significant negative effect of displacement rate ranking on the likelihood of being peered at (z = -2.328, p < 0.05), and a significant positive effect of bout duration ranking on the likelihood of being peered at (z = 1.997, p < 0.05). There were no effects of strikes per nut ranking, success rate ranking, model sex, or model age on the likelihood of being peered at (see Table S4).

Discussion

Assessing the presence of social learning strategies used during the acquisition of tool use by wild infant and juvenile chimpanzees is crucial for determining how material culture is transmitted and maintained across generations. Here, we establish that wild chimpanzees employ a "who" social learning strategy when selecting non-maternal models from whom to learn a naturally occurring extractive foraging behaviour. We find that, across a 25-year period, when the learner was learning from groupmates other than their mother, individuals were more likely to be peered at when they were not related to the young chimpanzee, even when their relatives were available models.

This longitudinal finding reiterates the central importance of non-kin during the transmission of cultural traits. For the 37 peering events where the model options were a mixture of kin and non-kin, being non-kin increased the likelihood of the model being

peered at. Although this is a small sample, it suggests a preference for non-kin models when peering at a group member other than their mother. This supports a view that non-kin appear to have played a central role in the transmission of a chimpanzee culture known to be over 4,000 years old[30]. Our findings complement previous research findings that semi-wild chimpanzees are just as likely to be influenced by non-kin as they are their mothers when learning the grooming handclasp social custom[40]. In wild chimpanzees, as in humans, ties with non-kin develop in childhood, allowing for learning and cultural exchange from individuals other than the mother[24]. Indeed, Bossou offspring peered at their mothers less and less as they aged, corroborating results of previous studies in chimpanzees[36], orangutans[33], and humans[24]. The role of non-kin in the transmission of technological behaviour may vary, likely being more important for more complex tasks that have longer learning periods. Research should now investigate the degree of shared knowledge between infants and non-kin in other tasks to further assess the similarities between human and chimpanzee cultural transmission[24].

We found that when infants were two years old, they peered at non-maternal models to a greater extent than they did at ages one and three. Although it is not until age five that non-maternal models are peered at more than maternal models (likely because the inter-birth interval of the Bossou chimpanzees is approximately 5 years[47], and so the mothers are caring for a new infant at this age), the increase in peering at non-maternal models at age two could suggest a few underlying processes. It may be due to noise in our data set, as there were an uneven amount of data points for each year of the learning period (see Figure 2). However, it could be that young chimpanzees at this stage of development are exhibiting the first milestone of independence by starting to feed and sit by themselves next to their mother. Although wild chimpanzees start introducing solid foods into their diet within their first year[48], they rely mainly on suckling until they commence weaning from ~2 years old[49]. Thus, from age two, young chimpanzees are starting the process of independence from their

mother, with the high prevalence of peering at matrilineal kin at this age reflecting their reliance on more well known, and perhaps more tolerant, individuals.

In fact, it may be that all non-maternal models are also more tolerant to peering and scrounging from learners when they are younger infants. Indeed, models were most tolerant to two-year-old peerers being in close proximity (< 1 m) to them whilst they were engaged in a nut-cracking bout. Tolerance to scrounging was highest when the learners were age four, suggesting that the high proportion of peering directed towards non-maternal models at age two was not due to an increased likelihood of successfully scrounging the nut. This is consistent with known changes in diet breadth across chimpanzee development[48,49], with scrounging of kernels remaining rare until age 3 (70% of scrounging events took place from ages 3–5). These findings point to a process whereby information exchange among matrilineal kin and non-kin is facilitated in early childhood.

If the goal of peering were to steal the calorie-rich and nutrient-dense resource, rather than solely to learn the mechanics of the skill, we would expect learners to select models based on the likelihood of successfully scrounging their extracted kernel (i.e., accessing the energetic reward). However, scrounging from non-maternal models was relatively rare (~10% of all peering events). Moreover, learners were less likely to scrounge from male than female non-maternal models, likely because it is riskier, but the sex of the model did not affect the likelihood of them being peered at. Together, this suggests that peering is not used by learners solely as a means to scrounge kernels. Rather, it appears that learners are peering to learn how to perform the behaviour from a knowledgeable group mate.

Moreover, we found that, when all peering events directed at non-maternal models were considered for the learners with nut-cracking mothers, non-kin were more likely to be peered at than kin. The relative ranking of the nut-cracking models in their bout durations and displacement rate also significantly affected the odds of being peered at. Specifically, we found that models who had lower displacement rate ranks (i.e., who displaced the nut from the anvil fewer times) were more likely to be peered at, but also that models with

higher bout duration ranks (i.e., who took longer to extract the nut kernel) were more likely to be peered at. These results held true even when we considered only the 79 peering events where all learners had multiple potential models available to them. In these cases, models with higher success rate ranks (i.e., who were less likely to extract the whole kernel) were also more likely to be peered at.

These results were surprising given the apparent contradiction in the preference for individuals who displaced the nut fewer times but took longer to crack the nut and did not have the highest success rate out of the available models. The preference for models who displaced the nut fewer times may reflect that infants are trying to learn how to strike the nut. Moreover, it is possible that individuals with longer bout durations were more likely to be peered at because these models provided learners with a longer period within which to observe the behaviour. Further research from other nut-cracking communities is required to determine whether infants do indeed choose models who provide the greatest exposure to the skill.

Alternatively, the apparent preference for models with longer bouts may be because of another, currently unmeasured, variable. Indeed, the objective measure of efficiency used here may not fully reflect the learners' subjective judgement of what makes a "good" nutcracker or model. For example, infants may be selecting models who are most tolerant to peering[37]. An important next step would be to investigate whether a *copy tolerant models* strategy exists for the acquisition of stone tool use in Bossou.

Unlike previous research on the acquisition of stone tool use in wild tufted capuchins[15] and long-tailed macaques[18], we found that the age of the model did not significantly affect the likelihood of them being peered at. Here, we used the age of the nut-cracking models in years (6–58 years old), rather than using age categories, to achieve a more fine-grained understanding of the role of age in model selection. Although categories (such as infant, juvenile, and adult, as used in, for example, capuchin[15] and chimpanzee[31] research) are useful where the exact ages of individuals may be unknown, they can obscure behavioural

patterns. The increased sensitivity of age measurement in this research enabled a more accurate understanding of the role of model age (or lack thereof) on the model selection process.

Although there was no effect of model age on the likelihood of being peered at, no learners peered at models younger than themselves, supporting previous research from Bossou[31]. It is noteworthy, however, that there were five instances of learners peering at other individuals in their ELPs, perhaps reflecting that "friends" are tolerant to peering. As information transfer must be vertical (via older kin) or oblique (via older non-kin) for cultural traits to be inherited by younger generations[50], these cases of horizontal transmission (from the same generation) could indicate that learners supplement their learning from more knowledgeable, older conspecifics by peering at tolerant models from the same age-class. Further research is needed to investigate the prevalence and functional role of peer-to-peer learning during the acquisition and maintenance of material culture in wild chimpanzees.

This research is limited by the fact that patrilineal kinship could not be considered as paternity is not established at Bossou. More research is needed to assess the presence of social learning strategies in communities where patrilineal kinship is known, as chimpanzee fathers can recognise their offspring and have been found to associate with their offspring more than with unrelated infants[51,52]. Despite this, as patrilineal siblings do not preferentially associate with one another (because they cannot be reliably identified)[53], we believe our findings are likely to hold true even when considering patrilineal kinship.

Also, as the videos were archival, the filming was not targeted towards the present research questions. As such, some variables of interest could not be recorded. For example, there were 21 instances where potential nut-cracking models were identified via audio but were not visible on camera (recorded as "unknown offscreen"), so their data were excluded from analyses as no sex, age, kin, or efficiency information could be assigned to them. However, excluding their data meant that the choice made by the learner (peering at the selected

model instead of the offscreen model) was obscured. The selected models were non-kin in 17 of these instances and were kin in four. Although we may assume that at least some of these instances had both kin and non-kin as available options to peer at, this exemplifies one of the challenges of collecting data from archival video. Even so, using the long-term archive allowed us to sample all of the visible peering events at the experimental site during the experimental sessions in the dry season for every learner over multiple generations within the same population of wild chimpanzees. As such, this research shows the most comprehensive picture possible of the social learning of the nut-cracking material culture of this now almost extinct community.

Conclusion

This study investigated the changing role of mothers throughout a prolonged period of stone tool skill acquisition in young wild chimpanzees, and the presence of "who" social learning strategies in the selection of non-maternal models over a 25-year period. Our results highlight that non-kin play an increasingly central role in learning and cultural transmission throughout development. When learners are not peering at their mother, we establish that not being related to the learner, displacing the nut fewer times, and taking longer to extract the kernel all increase the likelihood of a model being peered at. Being non-kin still increases the chances of an individual being peered at even when there are kin models available. Learning from unrelated individuals has been central to the transmission and maintenance of this prehistoric chimpanzee culture. These findings complement previous research on the essential role of non-kin in knowledge exchange in humans and have important implications for the role of social network structure on cultural transmission in early hominins. It is probable that non-kin also played a critical role in the acquisition and maintenance of lithic technologies in hominins.

Methods

Study site. The Bossou chimpanzees inhabit a core area of 7km^2 within primary and secondary forest in the tropical wet seasonal climate of south-eastern Guinea, West Africa (7°38'71.7'N, 8°29'38.9'W)[54,55]. Researchers have been studying the chimpanzees since 1976, with the population always being relatively small (approximately 20 individuals but falling after a respiratory disease outbreak in 2003)[56–58].

Study materials and subjects. A long-term video archive has been established from footage taken of the Bossou chimpanzees during the dry season (December–February) each year from 1988 to 2018 (excluding 2001 and 2011)[55,59]. Footage was taken using zoomed, medium distance, and wide-angle lens from standardised angles[59]. The present study used over 680 hours of video from the 1992–2017 zoomed and medium distance video footage. This footage included 13 chimpanzees (six females, seven males; 0–5 years old) learning to use the stone hammer-and-anvil composite to crack oil palm nuts during the proposed early period of social learning lasting from ages 0–5[31,36]. Three of these individuals (Nto, Poni, and Peley) had mothers (Nina and Pama) who could not crack nuts, having presumably migrated from non-cracking communities[60].

Data collection. Behaviour was coded from the videos using *Behavioural Observation Research Interactive Software* (BORIS v. 7.13.9)[61]. Data obtained in previous research, which showed substantial–excellent inter-rater reliability, were used in this study[35,62]. All peering events (defined as the period where a learner was watching a nut-cracking model's hand, arm, nut, or hammer-and-anvil composite whilst they were cracking an oil palm nut) that were visible in the Bossou archive from 1992–2017 were recorded. The only peering events in 2009 were directed towards models cracking coula nuts, so 2009 was excluded.

For each peering event, the model's name, whether the model was the learner's mother or not, and the names of any other conspecifics cracking oil palm nuts at the same time ("cracking conspecifics") were recorded. Any tolerance (i.e., permitting proximity, interaction, or scrounging) or intolerance (i.e., vocally or physically rejecting proximity,

interaction, or scrounging attempts) the model showed towards the learner was also recorded[62]. Because the nut-cracking behaviour produces a distinctive sound[63], "unknown offscreen" was inputted for "cracking conspecifics" if nut-cracking could be heard through the video's audio but the individual was not on camera. Where no conspecifics were visibly or audibly cracking nuts at the same time as the selected model, "none" was inputted. No rank data was gathered as, aside from the alpha male, dominance hierarchy data is not available for Bossou.

Where possible (n = 8), the "unknown offscreen" individuals were identified using the corresponding wide-angle lens footage of that day. For video files that had frame-level metadata, overlapping timestamps from alternative camera angles with parallel time/date information were retrieved using FFmpeg[64]. For video files that lacked temporal metadata, candidate overlapping camera angles were identified using field note data on the start time/date of the video tape, and the exact time point was located manually to identify the offscreen potential models.

Ethical approval and permissions. All original contributors to the Bossou archive obtained ethical approval and permission to carry out research in Bossou from the Direction Générale de la Recherche Scientifique et de l'Innovation Technologique (DGERSIT) and the Institut de Recherche Environmentale de Bossou (IREB) in Guinea. Tetsuro Matsuzawa and Kyoto University, Japan, gave access to the Bossou archive.

Statistical analysis. Data wrangling and analysis was performed using R (v. 4.3.2)[65] and RStudio (v. 2023.09.1+494)[66] for MacOS. We created a long data frame of peering events to determine whether particular characteristics affected the likelihood of a nut-cracking individual being peered at by a learner. The data frame consisted of the learner's name, model's name, the year, the model's relative efficiency rankings for *bout duration*, *strikes per nut*, *success rate*, and *displacement rate* for that year, the relationship between the learner and model ("kin", or not an established relation, "non-kin"), the model's age and sex, and whether the model was peered at or not (1 if they were peered at, n = 177, 0 if they were

not peered at, n = 94). Thus, for peering events where the model was the only option for the learner to peer at (i.e., no other individuals were cracking at the same time), there was only one row in the long data frame. For peering events where there were two or more options of who the learner could peer at (i.e., multiple individuals were cracking at the same time), there was one row in the data frame for the model who was peered at, and a row for each individual who was cracking but not peered at. This allowed us to test who specifically was selected to peer at when the learner had multiple available options.

The relative nut-cracking efficiency of the model was calculated using previously published data on the four stable and reliable measures of nut-cracking efficiency[35]. These measures were *bout duration* (the time it takes for one nut to be cracked), *strikes per nut* (number of hammer strikes required to open the nut), *success rate* (the proportion of each bout outcome: kernel not extracted, extracted a broken kernel, or extracted a whole kernel), and *displacement rate* (the number of times the nut came off the anvil because of a hammer strike). How chimpanzees were ranked based on these efficiency measures has previously been described[35]. Briefly, mixed-effect models were constructed for each measure, with age and sex as fixed effects and the subject included as a random intercept. The random intercept terms were extracted, ordered, and then given a rank, with lower values indicating greater relative nut-cracking efficiency (i.e., 1 was the most efficient individual for that measure). Our analyses of each peering event used the year-specific ranks of the four efficiency measures for each model for every year they were present in the dataset (1992–2017). Using the year-specific efficiency rank was important as high population turnover in the community affected the relative efficiency of each potential model year-on-year.

The instances where the "cracking conspecific" was recorded as "unknown offscreen" (and the wide-angled lens footage did not clarify their identity; n = 21), were not included in the final long data set, as their relative efficiency rankings, sex, model age (in years), learner age (in years), and kinship information were always unknown.

All analyses had a significance level set at $\alpha = 0.05$ (two-tailed). As the outcome variable was binomial (1 for peered at, 0 for not peered at), a mixed-effects binomial logistic regression with a "bobyqa" optimiser was fitted using the *glmer* function from the *lme4* package[67]. The four nut-cracking model efficiency rankings, model sex, model age, kinship (kin, non-kin), and learner age were included as fixed predictor variables, and the nut-cracking model ID was included as a random intercept. The *drop1* function was used to find the best fitting model (smallest AIC). Diagnostic *post hoc* analyses were performed to check the assumptions of the binomial logistic regressions were met and to identify any influential data points (see Supplementary Information). Multicollinearity was checked using the *vif* function in the *car* package[68]. The normality of the residuals was checked visually using QQ-plots. The presence of influential observations for the level-two parameter (nut-cracking model ID) was checked using the *dfbetas* function.

References

1. Heyes, C. Social learning in animals: categories and mechanisms. *Biol. Rev.* **69**, 207–231 (1994).
2. Kendal, R. L., Coolen, I., van Bergen, Y. & Laland, K. N. Trade-offs in the adaptive use of social and asocial learning. *Adv. Study Behav.* **35**, 333–379 (2005).
3. Laland, K. N. Social learning strategies. *Learn. Behav.* **32**, 4–14 (2004).
4. Jiménez, Á. V & Mesoudi, A. Prestige-biased social learning: current evidence and outstanding questions. *Palgrave Commun.* **5**, (2019).
5. Henrich, J. & Gil-White, F. J. The evolution of prestige: freely conferred deference as a mechanism for enhancing the benefits of cultural transmission. *Evol. Hum. Behav.* **22**, 165–196 (2001).
6. Wood, L. A., Kendal, R. L. & Flynn, E. G. Context-dependent model-based biases in cultural transmission: children's imitation is affected by model age over model knowledge state. *Evol. Hum. Behav.* **33**, 387–394 (2012).
7. Wood, L. A., Kendal, R. L. & Flynn, E. G. Whom do children copy? Model-based biases in social learning. *Dev. Rev.* **33**, 341–356 (2013).
8. Stroeymeyt, N., Giurfa, M. & Franks, N. R. Information certainty determines social and private information use in ants. *Sci. Rep.* **7**, 43607 (2017).
9. Grüter, C., Segers, F. H. I. D. & Ratnieks, F. L. W. Social learning strategies in honeybee foragers: do the costs of using private information affect the use of social information? *Anim. Behav.* **85**, 1443–1449 (2013).
10. Kendal, J. R., Rendell, L., Pike, T. W. & Laland, K. N. Nine-spined sticklebacks deploy a hill-climbing social learning strategy. *Behav. Ecol.* **20**, 238–244 (2009).
11. Riebel, K., Spierings, M. J., Holveck, M.-J. & Verhulst, S. Phenotypic plasticity of avian social-learning strategies. *Anim. Behav.* **84**, 1533–1539 (2012).
12. Guillette, L. M., Scott, A. C. Y. & Healy, S. D. Social learning in nest-building birds: a role for familiarity. *Proc. R. Soc. B Biol. Sci.* **283**, 20152685 (2016).
13. Aplin, L. M. *et al.* Experimentally induced innovations lead to persistent culture via conformity in wild birds. *Nature* **518**, 538–541 (2015).
14. Farine, D. R., Spencer, K. A. & Boogert, N. J. Early-life stress triggers juvenile zebra finches to switch social learning strategies. *Curr. Biol.* **25**, 2184–2188 (2015).
15. Coelho, C. G. *et al.* Social learning strategies for nut-cracking by tufted capuchin monkeys (*Sapajus* spp.). *Anim. Cogn.* **18**, 911–919 (2015).
16. Kendal, R. L. *et al.* Chimpanzees copy dominant and knowledgeable individuals: implications for cultural diversity. *Evol. Hum. Behav.* **36**, 65–72 (2015).

17. Garcia-Nisa, I., Evans, C. & Kendal, R. L. The influence of task difficulty, social tolerance, and model success on social learning in Barbary macaques. *Sci. Rep.* **13**, 1176 (2023).
18. Tan, A., Hemelrijk, C. K., Malaivijitnond, S. & Gumert, M. D. Young macaques (*Macaca fascicularis*) preferentially bias attention towards closer, older, and better tool users. *Anim. Cogn.* **21**, 551–5563 (2018).
19. Nagell, K., Olguin, R. S. & Tomasello, M. Processes of social learning in the tool use of chimpanzees (*Pan troglodytes*) and human children (*Homo sapiens*). *J. Comp. Psychol.* **107**, 174–186 (1993).
20. Tomasello, M., Davis-Dasilva, M., Camak, L. & Bard, K. Observational learning of tool-use by young chimpanzees. *Hum. Evol.* **2**, 175–183 (1987).
21. Horner, V. & Whiten, A. Causal knowledge and imitation/emulation switching in chimpanzees (*Pan troglodytes*) and children (*Homo sapiens*). *Anim. Cogn.* **8**, 164–181 (2005).
22. Call, J., Carpenter, M. & Tomasello, M. Copying results and copying actions in the process of social learning: chimpanzees (*Pan troglodytes*) and human children (*Homo sapiens*). *Anim. Cogn.* **8**, 151–163 (2005).
23. Boyd, R., Richerson, P. J. & Henrich, J. The cultural niche: why social learning is essential for human adaptation. *Proc. Natl. Acad. Sci.* **108**, 10918–10925 (2011).
24. Migliano, A. B. *et al.* Characterization of hunter-gatherer networks and implications for cumulative culture. *Nat. Hum. Behav.* **1**, 43 (2017).
25. Hill, K. R. *et al.* Hunter-gatherer inter-band interaction rates: implications for cumulative culture. *PLoS One* **9**, 1–9 (2014).
26. Boesch, C. *et al.* Chimpanzee ethnography reveals unexpected cultural diversity. *Nat. Hum. Behav.* **4**, 910–916 (2020).
27. Koops, K., Gaspard Soumah, A., van Leeuwen, K. L., Didier Camara, H. & Matsuzawa, T. Field experiments find no evidence that chimpanzee nut cracking can be independently innovated. *Nat. Hum. Behav.* **6**, 487–494 (2022).
28. Furuichi, T. Factors underlying party size differences between chimpanzees and bonobos: a review and hypotheses for future study. *Primates* **50**, 197–209 (2009).
29. Harmand, S. & Arroyo, A. Linking primatology and archaeology: the transversality of stone percussive behaviors. *J. Hum. Evol.* **181**, (2023).
30. Mercader, J. *et al.* 4,300-year-old chimpanzee sites and the origins of percussive stone technology. *PNAS* **104**, 3043–3048 (2007).
31. Biro, D. *et al.* Cultural innovation and transmission of tool use in wild chimpanzees: evidence from field experiments. *Anim. Cogn.* **6**, 213–223 (2003).

32. Matsuzawa, T. *et al.* Emergence of culture in wild chimpanzees: education by master-apprenticeship. in *Primate origins of human cognition and behavior* (ed. Matsuzawa, T.) 557–574 (Springer, 2001).
33. Schuppli, C. *et al.* Observational social learning and socially induced practice of routine skills in immature wild orang-utans. *Anim. Behav.* **119**, 87–98 (2016).
34. Biro, D., Sousa, C. & Matsuzawa, T. Ontogeny and cultural propagation of tool use by wild chimpanzees at Bossou, Guinea: case studies in nut cracking and leaf folding. in *Cognitive development in chimpanzees* (eds. Matsuzawa, T., Tomonaga, M. & Tanaka, M.) 476–506 (Springer, 2006).
35. Berdugo, S., Cohen, E., Davis, A. J., Matsuzawa, T. & Carvalho, S. Stable long-term individual variation in chimpanzee technological efficiency. *bioRxiv* 2023.11.21.568000 (2023).
36. Inoue-Nakamura, N. & Matsuzawa, T. Development of stone tool use by wild chimpanzees (*Pan troglodytes*). *J. Comp. Psychol.* **111**, 159–173 (1997).
37. Whiten, A. & van de Waal, E. The pervasive role of social learning in primate lifetime development. *Behav. Ecol. Sociobiol.* **72**, 80 (2018).
38. Canteloup, C., Hoppitt, W. J. E. & van de Waal, E. Wild primates copy higher-ranked individuals in a social transmission experiment. *Nat. Commun.* **11**, (2020).
39. Canteloup, C., Cera, M. B., Barrett, B. J. & van de Waal, E. Processing of novel food reveals payoff and rank-biased social learning in a wild primate. *Sci. Rep.* **11**, 9550 (2021).
40. van Leeuwen, E. J. C. & Hoppitt, W. J. E. Biased cultural transmission of a social custom in chimpanzees. *Sci. Adv.* **9**, eade5675 (2023).
41. Bonnie, K. E., Horner, V., Whiten, A. & de Waal, F. B. M. Spread of arbitrary conventions among chimpanzees: a controlled experiment. *Proc. R. Soc. B Biol. Sci.* **274**, 367–372 (2006).
42. Ottoni, E. B., Resende, B. D. & Izar, P. Watching the best nutcrackers: what capuchin monkeys (*Cebus apella*) know about others' tool-using skills. *Anim. Cogn.* **24**, 215–219 (2005).
43. Horner, V., Proctor, D., Bonnie, K. E., Whiten, A. & de Waal, F. B. M. Prestige affects cultural learning in chimpanzees. *PLoS One* **5**, e10625 (2010).
44. Luncz, L. V, Sirianni, G., Mundry, R. & Boesch, C. Costly culture: differences in nut-cracking efficiency between wild chimpanzee groups. *Anim. Behav.* **137**, 63–73 (2018).
45. Lamon, N., Neumann, C., Gruber, T. & Zuberbühler, K. Kin-based cultural transmission of tool use in wild chimpanzees. *Sci. Adv.* **3**, (2017).

46. Clutton-Brock, T. & Sheldon, B. C. Individuals and populations: the role of long-term, individual-based studies of animals in ecology and evolutionary biology. *Trends Ecol. Evol.* **25**, 562–573 (2010).
47. Sugiyama, Y. Demographic parameters and life history of chimpanzees at Bossou, Guinea. *Am. J. Phys. Anthropol.* **124**, 154–165 (2004).
48. Bray, J., Emery Thompson, M., Muller, M. N., Wrangham, R. W. & Machanda, Z. P. The development of feeding behavior in wild chimpanzees (*Pan troglodytes schweinfurthii*). *Am. J. Phys. Anthropol.* **165**, 34–46 (2018).
49. Fahy, G. E. *et al.* Stable nitrogen isotope analysis of dentine serial sections elucidate sex differences in weaning patterns of wild chimpanzees (*Pan troglodytes*). *Am. J. Phys. Anthropol.* **153**, 635–642 (2014).
50. Danchin, É. *et al.* Beyond DNA: integrating inclusive inheritance into an extended theory of evolution. *Nat. Rev. Genet.* **12**, 475–486 (2011).
51. Lehmann, J., Fickenscher, G. & Boesch, C. Kin biased investment in wild chimpanzees. *Behaviour* **143**, 931–955 (2006).
52. Murray, C. M., Stanton, M. A., Lonsdorf, E. V, Wroblewski, E. E. & Pusey, A. E. Chimpanzee fathers bias their behaviour towards their offspring. *R. Soc. Open Sci.* **3**, 160441 (2016).
53. Langergraber, K. E., Mitani, J. C. & Vigilant, L. The limited impact of kinship on cooperation in wild chimpanzees. *Proc. Natl. Acad. Sci.* **104**, 7786–7790 (2007).
54. Hockings, K. J., Anderson, J. R. & Matsuzawa, T. Socioecological adaptations by chimpanzees, *Pan troglodytes verus*, inhabiting an anthropogenically impacted habitat. *Anim. Behav.* **83**, 801–810 (2012).
55. Matsuzawa, T. Field experiments on use of stone tools by chimpanzees in the wild. in *Chimpanzee cultures* (eds. Wrangham, R. W., McGrew, W. C., De Waal, F. B. M. & Heltne, P. G.) 351–370 (Harvard University Press, 1994).
56. Sugiyama, Y. & Koman, J. Social structure and dynamics of wild chimpanzees at Bossou, Guinea. *Primates* **20**, 323–339 (1979).
57. Matsuzawa, T. & Humle, T. Bossou: 33 years. in *The chimpanzees of Bossou and Nimba* (eds. Matsuzawa, T., Humle, T. & Sugiyama, Y.) 3–10 (Springer, 2011).
58. Humle, T. The 2003 epidemic of a flu-like respiratory disease at Bossou. in *The chimpanzees of Bossou and Nimba* (eds. Matsuzawa, T., Humle, T. & Sugiyama, Y.) 325–333 (Springer, 2011).
59. Schofield, D. Computational ethology for primate sociality: a novel paradigm for computer-vision-based analysis of animal behaviour. (University of Oxford, 2022).

60. Matsuzawa, T. Stone tools for nut-cracking. in *The chimpanzees of Bossou and Nimba* (eds. Matsuzawa, T., Humle, T. & Sugiyama, Y.) 73–84 (Springer, 2011).
61. Friard, O. & Gamba, M. BORIS: a free, versatile open-source event-logging software for video/audio coding and live observations. *Methods Ecol. Evol.* **7**, 1325–1330 (2016).
62. Berdugo, S., Cohen, E., Davis, A. J., Matsuzawa, T. & Carvalho, S. The ontogeny of chimpanzee technological efficiency. (2024).
63. Bain, M. *et al.* Automated audiovisual behavior recognition in wild primates. *Sci. Adv.* **7**, eabi4883 (2021).
64. Tomar, S. Converting video formats with FFmpeg. *Linux J.* **2006**, 10 (2006).
65. R Core Team. R: a language and environment for statistical computing. (2020).
66. Posit team. RStudio: integrated development environment for R. (2023).
67. Bates, D., Maechler, M., Bolker, B. & Walker, S. Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* **67**, 1–48 (2015).
68. Fox, J. & Weisberg, S. *An R companion to applied regression*. (Sage, 2019).

Acknowledgements

Thank you to the Direction Générale de la Recherche Scientifique et de l'Innovation Technologique (DGERSIT) and the Institut de Recherche Environnementale de Bossou (IREB) in Guinea for research authorisation. Special thanks to all the Bossou field assistants and researchers, specifically Henry Didier Camara, Cé Vincent Mami, Gouanou Zogbila, Boniface Zogbila, Jules Doré, Gouanou Goumy, Tino Camara, Pascal Goumy, Paquílé Cherif, Jiles Gondo Doré, and Marcel Doré. Thank you to all researchers who contributed footage to the Bossou video archive. Daniel Schofield digitised, organised, and systematised the video archive, and Alexander Mielke (Queen Mary University of London) and Sophie Berdugo catalogued the archive. Thank you to Alexander Mielke for the early discussions about this research. Thank you to Katarina Almeida-Warren, Jacinto Mathe, Rachel Hurwitz, Katya Herberg, Carolyn Gover, and Liam McClain for helpful comments and discussion.

Author contributions

S.B. conceived of the study, designed, and coordinated the study, collected data, analysed and visualised the data, and wrote the manuscript. **E.C.** provided supervision, participated in the design of the study, and commented on the manuscript. **A.J.D.** analysed and visualised the data and commented on the manuscript. **T.M.** collected the original data set and commented on the manuscript. **D.P.S.** curated data and commented on the manuscript. **S.C.** collected the original data set, provided supervision, participated in the design of the study, and commented on the manuscript.

Funding

This research was supported by the Clarendon Fund (University of Oxford, UK), and the Keble College Sloane-Robinson Clarendon Scholarship (University of Oxford, UK) to **S.B.**, and by the Ministry of Education, Culture, Sports, Science, and Technology (MEXT), Japan, (grant nos. 07102010, 12002009, 16002001, 20002001, 24000001, and 16H06283) to **T.M.**. The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Competing interests

The authors declare no competing interests.

Supplementary information is available for this paper.

Correspondence and requests for materials should be addressed to Sophie Berdugo.

Supplementary Information

Table S1. Availability of nut-cracking kin models for learners during their early learning period (0–5 years old).

Learner	Sex	Early learning period	Mother	Available nut-cracking kin models
Fotaiu	Female	1992–1997	Fana	Fana (1992–1997) Foaf (1992–1997)
Vuavua	Female	1992–1997	Velu	Velu (1992–1997) Vui (1992–1997)
Yolo	Male	1992–1997	Yo	Yo (1992–1997)
Juru	Female	1994–1998	Jire	Jire (1994–1998)
Nto	Female	1994–1998	Nina*	Na (1994–1996)
Poni	Male	1994–1998	Pama*	Pili (1994–1998)
Pokuru	Male	1997–2000	Pili	Pili (1992–1997) Poni (1999–2000)
Fanle	Female	1998–2003	Fana	Fana (1998–2003) Foaf (1998–2003) Fotaiu (1998–2003)
Jeje	Male	1998–2003	Jire	Jire (1998–2003) Juru (1998–2001)
Peley	Male	1999–2004	Pama*	Pili (1999–2001) Poni (1999–2003)
Joya	Female	2004–2009	Jire	Jire (1998–2001) Jeje (2004–2009)
Flanle	Male	2008–2013	Fanle	Fana (2008–2013) Foaf (2008–2013)
Fanwa	Male	2012–2017	Fanle	Fanle (2012–2017) Fana (2012–2017) Foaf (2012–2017) Flanle (2012–2016)

Notes: * = could not crack nuts.

Table S2. Subject information and data summary.

Subject	Sex	Observation years	Nut-cracking mother	Maternal peering events	Non-maternal peering events
Fotaiu	Female	1992–1997	Yes	14	19
Vuavua	Female	1992–1997	Yes	5	5
Yolo	Male	1992–1997	Yes	44	7
Juru	Female	1994–1998	Yes	23	21
Nto	Female	1994–1998	No	0	34
Poni	Male	1994–1998	No	0	14
Pokuru*	Male	1997–2000	Yes	8	1
Fanle	Female	1998–2003	Yes	58	4
Jeje	Male	1998–2003	Yes	45	9
Peley	Male	1999–2004	No	0	15
Joya	Female	2004–2009	Yes	18	3
Flanle	Male	2008–2013	Yes	12	49
Fanwa	Male	2012–2017	Yes	30	1

Note: * = Died before the end of the early learning period.

Table S3. Output of the best fitting multilevel binomial logistic regression for all peering events where the nut-cracking model was not the learner's mother.

			Peered at	
Predictors	*Estimate*	*Odds Ratios*	*CI*	*p*
Intercept	2.238	9.38	1.91–46.16	**0.006**
Kin [Yes]	-3.093	0.05	0.01–0.21	**<0.001**
Bout duration rank	0.297	1.35	1.06–1.71	**0.016**
Displacement rate rank	-0.429	0.65	0.52–0.81	**<0.001**
Random Effects				
σ^2		3.29		
$\tau_{00\ model}$		1.51		
ICC		0.31		
$N_{\ model}$		17		
Observations		189		
Marginal R^2 / Conditional R^2		0.404 / 0.591		

Notes: σ^2 = Within-group (residual) variance. τ_{00} = Between-group (random intercept) variance. ICC = the correlation between randomly drawn observations from the same grouping variable[1].

Table S4. Output of the best fitting multilevel binomial logistic regression for the 79 peering events where all learners peered at a model other than their mother and had options for which model to peer at.

		Peered at		
Predictors	*Estimate*	*Odds Ratios*	*CI*	*p*
Intercept	-0.754	0.47	0.16–1.38	0.170
Kin [Yes]	-0.932	0.39	0.16–0.94	**0.035**
Bout duration rank	0.210	1.23	1.02–1.49	**0.030**
Success rate rank	0.159	1.17	1.01–1.36	**0.035**
Displacement rate rank	-0.212	0.81	0.69–0.95	**0.012**
Random Effects				
σ^2		3.29		
$\tau_{00\ model}$		0.04		
ICC		0.11		
$N_{\ model}$		17		
Observations		171		
Marginal R^2 / Conditional R^2		0.211 / 0.296		

Notes: σ^2 = Within-group (residual) variance. τ_{00} = Between-group (random intercept) variance. ICC = the correlation between randomly drawn observations from the same grouping variable[1].

Table S5. Output of the best fitting binomial logistic regression for the peering events where the learner had a choice between a kin and a non-kin nut-cracking model.

		Peered at	
Predictors	*Odds Ratios*	*CI*	*p*
Intercept	1.85	0.55–6.19	0.321
Kin [Yes]	0.10	0.03–0.31	**<0.001**
Bout duration rank	1.36	1.01–1.83	**0.046**
Displacement rate rank	0.75	0.58–0.95	**0.020**
Random Effects			
σ^2	3.29		
$\tau_{00\ model}$	0.00		
$N_{\ model}$	16		
Observations	90		
Marginal R^2 / Conditional R^2	0.392 / NA		

Notes: σ^2 = Within-group (residual) variance. τ_{00} = Between-group (random intercept) variance. ICC = the correlation between randomly drawn observations from the same grouping variable[1].

Model Diagnostics

Peering at non-maternal models. There were no issues of multicollinearity (all VIFS ≤ 2.31) when multicollinearity was checked using the *vif* function from the *car* package[2]. QQ-plots revealed the residuals did not deviate significantly from normality. Model diagnostics were performed to assess whether any nut-cracking models (the level two parameter) had an outsized influence on the regression model. Two models (Na and Tua) had DFBETA values greater than the $2/\sqrt{n}$ cut-off, so their data were considered to be influential[3]. We re-ran the regression (nut-cracking model ID as random intercept, kinship, bout duration ranking and displacement rate ranking as fixed effects) without their data. All effects remained unchanged.

"Who" social learning strategies. There were no issues of multicollinearity (all VIFs ≤ 2). QQ-plots revealed the residuals deviated significantly from normality. Influential observations were identified using the *cooks.distance* function from the *car* package. The model was rerun without the 11 observations that exceeded three times the mean of the Cooks Distance. All results remained unchanged, but the effect of one predictor—kinship—became insignificant (t = -1.616, p > 0.05). Removing these 11 observations normalised the residuals. Model diagnostics were performed to assess whether any nut-cracking models (the level two parameter) had an outsized influence on the regression model. One model (Velu) had DFBETA value greater than the $2/\sqrt{n}$ cut-off, so her data were considered to be influential[3]. We re-ran the regression (nut-cracking model ID as random intercept, kinship, bout duration ranking, success rate ranking, and displacement rate ranking as fixed effects) without her data. Two results changed: the effect of kinship on the likelihood of being peered at became non-significant (z = -1.074, p > 0.05), and the relationship between kinship, bout duration ranking, success rate ranking, and displacement rate ranking showed significant variance in intercepts across nut-cracking models (z = -2.150, p < 0.05).

References

1. Hox, J. J. *Multilevel analysis: techniques and applications*. (Routledge, 2010).
2. Fox, J. & Weisberg, S. *An R companion to applied regression*. (Sage, 2011).
3. Belsley, D. D., Kuh, E. & Welsch, R. E. *Regression diagnostics: identifying influential data and sources of collinearity*. (Wiley, 1980).

8

General Discussion

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8.1 SUMMARY

Stable individual variation in the efficiency of extractive foraging has wide-ranging repercussions, from the survival and reproductive success of the individual (Biro et al., 2013; Gruber et al., 2021) to how the archaeological record is interpreted (Pascual-Garrido et al., 2023), and to our understanding of social and cultural learning (Gruber et al., 2021; Mesoudi et al., 2016). Investigating individual differences in stone tools used for pounding is of particular interest, given the importance of percussion in early hominin technological evolution and the durability of stone in the archaeological record (Harmand & Arroyo, 2023). Indeed, investigations on the transmission and maintenance of chimpanzee stone tool technology provide insights into the acquisition of the Oldowan techno-complex and offer vital behavioural resolution to assist in interpreting artefacts.

The long-term video archive of the Bossou chimpanzees using stone tools therefore offers a unique opportunity to address many important research questions pertaining to the evolution of cognitive and technological abilities among our closest relatives. For example, it provides the context to contribute to ongoing debates regarding the social learning capabilities of chimpanzees within a natural (albeit experimentally provisioned) setting, and it allows for lifetime-scale research, which is critical for addressing ontogenetic questions with evolutionary relevance (Clutton-Brock & Sheldon, 2010). Short term research—although often necessary given monetary and time constraints—cannot provide the full developmental picture for a long-lived species such as chimpanzees (Hayes & Schradin, 2017; Kappeler et al., 2012). As such, the systematic yearly footage of the same individuals engaging in the same technological behaviour at the same location makes Bossou uniquely positioned for understanding the ontogeny of tool use in wild chimpanzees (Matsuzawa, 2011a). In fact, the Bossou archive may offer the only systematic longitudinal glimpse into wild individuals habitually using stone tools we will ever have.

In this thesis, I have addressed many of the longstanding questions surrounding wild chimpanzee social learning and the acquisition of lithic technology from a longitudinal perspective. In Chapter 1, I introduced the motivations for investigating the extent and causes of individual variation in chimpanzee technological efficiency. In Chapters 2 and 3, I reviewed the theoretical and empirical underpinnings of the research presented in the thesis, from the use of chimpanzees as models for early hominin percussive technological behaviour, to the ongoing "Chimpanzee Culture Wars" surrounding social and cultural learning in our closest living relatives (Langlitz, 2020; McGrew, 2003). I also discussed the essential role of long-term ethological research of known individuals in the wild for addressing evolutionarily relevant questions, especially those pertaining to ontogeny. In Chapter 4, I introduced the Bossou field site and its rich research history. I also outlined the video data systematisation, pilot research, and the key measures used in this thesis, and explained how behavioural data were collected from the archival video footage of the Bossou chimpanzees.

Thereafter, I presented the empirical contributions of the thesis. In Chapter 5, I showed that stable and reliable individual-level variation exists in the efficiency of stone tool use in Bossou. In Chapter 6, I showed that this variation likely resulted from differing experiences during the social learning of the skill early in development. Here, I presented the first longitudinal evidence that variation in the number of social learning opportunities mothers exposed their infants to, and the amount of tolerance and intolerance learners experienced from nut-cracking models, predicted their subsequent efficiency. I also tentatively suggested that some individuals in Bossou may be imitating, rather than solely emulating, their selected nut-cracking models. In Chapter 7, I expanded on previous research findings on the changing importance of mothers and other groupmates during the development of complex skills in chimpanzees and investigated whether infants employed social learning strategies when selecting which non-maternal models to observe. I demonstrated that non-

kin are peered at even when kin models are available, hinting at the importance of non-kin in the transmission and maintenance of stone tool use in Bossou.

8.2 CONTRIBUTIONS AND IMPLICATIONS

The research presented in this thesis addressed the following three questions:

1. Do chimpanzees vary in the efficiency of their stone tool use at the individual level, beyond any differences relating to age or sex?
2. Does variation in the period during which chimpanzees learn how to use stone tools predict the subsequent technological efficiency of individuals?
3. Do wild chimpanzees select conspecifics from whom to learn how to use stone tools based on specific characteristics?

In answer to the first question, I established significant stable and reliable individual-level differences in nut-cracking efficiency. This is the first time such individual differences have been identified in wild chimpanzee stone tool use, and in technological efficiency more broadly. As such, this finding contributes to the growing body of evidence demonstrating individual variation in cognition and behaviour in primates (e.g., Bohn et al., 2023). The specific implications are discussed in more detail in sections 8.2.2 and 8.2.4.

Surprisingly, there were no sex differences in the technological efficiency of the Bossou chimpanzees, which is counter to previous research findings that establish a female bias in tool use across the *Pan* species and subspecies (Boesch & Boesch, 1981; Gruber et al., 2010; Lonsdorf, 2005). This may result from circumstances specific to the Bossou population. The community has decreased in size and has been geographically isolated for many years (see section 4.1.2), which may have resulted in unusual patterns compared to other communities. However, it may also be that the previous findings of a female bias are an artefact of short-term, cross-sectional investigations, and that the bias dissipates when variation is considered longitudinally (Berdugo et al., 2023; Chapman et al., 2017). This further illustrates the importance of long-term behavioural research.

In answer to the second question, I showed that the individual differences in post-ELP technological efficiency stemmed at least in part from divergent social learning experiences during the acquisition period of the skill. This offers support for Lonsdorf's (2005) social learning hypothesis for explaining the cause of variation in chimpanzee technological behaviour and provides the first example of its relevance for explaining differences at the individual-level and in lithic technology (see section 2.2.4). In turn, this is the first direct evidence of the long-term consequences of variation in tolerance and exposure to social learning opportunities on technological proficiency in any tool-using primate (Humle et al., 2009; van Schaik et al., 2003). As such, the answer to the second question contributes theoretically to our understanding of the social context that enabled primates, including hominins, to evolve to use complex tools (discussed further in section 8.2.3). Indeed, given the similarities between the stone tools used by the Bossou chimpanzees and early hominin lithic techno-complexes (see section 3.3.3), this ontogenetic research potentially provides an insight into the acquisition and transmission of Oldowan tools. This adds to the body of work conducting controlled laboratory experiments on modern human adults (see section 2.1.1) by investigating the acquisition of stone technological skills by young chimpanzees in natural settings over multiple generations.

In answer to the third question, I found that although young chimpanzees predominantly learned the complex stone tool behaviour from their mother, when not learning from their mother, individuals who are unrelated to the learner and who have longer bouts and displace the nut fewer times are more likely to be peered at. This furthers our understanding of the role of social learning throughout primate development (Whiten & van de Waal, 2018), and provides the first example of a "who" social learning strategy being employed by wild chimpanzees learning a pre-existing cultural behaviour. This may offer insights into the potential transmission strategies underlying early hominin lithic technology, which has relevance for modelling hominin cultural and technological evolution more generally.

Although the empirical contributions presented in this thesis do not speak directly to the importance of terrestriality in supporting the social learning of tool use, collectively they demonstrate the value of being in close proximity to multiple potential models, including non-kin, when acquiring the skills. A valuable next step would be to conduct long-term research on the ontogeny of the arboreal nut-cracking behaviour in the Taï chimpanzees to compare to the solely terrestrial behaviour in Bossou. This would contribute to our understanding of the so-called "terrestriality premium" that supported the acquisition of increasingly complex technology in hominins (Meulman et al., 2012, p. 58).

Alongside these questions, this thesis also had three broad aims:

1. Develop a comprehensive inter-generational data set of the stone tool behaviour of the Bossou chimpanzee population to provide a long-term record of the material culture of the critically endangered population and subspecies.
2. Establish a stable and reliable measure of chimpanzee nut-cracking efficiency.
3. Demonstrate the key value of long-term video archives for answering questions on social learning in skill acquisition in a long-lived species.

In realising these aims, I have made significant contributions to the fields of chimpanzee learning and behaviour, with broader implications for primate archaeology and conservation. By developing a comprehensive data set of the stone tool behaviour of all the wild Bossou chimpanzees, I hope to make a contribution to the preservation of the behaviours and cultural heritage of the population (Carvalho et al., 2022). By establishing a stable and reliable measure of chimpanzee nut-cracking efficiency, which expands on prior definitions used by Boesch & Boesch (1981) and Humle (2003) to incorporate the "strike accuracy" component—termed "displacement rate" in this thesis—used in long-tailed macaques (Tan et al., 2015), I have produced a reliable metric that can be replicated in future research. Moreover, I identified that "tool switch rate" was not a reliable measure of efficiency, which will inform its use in future research. Individuals in Bossou did vary in how frequently they changed their tools during a nut-cracking bout, but this does not appear to

reflect the same underlying construct as bout duration, strikes per nut, success rate, and displacement rate. Finally, by demonstrating the value of video archives for answering questions on social learning in skill acquisition, I hope that further research can be undertaken to continue to investigate the learning mechanisms employed by chimpanzees in the wild.

In this thesis, I was the first to take such a longitudinal approach in the study of wild chimpanzee learning and technological behaviour. In doing so, I have also provided specific methodological, empirical, and theoretical contributions to the literature, explored below.

8.2.1 Longitudinal Research on Wild Chimpanzee Behaviour

A key contribution made as part of this thesis was the production of a behavioural catalogue of the Bossou archive, alongside the long-term data set. As part of the data collection phase of this thesis, Alexander Mielke and I produced a near-complete catalogue of behaviours for the entirety of the Bossou archive from 1992–2018. The party composition was noted for each video, along with information on various behaviours to aid future research that makes use of the archive. This will support future studies by allowing researchers to instantly search for videos containing behaviours of interest. This can also be used to support machine learning algorithms which are being trained for use in computational ethological research (e.g., Schofield, 2022), such as by acting as the ground-truthing for social networks or by providing an immediate subset of videos to be used for algorithm training.

Moreover, I have created a comprehensive longitudinal data set on the acquisition and use of stone tools by chimpanzees across three generations, with a substantial number of data points for each individual. This is particularly important given that only two communities have long-term studies on stone tool use (Bossou and Taï, although the Taï chimpanzees also use wooden hammers; Boesch & Boesch, 1981), and only Bossou has a systematic video archive of yearly footage on the technological behaviour of the same individuals. The present research has produced an invaluable record of intergenerational cultural

transmission and maintenance in a wild primate population and the data set produced will provide further unique opportunities to undergo long-term investigations of cognition and behaviour in the critically endangered species.

8.2.2 Fitness Consequences of Individual Variation in Tool Use

This thesis lays the groundwork for determining the fitness gains incurred (such as through number of offspring) from efficient tool use, which would provide insights into the adaptive advantages of using stone tools to extract nut kernels (Biro et al., 2013). Indeed, Biro et al. (2013) explained that 'we cannot identify adaptations without first qualifying, and where possible quantifying, the variation on which natural selection may act' (p. 6). The research presented in Chapter 5 establishing stable individual differences in the efficiency of cracking oil palm nuts using stone tools has quantified the variation in the Bossou chimpanzees.

It was beyond the scope of the thesis to conduct dedicated research on the role of nut-cracking efficiency on longevity and (lifetime) reproductive success in Bossou. Although genealogy data are available for Bossou, this is constrained to matrilineal relationships as paternity was not established. As such, reproductive data exists for only eight females out of the 21 chimpanzees included in the research. Moreover, it is not possible to establish a causal link between nut-cracking efficiency and longevity based on the archival data alone. If less efficient nutcrackers died earlier, it may not be possible to distinguish between this being a consequence of relatively poor technological efficiency, or the low efficiency being an indicator of another factor affecting survival (e.g., general weakness or ill-health).

Finally, research specifically addressing these questions surrounding the fitness consequences of individual variation in tool use should incorporate broader trade-offs in activity budgets and energy expenditure, as it is possible that less efficient nutcrackers compensate for their relative energy disadvantages elsewhere. For example, they may be more efficient in other subsistence-related tasks, or they may increase their net acquisition rate (energy gained minus lost divided by total time spent) to increase their energy

availability (Kraft et al., 2021; Smith, 1979). Understanding how the time and energy costs associated with extractive foraging impact total energy expenditure will make substantial contributions to our understanding of foraging ecology and life history adaptations (Kraft et al., 2021).

8.2.3 Social Learning and Cultural Evolution

The research presented in Chapter 6 was the first to investigate the combined role of the "master" and the "apprentice" during the learning period of the stone tool use skill. In doing so, we found that mothers providing opportunities to learn to crack nuts socially, model tolerance to peering, and model intolerance to peering all significantly affected the future strikes per nut of the learners, with the latter two also significantly affecting the learner's subsequent bout duration. However, none of these developmental experiences predicted the success rate or displacement rate of the learner, suggesting that these components of efficiency are honed via different learning processes, perhaps via individual learning.

Although further research is required to determine the exact mechanism(s) that produce variation in success rate and displacement rate, the known incorporation of individual learning in the nut-cracking learning period may be a source of innovation within the community. As innovations appear to be rooted in motivation to obtain rewards (Thornton & Mesoudi, 2023), innovations may arise in Bossou that are specifically targeted at improving the success rate and decreasing the displacement rate of individuals. Thornton & Mesoudi (2023) explained that understanding the developmental conditions that foster innovation has important implications for the potential for cumulative cultural evolution across species. The developmental conditions established in Chapter 6 may lay the groundwork for cumulative cultural evolution in nut-cracking in Bossou.

Moreover, the research contributes to the theoretical literature on the role of model tolerance during behavioural acquisition, and the consequence of this on technological cultural transmission (Coussi-Korbel & Fragaszy, 1995; van Schaik et al., 1999). Our finding

that experiences of model *in*tolerance also predict the learner's subsequent tool use efficiency complements and advances these accounts. Building on this, in Chapter 7 we suggest that learners may select more tolerant models to peer at. Further research is required to assess whether a *copy tolerant models* social learning strategy exists in Bossou, and in other populations.

Combined, the findings from this thesis reiterate the critical need to investigate social learning and cultural transmission and maintenance in wild primates. By taking a longitudinal approach, I established that learners who were more likely to peer at the models' whole nut-cracking bout were subsequently less efficient at the skill, contributing important data to the imitation *versus* emulation debate. I discuss suggested future research directions based on this finding in section 8.4.1, below.

8.2.4 Primate Archaeology

The research findings from this thesis, particularly those pertaining to stable individual differences in stone tool efficiency presented in Chapter 5, have important implications for the field of primate archaeology. Indeed, variation in Oldowan flaking technique has previously been found within the same site in the Nachukui Formation in West Turkana, dated to 1.8–1.7 Ma (Roche et al., 2018). By demonstrating that individuals using stone tools in Bossou vary considerably in their displacement rate, which may increase the likelihood of fracture because of the repeated percussion of stone-on-stone (Carvalho et al., 2009; Luncz, Arroyo, et al., 2022), we highlight a potential process that may have produced the known variation within hominin archaeological assemblages.

Moreover, the findings presented in Chapter 6 on the social learning processes involved in producing this individual-level variation, and those in Chapter 7 highlighting the social learning strategies that make use of the individual variation in efficiency, contribute to an expanded link between primatology and archaeology (Harmand & Arroyo, 2023). Indeed, Harmand & Arroyo (2023) argued that,

> Our next efforts should go towards exploring learning processes in extant primates during tool-using and tool-producing… [as] only such an expanded and more informed knowledge will help generate alternatives to existing hypotheses accounting for the contrasts in technological proficiency among primates and, perhaps more puzzling, the uniqueness of hominin flaking as it emerged at least 3.3 Ma. (p. 10)

There is now an essential need for more work on the archaeology of perishable material, as outlined by Pascual-Garrido & Almeida-Warren (2021), so that we can take a 'step away from the lithic mania' (Carvalho, 2021, p. 347) of primate archaeology and gain a more holistic understanding of the material record produced by primates, including hominins (Pascual-Garrido et al., 2023).

8.2.5 Conservation

Not least, the research presented in this thesis contributes to the ongoing discussion surrounding the use of culture in conservation. Although chimpanzees are known to be behaviourally flexible in the face of anthropogenic disturbance (Hockings et al., 2015), some novel behaviours (such as crop-raiding) can incite tensions with the local human populations and increase the risk of pathogenic transmission from humans or livestock (Hockings et al., 2015; McLennan & Hill, 2010; Parsons et al., 2014).

Moreover, chimpanzee communities living in areas with a high "human footprint" (e.g., high population density and large amounts of infrastructure) have an 88% lower mean probability of a behaviour occurring than communities in low-impact locations (Kühl et al., 2019). This finding corroborates van Schaik's (2002) Disturbance Hypothesis for the loss of traditions in great apes, namely orangutans and chimpanzees. The Disturbance Hypothesis states that the core components of the social transmission of traditions—innovation, diffusion, and horizontal and vertical transmission—are impacted by human pressures such as hunting and habitat fragmentation, and hence behavioural repertoires will be significantly depleted in these environments (van Schaik, 2002). Likewise, as noted by

Gruber et al. (2021), 'if [population] turnover is too fast, and the cost of acquisition is too high, cultural traits could become extinct' (p. 7).

The research presented in Chapters 6 and 7 reiterates the importance of social learning in the acquisition of stone tool use in chimpanzees, and that specific strategies appear to be guiding this learning. As argued in the conclusion of Chapter 6, these social learning processes throughout the extended learning period must be protected if nut-cracking is to be used in conservation efforts. Indeed, nut-cracking is protected by the United Nations' Convention on the Conservation of Migratory Species of Wild Animals given the importance of the behaviour for the conservation of the West African chimpanzee subspecies (Expert Working Group on Animal Culture and Social Complexity, 2023). Knowing the social learning strategies employed during the transmission of nut-cracking may support targeted protection efforts (Greggor et al., 2017).

In fact, there is increasing recognition of the role of social learning and cultural transmission in conservation given their role in adaptability to changing environments and in maintaining evolutionary trajectories (Brakes et al., 2019). For example, Brakes et al. (2019) highlighted the importance of targeted protection of older individuals known to possess key social and ecological knowledge, as in African elephant matriarchs (*Loxodonta Africana*; McComb et al., 2001). Furthermore, they argued that,

> Understanding the importance of behavioural diversity will benefit conservation policies both when assessing the status of potentially vulnerable populations (e.g., when delineating units to conserve, by accounting for cultural segregation) and when devising effective conservation strategies (e.g., by identifying key repositories of social knowledge). (p. 1034)

However, Carvalho et al. (2022) cautioned against the use of "culture for conservation" without adequate consideration of the pros and cons on a case-by-case basis and context-dependent strategic deployment. They warned that using cultural traits in the conservation of species may delay what must be an immediate and rapid response to biodiversity loss, as

the necessary evidence base determining the cost-effectiveness and suitability of the policies may take too long to compile. Carvalho et al. (2022) argued that culture should not be a separate conservation tool, but instead should be one part of the conservation tool kit to 'both complement and enhance current conservation standards' (p. 2). The research presented in this thesis can potentially be used as part of the evidence-base to ascertain whether nut-cracking should be used in West African chimpanzee conservation efforts.

Also, there is increasing recognition that behavioural variability must be considered during conservation efforts, as it can impact the accuracy and precision of sign-based wildlife monitoring (Wessling & Surbeck, 2023). This is particularly relevant for the stone tool context given the durability of lithic artefacts. For example, efforts in November 2018 to monitor the status of the chimpanzee community in Diécké, Guinea, used remnants of nut-cracking activity as one of the proxies for chimpanzee presence (Almeida-Warren, 2023). It is important to consider how individual-level variation in this behaviour might affect the interpretation of traces left behind by tool users.

As it stands, there are only three chimpanzees remaining in Bossou: Jire, Jeje, and Fanwa (see Figure 19). During the course of this thesis project, five chimpanzees (Fangasi, Yo, Fana, Foaf, and Fanle) disappeared, with the cause for three losses (Foaf, Fangasi, and Fanle) being unknown as their bodies were never recovered. The Bossou chimpanzees have always lived in close proximity to humans and have previously been recognised as being the most human-disturbed chimpanzee population (Humle, 2011a; Wilson et al., 2014). However, in the current Anthropocene epoch, chimpanzees across Africa are living in increasingly anthropogenic environments (Hockings et al., 2015). As such, the findings of our research have important implications for all chimpanzee populations, not only for the nut-cracking behaviour of the Bossou chimpanzees and the West African subspecies more broadly.



Figure 19. A photograph taken in 2018 of what would become the three remaining Bossou chimpanzees at the end of this DPhil research in 2024 (from left to right: Jeje, Fanwa, and Jire). Photograph credit: Katarina Almeida-Warren.

8.3 LIMITATIONS

As well as the limitations pertaining to each of the three studies already discussed in Chapters 5, 6, and 7, the research undertaken for this thesis is limited by two main points.

The first limitation relates to the massive time investment required when collecting behavioural data from video. The data collection phase lasted approximately two years, which indicates just how time consuming this type of research can be. However, because of this, data on some relevant variables for the ontogeny of technology and technological efficiency (namely, individual trial-and-error learning) could not be gathered. In fact, the original intention was to also collect data on so-called "behavioural episodes", where a learner manipulates the stones and nuts (the "objects"), either together or independently, by themselves (Inoue-Nakamura & Matsuzawa, 1997). Behavioural episodes were previously delineated to represent the progression from those consisting of single actions on a single object to those involving multiple actions on multiple objects (Inoue-Nakamura & Matsuzawa, 1997).

Despite the known importance of trial-and-error learning for behavioural efficiency (Gruber et al., 2021), this element was dropped given the infeasibility of further data collection within the timespan of the DPhil. Instead, the research focussed specifically on the social learning components relevant to the acquisition of the stone tool use skill. Additional research is now needed to determine whether there are individual differences in the asocial learning of the nut-cracking skill, and whether this variation predicts the subsequent efficiency of the individual. This would provide a fuller picture as to the ontogeny of stone tool technology.

Second, I was not able to draw from the whole suite of previous research on animal learning and behavioural variation, meaning that I have not been able to compare my findings to other taxa beyond the tool using primates. For example, in the introduction to the research presented in Chapter 5, I highlighted the potential fitness implications of individual variation in wood-boring beetle larvae extraction by New Caledonian crows (Rutz et al., 2010). However, due to time and space constraints, I have not been able to delve deeply into the behavioural variation found in New Caledonian crow tool use, nor the ontogeny of these skills (Visalberghi et al., 2017). For example, the shape of their hooked stick tools is known to vary, being influenced by age, manufacture method, and the properties of the raw material (Sugasawa et al., 2017). Whilst I have attempted to demonstrate the broader foundations and implications of the research throughout, there will undoubtedly be examples I have missed.

8.4 FUTURE DIRECTIONS

The data set collated as part of this research and the findings presented throughout this thesis opens the door for many future research directions. The complete data set will be published to support these endeavours and allow the full potential of the data to be realised. This will also allow for further insights into the behaviours of the Bossou chimpanzees, which is a population on the cusp of extinction.

The specific future research directions for each study were discussed in their respective Chapters, but here two avenues of particular interest are outlined. These directions will add vital longitudinal data from wild chimpanzees to ongoing debates.

8.4.1 Imitation versus Emulation

An important next step would be to conduct dedicated research investigating whether the Bossou chimpanzees learn to use stone tools via imitation or emulation learning, and if there is variation in the use of these mechanisms. Results would build upon Lonsdorf's (2005) tentative conclusion that female chimpanzees learn to termite-fish via imitation, and male chimpanzees learn the skill via emulation. This conclusion was reached based on the finding that the similarity in termite-fishing techniques between mothers and daughters was greater than between mothers and sons.

An important follow-up study to the research presented in Chapter 6 would be to similarly test the congruence between the nut-cracking technique of infants who spent more time peering at the whole nut-cracking bout of models, and the technique of those models. The nut-cracking technique of individuals can be characterised using an action grammar perspective, whereby actions within a sequence follow grammatical rules (Greenfield et al., 1972; Hayashi, 2015). An investigation into the subsequent action grammars employed by learners would add fruitful new data to the imitation *versus* emulation debate. Indeed, if learners who peer at the whole nut-cracking bout of models go on to have similar action grammars, regardless of the efficiency of the skill, this would suggest that high-fidelity imitation is used by the Bossou chimpanzees. This follow-up study could also include whether learners preferentially imitate some models and emulate others, which would add further important insights into the transmission of the skill.

This research would also speak directly to the ongoing "Chimpanzee Culture Wars" (outlined in section 3.2) and could have far reaching implications for the field of animal learning. Indeed, Whiten (2022) noted that 'the concept of transmission fidelity begs more

conceptual analysis and dissection in the context of long-term cultural stability and change' (p. 228). By following the ontogeny of tool use techniques, the Bossou archive could be used to '[trace] such fidelity in animals in real time' to assess whether there is 'sufficient fidelity' for maintaining the long-lasting cultural behaviour of using stones to crack open nuts (p. 229). Moreover, data on how and from whom chimpanzees learn complex technological behaviours, and when these strategies develop in ontogeny, will provide a useful evolutionary perspective to inform our understanding of the evolution and transmission of tool use in hominins (Harmand & Arroyo, 2023; Whiten, 2022).

8.4.2 Cumulative Cultural Evolution

Building on this, another important avenue of future research would be to assess whether the efficiency of nut-cracking in Bossou changed through time. Indeed, Whiten (2022) argued that 'the millennia-long fidelity and stability of primate nut-cracking culture… is quite sufficient in principle to permit further cumulative cultural changes if they enhanced fitness' (p. 229). Mesoudi & Thornton (2018) laid out the four core criteria for cumulative cultural evolution: i) a behavioural change, likely resulting from individual learning, ii) the transmission of that modification to other individuals via social learning, iii) the learned behavioural change improving performance, and iv) the sequential repetition of the previous three criteria, such that there are step-wise improvements in performance over time. Mesoudi & Thornton (2018) use increases in the efficiency of extractive foraging as one of their examples of the third criterion (the learned behavioural change improving performance).

This topic would be a natural next step to investigate using the data set produced during this research. It would be possible to detect whether the bout duration, number of strikes per nut, success rate, and displacement rate (and also the separate aspect of tool switch rate) of the Bossou chimpanzees changed over time. Moreover, changes in the learnability

of the skill could be assessed, which Gruber et al. (2021) argued also constitutes an improvement in performance as it would improve the fitness of the cultural trait itself.

Schofield (2022) suggested that individual variation in action patterns and efficiency may change over time, such as changes in hand grips or nut selection. However, Schofield noted that these changes need not be unidirectional, with efficiency potentially decreasing over time because of changes in learning opportunities resulting from the decreases in population size and changes to network structure. Regardless of the findings of this future research, the results will have implications in terms of conservation policy (as mentioned in section 8.2.5) as well as for our understanding of cumulative cultural evolution in wild animals.

8.5 CONCLUSION

To unpack the complexities of animal behaviour, it is essential to study the same individuals over the course of their lifetime. By examining the presence, extent, and causes of individual-level variation in extractive foraging efficiency across 25 years, the research presented here has produced an unprecedented record of wild chimpanzee technological and cultural behaviour spanning three generations. Variation in efficiency can have profound fitness consequences, with stable individual differences in technological efficiency shedding light on the potential adaptive advantages of tool use. The research presented in this thesis establishes a reliable measure of nut-cracking efficiency for wild chimpanzees, which can be used in future research on chimpanzee tool use and cultural evolution. Moreover, it demonstrates the value of using long-term video archives for answering questions on social learning, which is critical for generating lifetime-scale data rather than snapshots from relatively short-term studies. Finally, it provides an insight into the social and cognitive processes that supported the acquisition of early lithic technologies in the hominin lineage.

Chimpanzees remain a relevant model for early hominin behaviour, but it is a model that is under threat. The Bossou community is on the cusp of extinction. We must act to ensure that no other populations follow suit.

REFERENCES

Almécija, S., Smaers, J. B., & Jungers, W. L. (2015). The evolution of human and ape hand proportions. *Nature Communications*, *6*(7717), 1–11. https://doi.org/10.1038/ncomms8717

Almeida-Warren, K. (2023). The chimpanzees of Korohouan, Diécké: an update on presence, conservation status and threats from the second largest forest reserve of Guinea. *International Primatological Society - Malaysian Primatological Society Congress*.

Almeida-Warren, K., Didier Camara, H., Matsuzawa, T., & Carvalho, S. (2022). Landscaping the behavioural ecology of primate stone tool use. *International Journal of Primatology*, *43*, 885–912. https://doi.org/10.1007/s10764-022-00305-y

Aplin, L. M., Sheldon, B. C., & McElreath, R. L. (2017). Conformity does not perpetuate suboptimal traditions in a wild population of songbirds. *Proceedings of the National Academy of Sciences*, *114*(30), 7830–7837. https://doi.org/10.1073/pnas.1621067114

Aplin, L. M., Sheldon, B. C., & Morand-Ferron, J. (2013). Milk bottles revisited: social learning and individual variation in the blue tit, *Cyanistes caeruleus*. *Animal Behaviour*, *85*(6), 1225–1232. https://doi.org/10.1016/j.anbehav.2013.03.009

Archer, W., Aldeias, V., & McPherron, S. P. (2020). What is "*in situ*"? A reply to Harmand et al. (2015). *Journal of Human Evolution*, *142*(102740), 1–5. https://doi.org/10.1016/j.jhevol.2020.102740

Atkisson, C., O'Brien, M. J., & Mesoudi, A. (2012). Adult learners in a novel environment use prestige-biased social learning. *Evolutionary Psychology*, *10*(3), 519–537. https://doi.org/10.1177/147470491201000309

Bain, M., Nagrani, A., Schofield, D., Berdugo, S., Bessa, J., Owen, J., Hockings, K. J., Matsuzawa, T., Hayashi, M., Biro, D., Carvalho, S., & Zisserman, A. (2021). Automated audiovisual behavior recognition in wild primates. *Science Advances*, *7*(46), eabi4883. https://doi.org/10.1126/sciadv.abi4883

Bandini, E., & Harrison, R. A. (2020). Innovation in chimpanzees. *Biological Reviews*, *95*(5), 1167–1197. https://doi.org/10.1111/brv.12604

Bard, K. A., & Leavens, D. A. (2014). The importance of development for comparative primatology. *Annual Review of Anthropology*, *43*, 183–200. https://doi.org/10.1146/annurev-anthro-102313-030223

Barham, L., Duller, G. A. T., Candy, I., Scott, C., Cartwright, C. R., Peterson, J. R., Kabukcu, C., Chapot, M. S., Melia, F., Rots, V., George, N., Taipale, N., Gethin, P., & Nkombwe, P. (2023). Evidence for the earliest structural use of wood at least 476,000 years ago. *Nature*,

622(7981), 107–111. https://doi.org/10.1038/s41586-023-06557-9

Barrett, B. J., McElreath, R. L., & Perry, S. E. (2017). Pay-off-biased social learning underlies the diffusion of novel extractive foraging traditions in a wild primate. *Proceedings of the Royal Society B: Biological Sciences*, *284*(1856), 20170358. https://doi.org/10.1098/rspb.2017.0358

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*(8), 181002. https://doi.org/10.1098/rsos.181002

Beck, B. B. (1980). *Animal tool behavior: the use and manufacture of tools by animals*. Garland STPM Press.

Belitzky, S., Goren-Inbar, N., & Werker, E. (1991). A Middle Pleistocene wooden plank with man-made polish. *Journal of Human Evolution*, *20*(4), 349–353. https://doi.org/10.1016/0047-2484(91)90015-N

Benito-Calvo, A., Carvalho, S., Arroyo, A., Matsuzawa, T., & De La Torre, I. (2015). First GIS analysis of modern stone tools used by wild chimpanzees (Pan troglodytes verus) in Bossou, Guinea, West Africa. *PLoS ONE*, *10*(3), e0121613. https://doi.org/10.1371/journal.pone.0121613

Berdugo, S. (2019). *Why do female chimpanzees become more frequent and efficient nutcrackers? An investigation into the developmental origins of the female bias in chimpanzee nut-cracking*. University of Oxford.

Berdugo, S., Cohen, E., Davis, A. J., Matsuzawa, T., & Carvalho, S. (2023). Stable long-term individual variation in chimpanzee technological efficiency. *BioRxiv*, 2023.11.21.568000. https://doi.org/10.1101/2023.11.21.568000

Bessa, J., Biro, D., & Hockings, K. J. (2022). Inter-community behavioural variation confirmed through indirect methods in four neighbouring chimpanzee communities in Cantanhez NP, Guinea-Bissau. *Royal Society Open Science*, *9*(211518). https://doi.org/10.1098/rsos.211518

Bessa, J., Hockings, K. J., & Biro, D. (2021). First evidence of chimpanzee extractive tool use in Cantanhez, Guinea-Bissau: cross-community variation in honey dipping. *Frontiers in Ecology and Evolution*, *9*(625303), 1–14. https://doi.org/10.3389/fevo.2021.625303

Biro, D., Haslam, M., & Rutz, C. (2013). Tool use as adaptation. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *368*(1630). https://doi.org/10.1098/rstb.2012.0408

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. https://doi.org/10.1007/s10071-003-0183-x

Biro, D., Sousa, C., & Matsuzawa, T. (2006). Ontogeny and cultural propagation of tool use by wild chimpanzees at Bossou, Guinea: Case studies in nut cracking and leaf folding. In T. Matsuzawa, M. Tomonaga, & M. Tanaka (Eds.), *Cognitive development in chimpanzees* (pp. 476–506). Springer.

Bobe, R., & Reynolds, S. C. (2022). Introduction: African paleoecology and human evolution. In S. C. Reynolds & R. Bobe (Eds.), *African paleoecology and human evolution* (pp. 1–6). Cambridge University Press.

Boesch, C. (1991). Teaching among wild chimpanzees. *Animal Behaviour*, *41*(3), 530–532. https://doi.org/101016/S0003-3472(05)80857-7

Boesch, C. (1993). Towards a new image of culture in wild chimpanzees? *Behavioral and Brain Sciences*, *16*(3), 514–515. https://doi.org/10.1017/S0140525X00031277

Boesch, C. (2013). Ecology and cognition of tool use in chimpanzees. In C. M. Sanz, J. Call, & C. Boesch (Eds.), *Tool use in animals: cognition and ecology* (pp. 21–47). Cambridge University Press.

Boesch, C., & Boesch-Achermann, H. (2000). *The chimpanzees of the Taï Forest : behavioural ecology and evolution*. Oxford University Press.

Boesch, C., & Boesch, H. (1981). Sex differences in the use of natural hammers by wild chimpanzees: a preliminary report. *Journal of Human Evolution*, *10*(7), 585–593. https://doi.org/10.1016/S0047-2484(81)80049-8

Boesch, C., & Boesch, H. (1983). Optimisation of nut-cracking with natural hammers by wild chimpanzees. *Behaviour*, *83*(3/4), 265–286. https://doi.org/10.1163/156853983X00192

Boesch, C., & Boesch, H. (1984). 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., Bombjaková, D., Meier, A., & Mundry, R. (2019). Learning curves and teaching when acquiring nut-cracking in humans and chimpanzees. *Scientific Reports*, *9*(1515). https://doi.org/10.1038/s41598-018-38392-8

Boesch, C., Kalan, A. K., Mundry, R., Arandjelovic, M., Pika, S., Dieguez, P., Ayimsin, E. A., Barciela, A., Coupland, C., Egbe, V. E., Eno-Nku, M., Michael Fay, J., Fine, D., Adriana Hernandez-Aguilar, R., 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

Bohn, M., Eckert, J., Hanus, D., Lugauer, B., Holtmann, J., & Haun, D. B. M. (2023). Great ape cognition is structured by stable cognitive abilities and predicted by developmental conditions. *Nature Ecology & Evolution*, *7*, 927–938. https://doi.org/10.1038/s41559-023-02050-8

Boose, K. J., White, F., & Meinelt, A. (2013). Sex differences in tool use acquisition in bonobos (*Pan paniscus*). *American Journal of Primatology*, *75*(9), 917–926. https://doi.org/10.1002/ajp.22155

Bouwhuis, S., Charmantier, A., Verhulst, S., & Sheldon, B. C. (2010). Individual variation in rates of senescence: natal origin effects and disposable soma in a wild bird population. *Journal of Animal Ecology*, *79*(6), 1251–1261. https://doi.org/10.1111/j.1365-2656.2010.01730.x

Boyd, R., & Richerson, P. J. (1985). *Culture and the evolutionary process*. University of Chicago Press.

Boyd, R., & Richerson, P. J. (1988). An evolutionary model for social learning: the effects of spatial and temporal variation. In T. R. Zentall & B. G. Galef (Eds.), *Social learning: psychological and biological perspectives* (pp. 29–48). Lawrence Erlbaum Associates.

Boyd, R., Richerson, P. J., & Henrich, J. (2011). The cultural niche: why social learning is essential for human adaptation. *Proceedings of the National Academy of Sciences*, *108*(suppl. 2), 10918–10925. https://doi.org/10.1073/pnas.1100290108

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., Notarbartolo di Sciara, G., 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

Brand, C. O., Heap, S., Morgan, J. H., & Mesoudi, A. (2020). The emergence and adaptive use of prestige in an online social learning task. *Scientific Reports*, *10*(12095). https://doi.org/10.1038/s41598-020-68982-4

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 origins* (pp. 222–244). Cambridge University Press. https://doi.org/10.1017/CBO9781139149327.011

Braun, D. R., Aldeias, V., Archer, W., Arrowsmith, 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. P., 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, 116*(24), 11712–11717. https://doi.org/10.1073/pnas.1820177116

Braun, D. R., Carvalho, S., Kaplan, R. S., Beardmore-Herd, M., Plummer, T. W., Biro, D., & Matsuzawa, T. (in review). *Stone selection by chimpanzees reveals parallel patterns to Oldowan hominins*.

Braun, D. R., & Hovers, E. (2009). Introduction: current issues in Oldowan research. In E. Hovers & D. R. Braun (Eds.), *Interdisciplinary approaches to the Oldowan* (pp. 1–14). Springer.

Bridges, A. D., Royka, A., Wilson, T., Lockwood, C., Richter, J., Juusola, M., & Chittka, L. (2024). Bumblebees socially learn behaviour too complex to innovate alone. *Nature*, *627*, 572–578. https://doi.org/10.1038/s41586-024-07126-4

Bril, B., Gilles, A. E., Ae, D., Foucart, J., Koki, A. E., Ae, F., & Hirata, S. (2009). Tool use as a way to assess cognition: how do captive chimpanzees handle the weight of the hammer when cracking a nut? *Animal Cognition*, *12*(2), 217–235. https://doi.org/10.1007/s10071-008-0184-x

Bril, B., Parry, R., & Dietrich, G. (2015). How similar are nut-cracking and stone-flaking? A functional approach to percussive technology. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *370*(20140355). https://doi.org/10.1098/rstb.2014.0355

Bründl, A. C., Tkaczynski, P., Nohon Kohou, G., Boesch, C., Wittig, R. M., & Crockford, C. (2020). Systematic mapping of developmental milestones in wild chimpanzees. *Developmental Science*, *24*(1), e12988. https://doi.org/10.1111/desc.12988

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), e23102. 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

Burke, C. J., Tobler, P. N., Baddeley, M., & Schultz, W. (2010). Neural mechanisms of observational learning. *Proceedings of the National Academy of Sciences*, *107*(32), 14431–14436. https://doi.org/10.1073/pnas.1003111107

Call, J., Carpenter, M., & Tomasello, M. (2005). Copying results and copying actions in the process of social learning: chimpanzees (*Pan troglodytes*) and human children (*Homo sapiens*). *Animal Cognition*, *8*(3), 151–163. https://doi.org/10.1007/s10071-004-0237-8

Carbonell, E., Sala, R., Barsky, D., & Celiberti, V. (2009). From homogeneity to multiplicity: a new approach to the study of archaic stone tools. In E. Hovers & D. R. Braun (Eds.), *Interdisciplinary approaches to the Oldowan* (pp. 25–38). Springer.

Caro, T. M., & Hauser, M. D. (1992). Is there teaching in nonhuman animals? *The Quarterly Review of Biology*, *67*(2), 151–174. https://doi.org/10.1086/417553

Carvalho, S. (2021). No country for old archaeology: comment on Archaeology of the Perishable. *Current Anthropology*, *62*(3), 346–347. https://doi.org/10.1086/713766

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*(1), 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., & McGrew, W. C. (2012). The origins of the Oldowan: why chimpanzees (*Pan troglodytes*) still are good models for technological evolution in Africa. In M. Dominguez-Rodrigo (Ed.), *Stone tools and fossil bones: debates in the archaeology of human origins* (pp. 201–221). Cambridge University Press.

Carvalho, S., Wessling, E. G., Abwe, E. E., Almeida-Warren, K., Arandjelovic, M., Boesch, C., Danquah, E., Diallo, M. S., Hobaiter, C., Hockings, K., Humle, T., Ikemeh, R. A., Kalan, A. K., Luncz, L., Ohashi, G., Pascual-Garrido, A., Piel, A., Samuni, L., Soiret, S., … Koops, K. (2022). Using nonhuman culture in conservation requires careful and concerted action. *Conservation Letters*, *15*(2), e12860. https://doi.org/10.1111/conl.12860

Chapman, C. A., Corriveau, A., Schoof, V. A. M., Twinomugisha, D., & Valenta, K. (2017). Long-term simian research sites: significance for theory and conservation. *Journal of Mammalogy*, *98*(3), 652–660. https://doi.org/10.1093/jmammal/gyw157

Chaudhary, N., Dyble, M., Major-Smith, D., Migliano, A. B., Page, A. E., Salali, G. D., Thompson, J., Viguier, S., & Vinicius, L. (2024). Hunter-gatherer children's close-proximity networks: similarities and differences with cooperative and communal breeding

systems. *Evolutionary Human Sciences*, *6*, e11. https://doi.org/10.1017/ehs.2024.1

Clutton-Brock, T., & Sheldon, B. C. (2010). Individuals and populations: the role of long-term, individual-based studies of animals in ecology and evolutionary biology. *Trends in Ecology & Evolution*, *25*(10), 562–573. https://doi.org/10.1016/j.tree.2010.08.002

Coolen, I., van Bergen, Y., Day, R. L., & Laland, K. N. (2003). Species difference in adaptive use of public information in sticklebacks. *Proceedings of the Royal Society B: Biological Sciences*, *270*(1531), 2413–2419. https://doi.org/10.1098/rspb.2003.2525

Coussi-Korbel, S., & Fragaszy, D. M. (1995). On the relation between social dynamics and social learning. *Animal Behaviour*, *50*(6), 1441–1453. https://doi.org/10.1016/0003-3472(95)80001-8

Crockford, C., & Boesch, C. (2003). Context-specific calls in wild chimpanzees, *Pan troglodytes verus*: analysis of barks. *Animal Behaviour*, *66*(1), 115–125. https://doi.org/10.1006/anbe.2003.2166

d'Oliveira Coelho, J., Anemone, R. L., Bobe, R., & Carvalho, S. (in review). *Parting ways:* Pan-Homo *divergence revisited*.

Danchin, É., Charmantier, A., Champagne, F. A., Mesoudi, A., Pujol, B., & Blanchet, S. (2011). Beyond DNA: integrating inclusive inheritance into an extended theory of evolution. *Nature Reviews Genetics*, *12*(7), 475–486. https://doi.org/10.1038/nrg3028

Darwin, C. (1859). *On the origin of species by means of natural selection*. John Murray.

de Beaune, S. A. (2004). The invention of technology: prehistory and cognition. *Current Anthropology*, *45*(2), 139–162. https://doi.org/10.1086/381045

De La Torre, I. (2011). The origins of stone tool technology in Africa: a historical perspective. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *366*, 1028–1037. https://doi.org/10.1098/rstb.2010.0350

De Waal, F. B. M. (2003). Silent invasion: Imanishi's primatology and cultural bias in science. *Animal Cognition*, *6*(4), 293–299. https://doi.org/10.1007/s10071-003-0197-4

Domínguez-Rodrigo, M., & Alcalá, L. (2016). 3.3-million-year-old stone tools and butchery traces? More evidence needed. *PaleoAnthropology*, *2016*, 46–53. https://doi.org/10.4207/PA.2016.ART99

Drummond-Clarke, R. C., Kivell, T. L., Sarringhaus, L., Stewart, F. A., Humle, T., & Piel, A. K. (2024). Wild chimpanzee behavior suggests that a savanna-mosaic habitat did not support the emergence of hominin terrestrial bipedalism. *Science Advances*, *8*(50), eadd9752. https://doi.org/10.1126/sciadv.add9752

Eppley, T. M., Hoeks, S., Chapman, C. A., Ganzhorn, J. U., Hall, K., Owen, M. A., Adams, D. B., Allgas, N., Amato, K. R., Andriamahaihavana, M., Aristizabal, J. F., Baden, A. L., Balestri, M., Barnett, A. A., Bicca-Marques, J. C., Bowler, M., Boyle, S. A., Brown, M., Caillaud, D., …

Santini, L. (2022). Factors influencing terrestriality in primates of the Americas and Madagascar. *Proceedings of the National Academy of Sciences*, *119*(42), e2121105119. https://doi.org/10.1073/pnas.2121105119

Eshchar, Y., Izar, P., Visalberghi, E., Resende, B. D., & Fragaszy, D. M. (2016). When and where to practice: social influences on the development of nut-cracking in bearded capuchins (*Sapajus libidinosus*). *Animal Cognition*, *19*(3), 605–618. https://doi.org/10.1007/s10071-016-0965-6

Estienne, V., Cohen, H., Wittig, R. M., & Boesch, C. (2019). Maternal influence on the development of nut-cracking skills in the chimpanzees of the Taï forest, Côte d'Ivoire (*Pan troglodytes verus*). *American Journal of Primatology*, *81*(7), e23022. https://doi.org/10.1002/ajp.23022

Estienne, V., Stephens, C., & Boesch, C. (2017). Extraction of honey from underground bee nests by central African chimpanzees (*Pan troglodytes troglodytes*) in Loango National Park, Gabon: techniques and individual differences. *American Journal of Primatology*, *79*(8), e22672. https://doi.org/10.1002/ajp.22672

Expert Working Group on Animal Culture and Social Complexity. (2023). *Reports of the Concerted Action Sub-Groups: Chimpanzees*. https://www.cms.int/sharks/en/document/reports-concerted-action-sub-groups-chimpanzees

Falótico, T., Bueno, C. Q., & Ottoni, E. B. (2021). Ontogeny and sex differences in object manipulation and probe tool use by wild tufted capuchin monkeys (*Sapajus libidinosus*). *American Journal of Primatology*, *83*(5). https://doi.org/10.1002/ajp.23251

Falótico, T., Valença, T., Verderane, M. P., Santana, B. C., & Sirianni, G. (2024). Mapping nut-cracking in a new population of wild capuchin monkeys (*Sapajus libidinosus*) at Ubajara National Park, Brazil. *American Journal of Primatology*, *86*(4), e23595. https://doi.org/10.1002/ajp.23595

Foley, R. A., & Gamble, C. (2009). The ecology of social transitions in human evolution. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *364*(1533), 3267–3279. https://doi.org/10.1098/rstb.2009.0136

Fox, E. A., Sitompul, A., & van Schaik, C. P. (1999). Intelligent tool use in wild Sumatran orangutans. In S. T. Parker, R. W. Mitchell, & H. L. Miles (Eds.), *The mentalities of gorillas and orangutans* (pp. 99–116). Cambridge University Press.

Fragaszy, D. M., Aiempichitkijkarn, N., Eshchar, Y., Mangalam, M., Izar, P., Resende, B. D., & Visalberghi, E. (2023). The development of expertise at cracking palm nuts by wild bearded capuchin monkeys, *Sapajus libidinosus*. *Animal Behaviour*, *197*, 1–14.

https://doi.org/10.1016/j.anbehav.2022.12.008

Fragaszy, D. M., Biro, D., Eshchar, Y., Humle, T., Izar, P., Resende, B. D., & Visalberghi, E. (2013). The fourth dimension of tool use: temporally enduring artefacts aid primates learning to use tools. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *368*(1630). https://doi.org/10.1098/rstb.2012.0410

Fragaszy, D. M., Izar, P., Visalberghi, E., Ottoni, E. B., & Gomes de Oliveira, M. (2004). Wild capuchin monkeys (*Cebus libidinosus*) use anvils and stone pounding tools. *American Journal of Primatology*, *64*(4), 359–366. https://doi.org/10.1002/ajp.20085

Friard, O., & Gamba, M. (2016). BORIS: a free, versatile open-source event-logging software for video/audio coding and live observations. *Methods in Ecology and Evolution*, *7*(11), 1325–1330. https://doi.org/10.1111/2041-210X.12584

Furuichi, T., Sanz, C. M., Koops, K., Sakamaki, T., Ryu, H., Tokuyama, N., & Morgan, D. B. (2015). Why do wild bonobos not use tools like chimpanzees do? *Behaviour*, *152*, 425–460. https://doi.org/10.1163/1568539X-00003226

Galef, B. G. (1988). Imitation in animals: history, definition, and interpretation of data from the psychological laboratory. In T. R. Zentall & B. G. Galef (Eds.), *Social learning: psychological and biological perspectives* (pp. 3–28). Lawrence Erlbaum Associates.

Gamer, M., Lemon, J., Fellows, I., & Singh, P. (2019). *irr: various coefficients of interrater reliability and agreement.* (R package version 0.84.1). https://cran.r-project.org/package=irr

Goldsborough, Z., Crofoot, M. C., & Barrett, B. J. (2024). Male-biased stone tool use by wild white-faced capuchins (*Cebus capucinus imitator*). *American Journal of Primatology*, *86*(4), e23594. https://doi.org/10.1002/ajp.23594

Goodall, J. (1964). Tool-using and aimed throwing in a community of free-living chimpanzees. *Nature*, *201*(4926), 1264–1266. https://doi.org/10.1038/2011264a0

Goren-Inbar, N., Gonen, S., Melamed, Y., & Kislev, M. (2002). Nuts, nut cracking, and pitted stones at Gesher Benot Ya'aqov, Israel. *Proceedings of the National Academy of Sciences*, *99*(4), 2455–2460. https://doi.org/10.1073/pnas.032570499

Gould, S. J. (1999). *The Human Difference*. The New York Times. http://www.nytimes.com/1999/07/02/opinion/the-human-difference.html

Grabowski, M., Hatala, K. G., & Jungers, W. L. (2018). Body mass estimates of the earliest possible hominins and implications for the last common ancestort. *Journal of Human Evolution*, *122*, 84–92. https://doi.org/10.1016/j.jhevol.2018.05.001

Greenfield, P. M., Nelson, K., & Saltzman, E. (1972). The development of rulebound strategies for manipulating seriated cups: a parallel between action and grammar. *Cognitive Psychology*, *3*(2), 291–310. https://doi.org/10.1016/0010-0285(72)90009-6

Greggor, A. L., Thornton, A., & Clayton, N. S. (2017). Harnessing learning biases is essential for applying social learning in conservation. *Behavioral Ecology and Sociobiology*, *71*(16). https://doi.org/10.1007/s00265-016-2238-4

Gruber, T., & Biro, D. (2023). Escaping a blind alley: the ZLS as a 'cultural crucible'?: Comment on "Blind alleys and fruitful pathways in the comparative study of cultural cognition" by Andrew Whiten. *Physics of Life Reviews*, *44*, 86–88. https://doi.org/10.1016/j.plrev.2022.12.012

Gruber, T., Chimento, M., Aplin, L. M., & Biro, D. (2021). Efficiency fosters cumulative culture across species. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *377*(1843), 20200308. https://doi.org/10.1098/rstb.2020.0308

Gruber, T., Clay, Z., & Zuberbühler, K. (2010). A comparison of bonobo and chimpanzee tool use: evidence for a female bias in the *Pan* lineage. *Animal Behaviour*, *80*(6), 1023–1033. https://doi.org/10.1016/j.anbehav.2010.09.005

Grund, C., Neumann, C., Zuberbühler, K., & Gruber, T. (2019). Necessity creates opportunity for chimpanzee tool use. *Behavioural Ecology*, *30*(4), 1136–1144. https://doi.org/10.1093/beheco/arz062

Gumert, M. D., Kuan Hoong, L., & Malaivijitnond, S. (2011). Sex differences in the stone tool-use behaviour 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

Hammond, P., Bobe, R., & Carvalho, S. (in review). *Insights from behavioural ecology on the evolution of primate terrestriality and hominin locomotion*.

Hammond, P., Lewis-Bevan, L., Biro, D., & Carvalho, S. (2022). Risk perception and terrestriality in primates: a quasi-experiment through habituation of chacma baboons (*Papio ursinus*) in Gorongosa National Park, Mozambique. *American Journal of Primatology*, *179*(1), 48–59. https://doi.org/10.1002/ajpa.24567

Harmand, S., & Arroyo, A. (2023). Linking primatology and archaeology: the transversality of stone percussive behaviors. *Journal of Human Evolution*, *181*, 103398. https://doi.org/10.1016/j.jhevol.2023.103398

Harmand, S., Lewis, J. E., Feibel, C. S., Lepre, C. J., Prat, S., Lenoble, A., Boes, X., Quinn, R. L., Brenet, M., Arroyo, A., Taylor, N., Clement, 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), 310–312. https://doi.org/10.1038/nature14464

Haslam, M. (2013). "Captivity bias" in animal tool use and its implications for the evolution of hominin technology. *Philosophical Transactions of the Royal Society B: Biological*

Sciences, *368*, 20120421. https://doi.org/10.1098/rstb.2012.0421

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*(7253), 339–344. https://doi.org/10.1038/nature08188

Hayashi, M. (2015). Perspectives on object manipulation and action grammar for percussive actions in primates. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *370*(1682), 20140350. https://doi.org/10.1098/rstb.2014.0350

Hayes, L. D., & Schradin, C. (2017). Long-term field studies of mammals: what the short-term study cannot tell us. *Journal of Mammalogy*, *98*(3), 600–602. https://doi.org/10.1093/jmammal/gyx027

Heldstab, S. A., Kosonen, Z. K., Koski, S. E., Burkart, J. M., van Schaik, C. P., & Isler, K. (2016). Manipulation complexity in primates coevolved with brain size and terrestriality. *Scientific Reports*, *6*(1), 24528. https://doi.org/10.1038/srep24528

Henrich, J., & Broesch, J. (2011). On the nature of cultural transmission networks: evidence from Fijian villages for adaptive learning biases. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *366*(1567), 1139–1148. https://doi.org/10.1098/rstb.2010.0323

Heyes, C. (1993). Imitation without perspective-taking. *Behavioral and Brain Sciences*, *16*(3), 524–525. https://doi.org/10.1017/S0140525X00031393

Heyes, C. (1994). Social learning in animals: categories and mechanisms. *Biological Reviews*, *69*(2), 207–231. https://doi.org/10.1111/j.1469-185x.1994.tb01506.x

Heyes, C. (2012). What's social about social learning? *Journal of Comparative Psychology*, *126*(2), 193–202. https://doi.org/10.1037/a0025180

Heyes, C. (2016). Blackboxing: social learning strategies and cultural evolution. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *371*(1693). https://doi.org/10.1098/rstb.2015.0369

Heyes, C. (2017). When does social learning become cultural learning? *Developmental Science*, *20*(e12350), 1–14. https://doi.org/10.1111/desc.12350

Hobaiter, C., Poisot, T., Zuberbühler, K., Hoppitt, W. J. E., & Gruber, T. (2014). Social network analysis shows direct evidence for social transmission of tool use in wild chimpanzees. *PLOS Biology*, *12*(9), e1001960. https://doi.org/10.1371/journal.pbio.1001960

Hockings, K. J. (2007). *Human-chimpanzee coexistence at Bossou, the Republic of Guinea: A chimpanzee perspective*. University of Stirling.

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.

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. (2010). Flexible feeding on cultivated underground storage organs by rainforest-dwelling chimpanzees at Bossou, West Africa. *Journal of Human Evolution*, *58*(3), 227–233. https://doi.org/10.1016/j.jhevol.2009.11.004

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., Wilson, M. L., Wood, B. A., Wrangham, R. W., & Hill, C. M. (2015). Apes in the Anthropocene: flexibility and survival. *Trends in Ecology & Evolution*, *30*(4), 215–222. https://doi.org/10.1016/j.tree.2015.02.002

Hoppitt, W. J. E., Brown, G. R., Kendal, R. L., Rendell, L., Thornton, A., Webster, M. M., & Laland, K. N. (2008). Lessons from animal teaching. *Trends in Ecology & Evolution*, *23*(9), 486–493. https://doi.org/10.1016/j.tree.2008.05.008

Hoppitt, W. J. E., & Laland, K. N. (2008). Social processes influencing learning in animals: a review of the evidence. *Advances in the Study of Behavior*, *38*, 105–165. https://doi.org/10.1016/S0065-3454(08)00003-X

Hoppitt, W. J. E., & Laland, K. N. (2013a). Introduction. In *Social learning: an introduction to mechanisms, methods, and models* (pp. 1–15). Princeton University Press. https://doi.org/10.23943/princeton/9780691150703.003.0001

Hoppitt, W. J. E., & Laland, K. N. (2013b). Social learning mechanisms. In *Social learning: an introduction to mechanisms, methods, and models* (pp. 62–101). Princeton University Press. https://doi.org/10.23943/princeton/9780691150703.003.0004

Horner, V., & Whiten, A. (2005). Causal knowledge and imitation/emulation switching in chimpanzees (*Pan troglodytes*) and children (*Homo sapiens*). *Animal Cognition*, *8*(3), 164–181. https://doi.org/10.1007/s10071-004-0239-6

Humle, T. (2003). *Culture and variation in wild chimpanzee behaviour: a study of three communities in West Africa*. University of Stirling, Stirling.

Humle, T. (2011a). Location and ecology. In T. Matsuzawa, T. Humle, & Y. Sugiyama (Eds.), *The chimpanzees of Bossou and Nimba* (pp. 13–21). Springer.

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.

Humle, T. (2016). Franco-Japanese and other collaborative contributions to understanding chimpanzee culture at Bossou and the Nimba Mountains. *Primates*, *57*(3), 339–348. https://doi.org/10.1007/s10329-016-0536-0

Humle, T., & Kormos, R. (2011). Chimpanzees in Guinea and in West Africa. In T. Matsuzawa, T. Humle, & Y. Sugiyama (Eds.), *The chimpanzees of Bossou and Nimba* (pp. 393–401). Springer.

Humle, T., Maisels, F., Oates, J. F., Plumptre, A., & Williamson, E. (2016). *Chimpanzee (Pan troglodytes)*. The IUCN Red List of Threatened Species. https://doi.org/10.2305/IUCN.UK.2016-2.RLTS.T15933A17964454.en

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*, 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*(Suppl 1), S37–S48. https://doi.org/10.1007/s10071-009-0272-6

Hunt, G. R., Gray, R. D., & Taylor, A. H. (2013). Why is tool use rare in animals? In C. M. Sanz, J. Call, & C. Boesch (Eds.), *Tool use in animals: cognition and ecology* (pp. 89–118). Cambridge University Press.

Inoue-Nakamura, N., & Matsuzawa, T. (1997). Development of stone tool use by wild chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology*, *111*(2), 159–173. https://doi.org/10.1037/0735-7036.111.2.159

Izar, P., Peternelli-dos-Santos, L., Rothman, J. M., Raubenheimer, D., Presotto, A., Gort, G., Visalberghi, E., & Fragaszy, D. M. (2022). Stone tools improve diet quality in wild monkeys. *Current Biology*, *32*(18), 4088–4092. https://doi.org/10.1016/j.cub.2022.07.056

Jones, J. H. (2011). Primates and the evolution of long, slow life histories. *Current Biology*, *21*(18), R708–R717. https://doi.org/10.1016/j.cub.2011.08.025

Jupyter. (2021, February 8). https://jupyter.org/index.html

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., Ayimsin, E. A., Bailey, E., Bessone, M., Brazzola,

G., Ebua Buh, V., Chancellor, R., Cohen, H., Coupland, C., … Kühl, H. S. (2020). Environmental variability supports chimpanzee behavioural diversity. *Nature Communications*, *11*(4451). https://doi.org/10.1038/s41467-020-18176-3

Kaplan, H. S., Hill, K. R., Lancaster, J., & Hurtado, A. M. (2000). A theory of human life history evolution: diet, intelligence, and longevity. *Evolutionary Anthropology*, *9*(7), 156–185. https://doi.org/10.1002/1520-6505(2000)9:4<156::AID-EVAN5>3.0.CO;2-7

Kappeler, P. M., van Schaik, C. P., & Watts, D. P. (2012). The values and challenges of long-term field studies. In P. M. Kappeler & D. P. Watts (Eds.), *Long-term field studies of primates* (pp. 3–18). Springer Berlin Heidelberg. https://doi.org/10.1007/978-3-642-22514-7_1

Kendal, R. L., Coolen, I., van Bergen, Y., & Laland, K. N. (2005). Trade-offs in the adaptive use of social and asocial learning. *Advances in the Study of Behavior*, *35*, 333–379. https://doi.org/10.1016/S0065-3454(05)35008-X

Kendal, R. L., Custance, D. M., Kendal, J. R., Vale, G., Stoinski, T. S., Rakotomalala, N. L., & Rasamimanana, H. (2010). Evidence for social learning in wild lemurs (*Lemur catta*). *Learning & Behavior*, *38*(3), 220–234. https://doi.org/10.3758/LB.38.3.220

Kendal, R. L., Galef, B. G., & van Schaik, C. P. (2010). Social learning research outside the laboratory: how and why? *Learning & Behavior*, *38*(3), 187–194. https://doi.org/10.3758/LB.38.3.187

King, G. E. (2020). Primate perspectives on the evolution of human behavior. In J. Vonk & T. Shackelford (Eds.), *Encyclopedia of animal cognition and behavior* (pp. 1–12). Springer International Publishing. https://doi.org/10.1007/978-3-319-47829-6_2099-1

Kinzey, W. G. (Ed.). (1987). *The evolution of human behaviour: primate models*. State University of New York Press.

Koops, K. (2023). The puzzle of *Pan* tool use: why are bonobos so different from chimpanzees in their use of tools? In T. Furuichi, G. Idani, D. Kimura, H. Ihobe, & C. Hashimoto (Eds.), *Bonobos and people at Wamba: 50 years of research* (pp. 133–147). Springer Nature Singapore. https://doi.org/10.1007/978-981-99-4788-1_12

Koops, K., Biro, D., Matsuzawa, T., McGrew, W. C., & Carvalho, S. (2023). Appropriate knowledge of wild chimpanzee behavior ('know-what') and field experimental protocols ('know-how') are essential prerequisites for testing the origins and spread of technological behavior. Response to "Unmotivated subjects cannot provide interpretable data and tasks with sensitive learning periods require appropriately aged subjects" by C. Tennie and J. Call. *Animal Behavior and Cognition*, *10*(2), 163–168. https://doi.org/10.26451/abc.10.02.05.2023

Koops, K., Furuichi, T., & Hashimoto, C. (2015). Chimpanzees and bonobos differ in intrinsic

motivation for tool use. *Scientific Reports*, *5*(11356), 1–6. https://doi.org/10.1038/srep11356

Koops, K., Furuichi, T., Hashimoto, C., & van Schaik, C. P. (2015). Sex differences in object manipulation in wild immature chimpanzees (*Pan troglodytes schweinfurthii*) and bonobos (*Pan paniscus*): preparation for tool use? *PLoS ONE*, *10*(10), e0139909. https://doi.org/10.1371/journal.pone.0139909

Koops, K., Gaspard Soumah, A., van Leeuwen, K. L., Didier Camara, H., & Matsuzawa, T. (2022). Field experiments find no evidence that chimpanzee nut cracking can be independently innovated. *Nature Human Behaviour*, *6*, 487–494. https://doi.org/10.1038/s41562-021-01272-9

Koops, K., McGrew, W. C., & Matsuzawa, T. (2010). Do chimpanzees (*Pan troglodytes*) use cleavers and anvils to fracture *Treculia africana* fruits? Preliminary data on a new form of percussive technology. *Primates*, *51*(2), 175–178. https://doi.org/10.1007/s10329-009-0178-6

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., & Sanz, C. M. (2022). Progress and prospects in primate tool use and cognition. In M. J. Beran & B. L. Schwartz (Eds.), *Primate cognitive studies* (pp. 238–259). Cambridge University Press. https://doi.org/10.1017/9781108955836.010

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*(12456). https://doi.org/10.1038/srep12456

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

Kortlandt, A. (1962). Chimpanzees in the wild. *Scientific American*, *206*(5), 128–140. https://doi.org/10.1038/scientificamerican0562-128

Kortlandt, A. (1986). The use of stone tools by wild-living chimpanzees and earliest hominids. *Journal of Human Evolution*, *15*(2), 77–132. https://doi.org/10.1016/S0047-2484(86)80068-9

Kraft, T. S., Venkataraman, V. V., Wallace, I. J., Crittenden, A. N., Holowka, N. B., Stieglitz, J., Harris, J., Raichlen, D. A., Wood, B., Gurven, M., & Pontzer, H. (2021). The energetics of

uniquely human subsistence strategies. *Science*, *374*(6575). https://doi.org/10.1126/science.abf0130

Kühl, H. S., Boesch, C., Kulik, L., Haas, F., Arandjelovic, M., Dieguez, P., Bocksberger, G., McElreath, M. B., Agbor, A., Angedakin, S., Ayimsin, E. A., Bailey, E., Barubiyo, D., Bessone, M., Brazzola, G., Chancellor, R., Cohen, H., Coupland, C., Danquah, E., … Kalan, A. K. (2019). Human impact erodes chimpanzee behavioural diversity. *Science*, *363*(6434), 1453–1455. https://doi.org/10.1126/science.aau4532

Kühl, H. S., Kalan, A. K., Arandjelovic, M., Aubert, F., D'Auvergne, L., Goedmakers, A., Jones, S., Kehoe, L., Regnaut, S., Tickle, A., Ton, E., van Schijndel, J., Abwe, E. E., Angedakin, S., Agbor, A., Ayimisin, E. A., Bailey, E., Bessone, M., Bonnet, M., … Boesch, C. (2016). Chimpanzee accumulative stone throwing. *Scientific Reports*, *6*(1), 22219. https://doi.org/10.1038/srep22219

Kutsukake, N. (2011). Lost in translation: field primatology, culture, and interdisciplinary approaches. In J. MacClancy & A. Fuentes (Eds.), *Centralizing fieldwork: critical perspectives from primatology, biological and social anthropology* (pp. 104–120). Berghahn Books.

Laland, K. N. (2004). Social learning strategies. *Learning & Behaviour*, *32*(1), 4–14. https://doi.org/10.3758/BF03196002

Laland, K. N., & Hoppitt, W. J. E. (2003). Do animals have culture? *Evolutionary Anthropology*, *12*(3), 150–159. https://doi.org/10.1002/evan.10111

Langlitz, N. (2020). *Chimpanzee culture wars*. Princeton University Press.

Legare, C. H. (2017). Cumulative cultural learning: development and diversity. *Proceedings of the National Academy of Sciences*, *114*(30), 7877–7883. https://doi.org/10.1073/pnas.1620743114

Lewin, R., & Foley, R. A. (2004). *Principles of human evolution* (Second). Blackwell Publishing.

Li, L., Reeves, J. S., Lin, S. C., Braun, D. R., & McPherron, S. P. (2023). Did Early Pleistocene hominins control hammer strike angles when making stone tools? *Journal of Human Evolution*, *183*, 103427. https://doi.org/10.1016/j.jhevol.2023.103427

Lind, J., Ghirlanda, S., & Enquist, M. (2019). Social learning through associative processes: a computational theory. *Royal Society Open Science*, *6*(3). https://doi.org/10.1098/rsos.181777

Lindshield, S., Rothman, J. M., Ortmann, S., & Pruetz, J. D. (2021). Western chimpanzees (*Pan troglodytes verus*) access a nutritionally balanced, high energy, and abundant food, baobab (*Adansonia digitata*) fruit, with extractive foraging and reingestion. *American Journal of Primatology*, *83*(9), e23307. https://doi.org/10.1002/ajp.23307

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*, 36–46. https://doi.org/10.1007/s10071-005-0002-7

Lonsdorf, E. V. (2013). The role of mothers in the development of complex skills in chimpanzees. In K. B. H. Clancy, K. Hinde, & J. N. Rutherford (Eds.), *Building babies: primate development in proximate and ultimate perspective* (pp. 303–318). Springer.

Lonsdorf, E. V, Eberly, L. E., & Pusey, A. E. (2004). Sex differences in learning in chimpanzees. *Nature Brief Communications*, *428*, 715–716. https://doi.org/10.1038/nature02527

Luncz, L. V, Arroyo, A., Falótico, T., Quinn, P., & Proffitt, T. (2022). A primate model for the origin of flake technology. *Journal of Human Evolution*, *171*, 103250. https://doi.org/10.1016/j.jhevol.2022.103250

Luncz, L. V, Braun, D. R., Marreiros, J., Bamford, M., Zeng, C., Pacome, S. S., Junghenn, P., Buckley, Z., Yao, X., & Carvalho, S. (2022). Chimpanzee wooden tool analysis advances the identification of percussive technology. *iScience*, *25*(11), 105315. https://doi.org/10.1016/j.isci.2022.105315

Luncz, L. V, Mundry, R., & Boesch, C. (2012). Evidence for cultural differences between neighboring chimpanzee communities. *Current Biology*, *22*(10), 922–926. https://doi.org/10.1016/j.cub.2012.03.031

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. https://doi.org/10.1016/j.anbehav.2017.12.017

Luncz, L. V, Svensson, M. S., Haslam, M., Malaivijitnond, S., Proffitt, T., & Gumert, M. (2017). Technological response of wild macaques (*Macaca fascicularis*) to anthropogenic change. *International Journal of Primatology*, *38*(5), 872–880. https://doi.org/10.1007/s10764-017-9985-6

Marchant, L. F., & McGrew, W. C. (2005). Percussive technology: chimpanzee baobab smashing and the evolutionary modelling of hominin knapping. In V. Rous & B. Bril (Eds.), *Stone knapping: the necessary conditions for a uniquely hominid behaviour* (pp. 341–350). McDonald Institute for Archaeological Research.

Martin, P., & Bateson, P. (2007). *Measuring behaviour: an introductory guide* (Third). Cambridge University Press.

Masi, S., Pouydebat, E., San-Galli, A., Meulman, E. J. M., Breuer, T., Reeves, J., & Tennie, C. (2022). Free hand hitting of stone-like objects in wild gorillas. *Scientific Reports*, *12*(1).

https://doi.org/10.1038/s41598-022-15542-7

Matsuzawa, T. (1994). Field experiments on use of stone tools by chimpanzees in the wild. In R. W. Wrangham, W. C. McGrew, F. B. M. De Waal, & P. G. Heltne (Eds.), *Chimpanzee cultures* (pp. 351–370). Harvard University Press.

Matsuzawa, T. (2003). Koshima monkeys and Bossou chimpanzees: long-term research on culture in nonhuman primates. In F. B. M. de Waal & P. L. Tyack (Eds.), *Animal social complexity: intelligence, culture, and individualized societies* (pp. 374–387). Harvard University Press.

Matsuzawa, T. (2011a). Field experiments of tool-use. In T. Matsuzawa, T. Humle, & Y. Sugiyama (Eds.), *The chimpanzees of Bossou and Nimba* (pp. 157–164). Springer.

Matsuzawa, T. (2011b). Stone tools for nut-cracking. In T. Matsuzawa, T. Humle, & Y. Sugiyama (Eds.), *The chimpanzees of Bossou and Nimba* (pp. 73–84). Springer.

Matsuzawa, T., Biro, D., Humle, T., Inoue-Nakamura, N., Tonooka, R., & Yamakoshi, G. (2001). Emergence of culture in wild chimpanzees: education by master-apprenticeship. In T. Matsuzawa (Ed.), *Primate origins of human cognition and behavior* (pp. 557–574). Springer.

Matsuzawa, T., Humle, T., & Sugiyama, Y. (Eds.). (2011). *The chimpanzees of Bossou and Nimba*. Springer.

Matsuzawa, T., Ohashi, G., Humle, T., Granier, N., Kourouma, M., & Gaspard Soumah, A. (2011). Green Corridor Project: planting trees in the savanna between Bossou and Nimba. In T. Matsuzawa, T. Humle, & Y. Sugiyama (Eds.), *The chimpanzees of Bossou and Nimba* (pp. 361–370). Springer.

McComb, K., Moss, C., Durant, S. M., Baker, L., & Sayialel, S. (2001). Matriarchs as repositories of social knowledge in African elephants. *Science*, *292*(5516), 491–494. https://doi.org/10.1126/science.1057895

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 Publishing Company.

McGrew, W. C. (1992a). *Chimpanzee material culture: implications for human evolution*. Cambridge University Press.

McGrew, W. C. (1992b). Chimpanzees as models. In *Chimpanzee material culture: implications for human evolution* (pp. 198–214). Cambridge University Press.

McGrew, W. C. (2003). Ten dispatches from the chimpanzee culture wars. In F. B. M. de Waal & P. L. Tyack (Eds.), *Animal social complexity: intelligence, culture, and individualized societies* (pp. 419–439). Harvard University Press.

McGrew, W. C. (2010). In search of the last common ancestor: new findings on wild

chimpanzees. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365*, 3267–3276. https://doi.org/10.1098/rstb.2010.0067

McGrew, W. C., Ham, R. M., White, L. J. T., Tutin, C. E. G., & Fernandez, M. (1997). Why don't chimpanzees in Gabon crack nuts? *International Journal of Primatology*, *18*(3), 353–374. https://doi.org/10.1023/A:1026382316131

McGrew, W. C., & Marchant, L. F. (1999). Laterality of hand use pays off in foraging success for wild chimpanzees. *Primates*, *40*(3), 509–513. https://doi.org/10.1007/BF02557586

McLennan, M. R. (2013). Diet and feeding ecology of chimpanzees (*Pan troglodytes*) in Bulindi, Uganda: foraging strategies at the forest-farm interface. *International Journal of Primatology*, *34*, 585–614. https://doi.org/10.1007/s10764-013-9683-y

McLennan, M. R., & Hill, C. M. (2010). Chimpanzee responses to researchers in a disturbed forest-farm mosaic at Bulindi, western Uganda. *American Journal of Primatology*, *72*(10), 907–918. https://doi.org/10.1002/ajp.20839

McPherron, S. P., Alemseged, Z., Marean, C. W., Wynn, J. G., Reed, D., Geraads, D., Bobe, R., & Béarat, H. A. (2010). Evidence for stone-tool-assisted consumption of animal tissues before 3.39 million years ago at Dikika, Ethiopia. *Nature*, *466*, 857–860. https://doi.org/10.1038/nature09248

Mercader, J., Barton, H., Gillespie, J., Jack, H., 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*, *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

Mesoudi, A. (2011). An experimental comparison of human social learning strategies: payoff-biased social learning is adaptive but underused. *Evolution and Human Behavior*, *32*(5), 334–342. https://doi.org/10.1016/j.evolhumbehav.2010.12.001

Mesoudi, A., Chang, L., Dall, S. R. X., & Thornton, A. (2016). The evolution of individual and cultural variation in social learning. *Trends in Ecology & Evolution*, *31*(3), 215–225. https://doi.org/10.1016/j.tree.2015.12.012

Mesoudi, A., & Thornton, A. (2018). What is cumulative cultural evolution? *Proceedings of the Royal Society B*, *385*(1880), 20180712. https://doi.org/10.1098/rspb.2018.0712

Meulman, E. J. M., Sanz, C. M., Visalberghi, E., & van Schaik, C. P. (2012). The role of terrestriality in promoting primate technology. *Evolutionary Anthropology*, *21*(2), 58–68. https://doi.org/10.1002/evan.21304

Migliano, A. B., Battiston, F., Viguier, S., Page, A. E., Dyble, M., Schlaepfer, R., Smith, D., Astete, L., Ngales, M., Gomez-Gardenes, J., Latora, V., & Vinicius, L. (2020). Hunter-gatherer multilevel sociality accelerates cumulative cultural evolution. *Science Advances*, *6*(9), eaax5913. https://doi.org/10.1126/sciadv.aax5913

Migliano, A. B., Page, A. E., Gómez-Gardeñes, J., Salali, G. D., Viguier, S., Dyble, M., Thompson, J., Chaudhary, N., Smith, D., Strods, J., Mace, R., Thomas, M. G., Latora, V., & Vinicius, L. (2017). Characterization of hunter-gatherer networks and implications for cumulative culture. *Nature Human Behaviour*, *1*(2), 43. https://doi.org/10.1038/s41562-016-0043

Milton, K. (1999). A hypothesis to explain the role of meat-eating in human evolution. *Evolutionary Anthropology*, *8*(1), 11–21. https://doi.org/10.1002/(SICI)1520-6505(1999)8:1<11::AID-EVAN6>3.0.CO;2-M

Miu, E., Gulley, N., Laland, K. N., & Rendell, L. (2020). Flexible learning, rather than inveterate innovation or copying, drives cumulative knowledge gain. *Science Advances*, *6*(23), eaaz0286. https://doi.org/10.1126/sciadv.aaz0286

Moore, J. (1998). 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 University Press.

Moore, M. W., & Perston, Y. (2016). Experimental insights into the cognitive significance of early stone tools. *PLoS ONE*, *11*(7), e0158803. https://doi.org/10.1371/journal.pone.0158803

Morgan, B., & Abwe, E. E. (2006). Chimpanzees use stone hammers in Cameroon. *Current Biology*, *16*(16), R632–R633. https://doi.org/10.1016/j.cub.2006.07.045.

Morgan, T. J. H., Uomini, N. T., Rendell, L., Chouinard-Thuly, L., Street, S. E., Lewis, H. M., Cross, C. P., Evans, C., Kearney, R., De La Torre, I., Whiten, A., & Laland, K. N. (2015). Experimental evidence for the co-evolution of hominin tool-making teaching and language. *Nature Communications*, *6*(1), 6029. https://doi.org/10.1038/ncomms7029

Muhammad, R., Kaikaew, T., Panjan, S., Meesawat, S., Thabthimthong, W., Payungporn, S., Apipattarachaiwong, J., Kanthaswamy, S., Hamada, Y., Luncz, L. V, & Malaivijitnond, S. (2023). Influence of COVID-19 on the emergence of stone-tool use behavior in a population of common long-tailed macaques (*Macaca fascicularis fascicularis*) in Thailand. *American Journal of Primatology*, *86*(2), e23580. https://doi.org/10.1002/ajp.23580

Muller, M. N. (2017). Introduction: chimpanzees and human evolution. In M. N. Muller, R. W. Wrangham, & D. R. Pilbeam (Eds.), *Chimpanzees and human evolution* (pp. 3–21). The Belknap Press of Harvard University.

Musgrave, S., Lonsdorf, E. V, Morgan, D. B., 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*, *117*(2), 969–976. https://doi.org/10.1073/pnas.1907476116

Nagell, K., Olguin, R. S., & Tomasello, M. (1993). Processes of social learning in the tool use of chimpanzees (*Pan troglodytes*) and human children (*Homo sapiens*). *Journal of Comparative Psychology*, *107*(2), 174–186. https://doi.org/10.1037/0735-7036.107.2.174

Neadle, D., Bandini, E., & Tennie, C. (2020). Testing the individual and social learning abilities of task-naïve captive chimpanzees (*Pan troglodytes* sp.) in a nut-cracking task. *PeerJ*, *8*(e8734). https://doi.org/10.7717/peerj.8734

Neufuss, J., Humle, T., Cremaschi, A., & Kivell, T. L. (2017). Nut-cracking behaviour in wild-born, rehabilitated bonobos (*Pan paniscus*): a comprehensive study of hand-preference, hand grips and efficiency. *American Journal of Primatology*, *79*(2), e22589. https://doi.org/10.1002/ajp.22589

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

Olsson, A., Knapska, E., & Lindström, B. (2020). The neural and computational systems of social learning. *Nature Reviews Neuroscience*, *21*(4), 197–212. https://doi.org/10.1038/s41583-020-0276-4

Pandolfi, S. S., van Schaik, C. P., & Pusey, A. E. (2003). Sex differences in termite fishing among Gombe chimpanzees. In F. B. M. de Waal & P. L. Tyack (Eds.), *Animal social complexity: intelligence, culture, and individualized societies* (pp. 414–418). Harvard University Press.

Pargeter, J., Khreisheh, N., & Stout, D. (2019). Understanding stone tool-making skill acquisition: experimental methods and evolutionary implications. *Journal of Human Evolution*, *133*, 146–166. https://doi.org/10.1016/j.jhevol.2019.05.010

Pargeter, J., Liu, C., Kilgore, M. B., Majoe, A., & Stout, D. (2023). Testing the effect of learning conditions and individual motor/cognitive differences on knapping skill acquisition. *Journal of Archaeological Method and Theory*, *30*(1), 127–171. https://doi.org/10.1007/s10816-022-09592-4

Parsons, M. B., Gillespie, T. R., Lonsdorf, E. V, Travis, D., Lipende, I., Gilagiza, B., Kamenya, S., Pintea, L., & Vazquez-Prokopec, G. M. (2014). Global positioning system data-loggers: a tool to quantify fine-scale movement of domestic animals to evaluate potential for zoonotic transmission to an endangered wildlife population. *PLoS ONE*, *9*(11), e110984. https://doi.org/10.1371/journal.pone.0110984

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*(8260). https://doi.org/10.1038/s41598-019-44703-4

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

Pascual-Garrido, A., Carvalho, S., & Almeida-Warren, K. (2023). Primate archaeology 3.0. *American Journal of Biological Anthropology*, *183*(3), 1–17. https://doi.org/10.1002/ajpa.24835

Pika, S., Klein, H., Bunel, S., Baas, P., Théleste, E., & Deschner, T. (2019). Wild chimpanzees (*Pan troglodytes troglodytes*) exploit tortoises (*Kinixys erosa*) via percussive technology. *Scientific Reports*, *9*(7661). https://doi.org/10.1038/s41598-019-43301-8

Pilbeam, D. R., & Lieberman, D. E. (2017). Reconstructing the last common ancestor of chimpanzees and humans. In M. N. Muller, R. W. Wrangham, & D. R. Pilbeam (Eds.), *Chimpanzees and human evolution* (pp. 22–141). The Belknap Press of Harvard University.

Plummer, T. W., Oliver, J. S., Finestone, E. M., Ditchfield, P. W., Bishop, L. C., Blumenthal, S. A., Lemorini, C., Caricola, I., Bailey, S. E., Herries, A. I. R., Parkinson, J. A., Whitfield, E., Hertel, F., Kinyanjui, R. N., Vincent, T. H., Li, Y., Louys, J., Frost, S. R., Braun, D. R., … Potts, R. (2023). Expanded geographic distribution and dietary strategies of the earliest Oldowan hominins and *Paranthropus*. *Science*, *379*(6632), 561–566. https://doi.org/10.1126/science.abo7452

Proffitt, T., Luncz, L. V, Falótico, T., Ottoni, E. B., De La Torre, I., & Haslam, M. (2016). Wild monkeys flake stone tools. *Nature*, *539*, 85–88. https://doi.org/10.1038/nature20112

Proffitt, T., Reeves, J. S., Braun, D. R., Malaivijitnond, S., & Luncz, L. V. (2023). Wild macaques challenge the origin of intentional tool production. *Science Advances*, *9*(10). https://doi.org/10.1126/sciadv.ade8159

Proffitt, T., Reeves, J. S., Pacome, S. S., & Luncz, L. V. (2022). Identifying functional and regional differences in chimpanzee stone tool technology. *Royal Society Open Science*, *9*(220826). https://doi.org/10.1098/rsos.220826

Pruetz, J. D. (2006). Feeding ecology of savanna chimpanzees at Fongoli, Senegal. In G. Hohmann, M. M. Robbins, & C. Boesch (Eds.), *Feeding ecology in apes and other*

primates: ecological, physiological and behavioural aspect (pp. 161–182). Cambridge University Press.

Pruetz, J. D., Bertolani, Boyer Ontl, K., Lindshield, S., Shelley, M., & Wessling, E. G. (2015). New evidence on the tool-assisted hunting exhibited by chimpanzees (*Pan troglodytes verus*) in a savannah habitat at Fongoli, Senegal. *Royal Society of Open Science*, *2*(140507). https://doi.org/10.1098/rsos.140507

Pruetz, J. D., & Bertolani, P. (2007). Savanna chimpanzees, *Pan troglodytes verus*, hunt with tools. *Current Biology*, *17*(5), 412–417. https://doi.org/10.1016/j.cub.2006.12.042

Pruetz, J. D., Bogart, S. L., & Lindshield, S. (2021). Extractive foraging in an extreme environment: tool and proto-tool use by chimpanzees at Fongoli, Senegal. In L. M. Hopper & S. R. Ross (Eds.), *Chimpanzees in context: a comparative perspective on chimpanzee behavior, cognition conservation, and welfare* (pp. 391–409). The University of Chicago Press. https://doi.org/10.7208/9780226728032

Pruetz, J. D., & McGrew, W. C. (2001). What does a chimpanzee need? Using natural behaviour to guide the care and management of captive populations. In L. Brent (Ed.), *The care and management of captive chimpanzees* (Vol. 2, pp. 17–37). American Society of Primatologists.

Putt, S. S., Woods, A. D., & Franciscus, R. G. (2014). The role of verbal interaction during experimental bifacial stone tool manufacture. *Lithic Technology*, *39*(2), 96–122. https://doi.org/10.1179/0197726114S.00000000036

R Core Team. (2020). *R: a language and environment for statistical computing*. R Foundation for Statistical Computing. https://www.r-project.org/

Rapaport, L. G., & Brown, G. R. (2008). Social influences on foraging behavior in young nonhuman primates: learning what, where, and how to eat. *Evolutionary Anthropology*, *17*(4), 189–201. https://doi.org/10.1002/evan.20180

Reader, S. M., & Biro, D. (2010). Experimental identification of social learning in wild animals. *Learning & Behavior*, *38*(3), 265–283. https://doi.org/10.3758/LB.38.3.265

Reeves, J. S., Proffitt, T., Malaivijitnond, S., & Luncz, L. V. (2023). Emergent technological variation in archaeological landscapes: a primate perspective. *Journal of The Royal Society Interface*, *20*(203), 20230118. https://doi.org/10.1098/rsif.2023.0118

Resende, B. D., Nagy-Reis, M. B., Lacerda, F. N., Pagnotta, M., & Savalli, C. (2014). Tufted capuchin monkeys (*Sapajus* sp.) learning how to crack nuts: does variability decline throughout development? *Behavioural Processes*, *109*, 89–94. https://doi.org/10.1016/j.beproc.2014.09.002

Resende, B. D., Ottoni, E. B., & Fragaszy, D. M. (2008). Ontogeny of manipulative behavior and nut-cracking in young tufted capuchin monkeys (*Cebus apella*): a perception–

action perspective. *Developmental Science*, *11*(6), 828–840. https://doi.org/10.1111/j.1467-7687.2008.00731.x

Richerson, P. J., & Boyd, R. (2020). The human life history is adapted to exploit the adaptive advantages of culture. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *375*(1803), 20190498. https://doi.org/10.1098/rstb.2019.0498

Roche, H., de la Torre, I., Arroyo, A., Brugal, J.-P., & Harmand, S. (2018). Naiyena Engol 2 (West Turkana, Kenya): a case study on variability in the Oldowan. *African Archaeological Review*, *35*(1), 57–85. https://doi.org/10.1007/s10437-018-9283-5

Rodrigues, E. D., Santos, A. J., Hayashi, M., Matsuzawa, T., & Hobaiter, C. (2022). Exploring greetings and leave-takings: communication during arrivals and departures by chimpanzees of the Bossou community, Guinea. *Primates*, *63*(5), 443–461. https://doi.org/10.1007/s10329-021-00957-z

Rolian, C., & Carvalho, S. (2017). Tool use and manufacture in the lact common ancestor of Pan and Homo. In M. N. Muller, R. W. Wrangham, & D. R. Pilbeam (Eds.), *Chimpanzees and human evolution* (pp. 602–644). The Belknap Press of Harvard University Press.

Rosati, A. G., Hagberg, L., Enigk, D. K., Otali, E., Emery Thompson, M., Muller, M. N., Wrangham, R. W., & Machanda, Z. P. (2020). Social selectivity in aging wild chimpanzees. *Science*, *370*(6515), 473–476. https://doi.org/10.1126/science.aaz9129

Rutz, C., Bluff, L. A., Reed, N., Troscianko, J., Newton, J., Inger, R., Kacelnik, A., & Bearhop, S. (2010). The ecological significance of tool use in New Caledonian crows. *Science*, *329*(5998), 1523–1526. https://doi.org/10.1126/science.1192053

Rutz, C., & St Clair, J. J. H. (2012). The evolutionary origins and ecological context of tool use in New Caledonian crows. *Behavioural Processses*, *89*(2), 153–165. https://doi.org/10.1016/j.beproc.2011.11.005

Sanz, C. M., Call, J., & Morgan, D. B. (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., & Morgan, D. B. (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. (2013). Ecological and social correlates of chimpanzee tool use. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *368*(20120416), 1–14. https://doi.org/10.1098/rstb.2012.0416

Sanz, C. M., Morgan, D. B., & 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

Sanz, C. M., Schöning, C., & 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

Sayers, K., & Lovejoy, C. O. (2008). The chimpanzee has no clothes: a critical examination of *Pan troglodytes* in models of human evolution. *Current Anthropology*, *49*(1), 87–114. https://doi.org/10.1086/523675

Schick, K. (2013). The origins and evolution of technology. In D. R. Begun (Ed.), *A companion to paleoanthropology* (First, pp. 265–289). Blackwell Publishing.

Schick, K., Toth, N., Garufi, G., Savage-Rumbaugh, E. S., Rumbaugh, D., & Sevcik, R. (1999). Continuing investigations into the stone tool-making and tool-using capabilities of a bonobo (*Pan paniscus*). *Journal of Archaeological Science*, *26*(7), 821–832. https://doi.org/10.1006/jasc.1998.0350

Schofield, D. (2022). *Computational ethology for primate sociality: a novel paradigm for computer-vision-based analysis of animal behaviour*. University of Oxford.

Schofield, D., Albery, G. F., Firth, J. A., Mielke, A., Hayashi, M., Matsuzawa, T., Biro, D., & Carvalho, S. (2023). Automated face recognition using deep neural networks produces robust primate social networks and sociality measures. *Methods in Ecology and Evolution*, *14*(8), 1937–1951. https://doi.org/10.1111/2041-210X.14181

Schofield, D., McGrew, W. C., Takahashi, A., & Hirata, S. (2018). Cumulative culture in nonhumans: overlooked fndings from Japanese monkeys? *Primates*, *59*, 113–122. https://doi.org/10.1007/s10329-017-0642-7

Schofield, D., Nagrani, A., Zisserman, A., Hayashi, M., Matsuzawa, T., Biro, D., & Carvalho, S. (2019). Chimpanzee face recognition from videos in the wild using deep learning. *Science Advances*, *5*(9), eaaw0736. https://doi.org/10.1126/sciadv.aaw0736

Schrauf, C., Call, J., Fuwa, K., & Hirata, S. (2012). Do chimpanzees use weight to select hammer tools? *PLoS ONE*, *7*(7), 1–12. https://doi.org/10.1371/journal.pone.0041044

Schuppli, C., Isler, K., & van Schaik, C. P. (2012). How to explain the unusually late age at skill competence among humans. *Journal of Human Evolution*, *63*(6), 843–850. https://doi.org/10.1016/j.jhevol.2012.08.009

Schuppli, C., Meulman, E. J. M., Forss, S. I. F., Aprilinayati, F., Van Noordwijk, M. A., & Van Schaik, C. P. (2016). Observational social learning and socially induced practice of routine skills in immature wild orang-utans. *Animal Behaviour*, *119*, 87–98. https://doi.org/10.1016/j.anbehav.2016.06.014

Schuppli, C., & van Schaik, C. P. (2019). Animal cultures: how we've only seen the tip of the iceberg. *Evolutionary Human Sciences*, *1*(e2), 1–13. https://doi.org/10.1017/ehs.2019.1

Semaw, S. (2006). The oldest stone artifacts from Gona (2.6-2.5 Ma), Afar, Ethiopia: implications for understanding the earliest stages of stone knapping. In N. Toth & K. Schick (Eds.), *The Oldowan: case studies into the earliest stone age* (pp. 43–75). Stone Age Institute Press.

Semaw, S., Renne, P. R., Harris, J. W. K., Feibel, C. S., Bernor, R. L., Fesseha, N., & Mowbray, K. (1997). 2.5-million-year-old stone tools from Gona, Ethiopia. *Nature*, *385*(6614), 333–336. https://doi.org/10.1038/385333a0

Setchell, J. M. (2019). *Studying primates: how to design, conduct and report primatological research*. Cambridge University Press.

Shea, J. J. (2006). Child's play: reflections on the invisibility of children in the paleolithic record. *Evolutionary Anthropology*, *15*(6), 212–216. https://doi.org/10.1002/evan.20112

Shick, K. D. (1987). Modeling the formation of Early Stone Age artifact concentrations. *Journal of Human Evolution*, *16*(7), 789–807. https://doi.org/10.1016/0047-2484(87)90024-8

Siepielski, A. M., DiBattista, J. D., & Carlson, S. M. (2009). It's about time: the temporal dynamics of phenotypic selection in the wild. *Ecology Letters*, *12*(11), 1261–1276. https://doi.org/10.1111/j.1461-0248.2009.01381.x

Silk, J. B., & House, B. R. (2016). The evolution of altruistic social preferences in human groups. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *371*(1687). https://doi.org/10.1098/rstb.2015.0097

Sirianni, G., Luncz, L. V, & Gratton, P. (2019). An energetic model of foraging optimization: wild chimpanzee hammer selection for nut-cracking. In C. Boesch & R. Wittig (Eds.), *The chimpanzees of the Taï forest: 40 years of research* (pp. 104–124). Cambridge University Press. https://doi.org/10.1017/9781108674218.009

Smith, E. A. (1979). Human adaptation and energetic efficiency. *Human Ecology*, *7*(1), 53–74. https://doi.org/10.1007/BF00889352

Snyder, W. D., Reeves, J. S., & Tennie, C. (2022). Early knapping techniques do not necessitate cultural transmission. *Science Advances*, *8*(27), eabo2894. https://doi.org/10.1126/sciadv.abo2894

Sousa, C., Biro, D., & Matsuzawa, T. (2009). Leaf-tool use for drinking water by wild chimpanzees (*Pan troglodytes*): acquisition patterns and handedness. *Animal Cognition*, *12*(Suppl 1), S115–S125. https://doi.org/10.1007/s10071-009-0278-0

Stanford, C. B. (2012). Chimpanzees and the behaviour of *Ardipithecus ramidus*. *Annual Review of Anthropology*, *41*, 139–149. https://doi.org/10.1146/annurev-anthro-092611-145724

Stout, D., Rogers, M. J., Jaeggi, A. V, & Semaw, S. (2019). Archaeology and the origins of human cumulative culture: a case study from the earliest Oldowan at Gona, Ethiopia. *Current Anthropology*, *60*(3), 309–340. https://doi.org/10.1086/703173

Sugasawa, S., Klump, B. C., St Clair, J. J. H., & Rutz, C. (2017). Causes and consequences of tool shape variation in New Caledonian crows. *Current Biology*, *27*(24), 3885–3890. https://doi.org/10.1016/j.cub.2017.11.028

Sugiyama, Y. (1995). Tool-use for catching ants by chimpanzees at Bossou and Monts Nimba, West Africa. *Primates*, *36*(2), 193–205. https://doi.org/10.1007/BF02381345

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.

Sugiyama, Y., Fushimi, T., Sakura, O., & Matsuzawa, T. (1993). Hand preference and tool use in wild chimpanzees. *Primates*, *34*(2), 151–159. https://doi.org/10.1007/BF02381386

Sugiyama, Y., & Koman, J. (1979a). Social structure and dynamics of wild chimpanzees at Bossou, Guinea. *Primates*, *20*(3), 323–339. https://doi.org/10.1007/BF02373387

Sugiyama, Y., & Koman, J. (1979b). Tool-using and -making behaviour in wild chimpanzees at Bossou, Guinea. *Primates*, *20*(4), 513–524. https://doi.org/10.1007/BF02373433

Sussman, R. W., & Hart, D. (2015). Modelling the past: the primatological approach. In W. Henke & I. Tattersall (Eds.), *Handbook of paleoanthropology* (Second, pp. 791–815). Springer-Verlag.

Tan, A. (2017). From play to proficiency: the ontogeny of stone-tool use in coastal-foraging long-tailed macaques (*Macaca fascicularis*) from a comparative perception-action perspective. *Journal of Comparative Psychology*, *131*(2), 89–114. https://doi.org/10.1037/com0000068

Tan, A., Tan, S. H., Vyas, D., Malaivijitnond, S., & Gumert, M. D. (2015). There is more than one way to crack an oyster: identifying variation in Burmese long-tailed macaque (*Macaca fascicularis aurea*) stone-tool use. *PLoS ONE*, *10*(5), e0124733. https://doi.org/10.1371/journal.pone.0124733

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 & Philosophy*, *35*(55). https://doi.org/10.1007/s10539-020-09769-9

Tennie, C., Braun, D. R., Premo, L. S., & McPherron, S. P. (2016). The island test for cumulative culture in the Paleolithic. In M. N. Haidle, N. J. Conard, & M. Bolus (Eds.), *The nature of culture* (pp. 121–133). Springer Netherlands. https://doi.org/10.1007/978-94-017-7426-0_11

Tennie, C., & Call, J. (2023). Unmotivated subjects cannot provide interpretable data and tasks with sensitive learning periods require appropriately aged subjects: a Commentary on Koops et al. (2022) “Field experiments find no evidence that chimpanzee nut cracking can be independently innovated". *Animal Behavior and Cognition*, *10*(1), 89–94. https://doi.org/10.26451/abc.10.01.05.2023

Tennie, C., Call, J., & Tomasello, M. (2009). Ratcheting up the ratchet: on the evolution of cumulative culture. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *364*(1528), 2405–2415. https://doi.org/10.1098/rstb.2009.0052

Tennie, C., Hopper, L. M., & van Schaik, C. P. (2020). On the origin of cumulative culture: consideration of the role of copying in culture-dependent traits and a reappraisal of the zone of latent solutions hypothesis. In L. M. Hopper & S. R. Ross (Eds.), *Chimpanzees in context: a comparative perspective on chimpanzee behavior, cognition conservation, and welfare* (pp. 428–453). University of Chicago Press.

Tennie, C., Premo, L. S., Braun, D. R., & McPherron, S. P. (2017). Early stone tools and cultural transmission: resetting the null hypothesis. *Current Anthropology*, *58*(5), 652–654. https://doi.org/10.1086/693846

Thompson, J. C., McPherron, S. P., Bobe, R., Reed, D., Barr, W. A., Wynn, J. G., Marean, C. W., Geraads, D., & Alemseged, Z. (2015). Taphonomy of fossils from the hominin-bearing deposits at Dikika, Ethiopia. *Journal of Human Evolution*, *86*, 112–135. https://doi.org/10.1016/j.jhevol.2015.06.013

Thornton, A., & Mesoudi, A. (2023). Untenable propositions and alternative avenues: comment to “Blind alleys and fruitful pathways in the comparative study of cultural cognition” by Andrew Whiten. *Physics of Life Reviews*, *44*, 51–53. https://doi.org/10.1016/j.plrev.2022.11.009

Thorpe, W. H. (1956). *Learning and instinct in animals*. Harvard University Press.

Tinbergen, N. (1963). On aims and methods of ethology. *Zeitschrift Für Tierpsychologie*, *20*, 410–433. https://doi.org/10.1111/j.1439-0310.1963.tb01161.x

Tkaczynski, P., Mielke, A., Samuni, L., Preis, A., Wittig, R. M., & Crockford, C. (2020). Long-term repeatability in social behaviour suggests stable social phenotypes in wild chimpanzees. *Royal Society Open Science*, *7*(9), 200454. https://doi.org/10.1098/rsos.200454

Tomasello, M. (1990). Cultural transmission in the tool use and communicatory signaling of chimpanzees? In K. R. Gibson & S. T. Parker (Eds.), *“Language” and intelligence in monkeys and apes: comparative developmental perspectives* (pp. 274–311). Cambridge University Press. https://doi.org/10.1017/CBO9780511665486.012

Tomasello, M. (1999). The human adaptation for culture. *Annual Review of Anthropology*, *28*,

509–529. https://doi.org/10.1146/annurev.anthro.28.1.509

Tomasello, M., Davis-Dasilva, M., Camak, L., & Bard, K. (1987). Observational learning of tool-use by young chimpanzees. *Human Evolution*, *2*(2), 175–183. https://doi.org/10.1007/BF02436405

Tomasello, M., Kruger, A. C., & Ratner, H. H. (1993). Cultural learning. *Behavioral and Brain Sciences*, *16*(3), 495–511. https://doi.org/10.1017/S0140525X0003123X

Tooby, J., & DeVore, I. (1987). The reconstruction of hominid behavioural evolution through strategic modeling. In W. G. Kinzey (Ed.), *The evolution of human behaviour: primate models* (pp. 183–237). State University of New York Press.

Toth, N., & Schick, K. (2015). Overview of Paleolithic archaeology. In W Henke & I. Tattersall (Eds.), *Handbook of paleoanthropology* (pp. 2441–2464). Springer-Verlag.

Toth, N., & Schick, K. (2018). An overview of the cognitive implications of the Oldowan Industrial Complex. *Azania: Archaeological Research in Aftica*, *53*(1), 3–39. https://doi.org/10.1080/0067270X.2018.1439558

Toth, N., Schick, K., Savage-Rumbaugh, E. S., Sevcik, R. A., & Rumbaugh, D. M. (1993). *Pan* the tool-maker: investigations into the stone tool-making and tool-using capabilities of a bonobo (*Pan paniscus*). *Journal of Archaeological Science*, *20*(1), 81–91. https://doi.org/10.1006/jasc.1998.0350

Vaidyanathan, G. (2011). Apes in Africa: the cultured chimpanzees. *Nature*, *476*(7360), 266–269. https://doi.org/10.1038/476266a

van Schaik, C. P. (2002). Fragility of traditions: the disturbance hypothesis for the loss of local traditions in orangutans. *International Journal of Primatology*, *23*(2), 527–538. https://doi.org/10.1023/A:1014965516127

van Schaik, C. P. (2010). Social learning and culture in animals. In P. M. Kappeler (Ed.), *Animal behaviour: evolution and mechanisms* (pp. 623–653). Springer.

van Schaik, C. P., Deaner, R. O., & Merrill, M. Y. (1999). The conditions for tool use in primates: implications for the evolution of material culture. *Journal of Human Evolution*, *36*(6), 719–741. https://doi.org/10.1006/jhev.1999.0304

van Schaik, C. P., Fox, E. A., & Fechtman, L. T. (2003). Individual variation in the rate of use of tree-hole tools among wild orang-utans: implications for hominin evolution. *Journal of Human Evolution*, *44*(1), 11–23. https://doi.org/10.1016/S0047-2484(02)00164-1

van Schaik, C. P., & Pradhan, G. R. (2003). A model for tool-use traditions in primates: implications for the coevolution of culture and cognition. *Journal of Human Evolution*, *44*(6), 645–664. https://doi.org/10.1016/S0047-2484(03)00041-1

Venkataraman, V. V, Kraft, T. S., & Dominy, N. J. (2013). Tree climbing and human evolution. *Proceedings of the National Academy of Sciences*, *110*(4), 1237–1242.

https://doi.org/10.1073/pnas.1208717110

Visalberghi, E., Sabbatini, G., Taylor, A. H., & Hunt, G. R. (2017). Cognitive insights from tool use in nonhuman animals. In *APA handbook of comparative psychology: perception, learning, and cognition, Vol. 2* (pp. 673–701). American Psychological Association. https://doi.org/10.1037/0000012-030

Watson, S. K., Botting, J., Whiten, A., & van de Waal, E. (2018). Culture and selective social learning in wild and captive primates. In L. D. Di Paolo, F. Di Vincenzo, & F. De Petrillo (Eds.), *Evolution of primate social cognition* (pp. 211–230). Springer, Cham. https://doi.org/10.1007/978-3-319-93776-2_14

Watts, D. P. (2008). Tool use by chimpanzees at Ngogo, Kibale National Park, Uganda. *International Journal of Primatology*, *29*(1), 83–94. https://doi.org/10.1007/s10764-007-9227-4

Webster, M. M., & Laland, K. N. (2008). Social learning strategies and predation risk: minnows copy only when using private information would be costly. *Proceedings of the Royal Society B: Biological Sciences*, *275*(1653), 2869–2876. https://doi.org/10.1098/rspb.2008.0817

Wessling, E. G., & Surbeck, M. (2023). Failure to account for behavioral variability significantly compromises accuracy in indirect population monitoring. *Animal Conservation*, *26*(4), 558–572. https://doi.org/10.1111/acv.12844

White, T. D., Asfaw, B., Beyene, Y., Haile-Selassie, Y., Lovejoy, C. O., Suwa, G., & WoldeGabriel, G. (2009). *Ardipithecus ramidus* and the paleobiology of early hominids. *Science*, *326*(5949), 64–86. https://doi.org/10.1126/science.1175802

Whiten, A. (2005). The second inheritance system of chimpanzees and humans. *Nature*, *437*(7055), 52–55. https://doi.org/10.1038/nature04023

Whiten, A. (2017). Social learning and culture in child and chimpanzee. *Annual Review of Psychology*, *68*(1), 129–154. https://doi.org/10.1146/annurev-psych-010416-044108

Whiten, A. (2020). Wild chimpanzees scaffold youngsters' learning in a high-tech community. *Proceeding of the National Academy of Sciences*, *117*(2), 802–804. https://doi.org/10.1073/pnas.1920430117

Whiten, A. (2022). Blind alleys and fruitful pathways in the comparative study of cultural cognition. *Physics of Life Reviews*, *43*, 211–238. https://doi.org/10.1016/j.plrev.2022.10.003

Whiten, A., Goodall, J., McGrew, W. C., Nishida, T., Reynolds, V., Sugiyama, Y., Tutin, C. E. G., Wrangham, R. W., & Boesch, C. (1999). Culture in chimpanzees. *Nature*, *399*(6737), 682–685. https://doi.org/10.1038/21415

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*(4), 420–435. https://doi.org/10.1016/j.jhevol.2008.12.010

Whiten, A., & van de Waal, E. (2018). The pervasive role of social learning in primate lifetime development. *Behavioral Ecology and Sociobiology*, *72*(5), 1–16. https://doi.org/10.1007/s00265-018-2489-3

Wickham, H., Averick, M., Bryan, J., Chang, W., McGowan D'Agostino, L., François, R., Grolemund, G., Hayes, A., Henry, L., Hester, J., Kuhn, M., Lin Pedersen, T., Miller, E., Bache, S. M., Müller, K., Ooms, J., Robinson, D., Seidel, D. P., Spinu, V., … Yutani, H. (2019). Welcome to the tidyverse. *Journal of Open Source Software*, *4*(43), 1686. https://doi.org/10.21105/joss.01686

Wilson, M. L., Boesch, C., Fruth, B., Furuichi, T., Gilby, I. C., Hashimoto, C., Hobaiter, C., Hohmann, G., Itoh, N., Koops, K., Lloyd, J. N., Matsuzawa, T., Mitani, J. C., Mjungu, D. C., Morgan, D. B., Muller, M. N., Mundry, R., Nakamura, M., Pruetz, J. D., … Wrangham, R. W. (2014). Lethal aggression in *Pan* is better explained by adaptive strategies than human impacts. *Nature*, *513*, 414–417. https://doi.org/10.1038/nature13727

Wittig, R. M., & Boesch, C. (2019). Demography and life history of five chimpanzee communities in Taï National Park. In C. Boesch & R. M. Wittig (Eds.), *The chimpanzees of the Taï forest: 40 years of research* (pp. 125–140). Cambridge University Press. https://doi.org/10.1017/9781108674218.010

Wood, B. M., & Gibly, I. C. (2017). From *Pan* to man the hunter: hunting and meat sharing by chimpanzees, humans, and our common ancestor. In M. N. Muller, R. W. Wrangham, & D. R. Pilbeam (Eds.), *Chimpanzees and human evolution* (pp. 339–382). The Belknap Press of Harvard University Press.

Wood, L. A., Kendal, R. L., & Flynn, E. G. (2012). Context-dependent model-based biases in cultural transmission: children's imitation is affected by model age over model knowledge state. *Evolution and Human Behavior*, *33*(4), 387–394. https://doi.org/10.1016/j.evolhumbehav.2011.11.010

Wood, L. A., Kendal, R. L., & Flynn, E. G. (2013). Copy me or copy you? The effect of prior experience on social learning. *Cognition*, *127*(2), 203–213. https://doi.org/10.1016/j.cognition.2013.01.002

Wrangham, R. W. (2006). Chimpanzees: the culture-zone concept becomes untidy. *Current Biology*, *16*(16), R634–R635. https://doi.org/10.1016/j.cub.2006.07.031

Wrangham, R. W., Conklin-Brittain, N. Lou, & Hunt, K. D. (1998). Dietary response of chimpanzees and cercopithecines to seasonal variation in fruit abundance. I.

Antifeedants. *International Journal of Primatology*, *19*(6), 949–970. https://doi.org/10.1023/A:1020318102257

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

Yamagiwa, J., & Basabose, A. K. (2006). Effects of fruit scarcity on foraging strategies of sympatric gorillas and chimpanzees. In G. Hohmann, M. M. Robbins, & C. Boesch (Eds.), *Feeding ecology in apes and other primates: ecological, physiological and behavioural aspect* (pp. 73–96). Cambridge University Press.

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., & Sugiyama, Y. (1995). Pestle-pounding behaviour of wild chimpanzees at Bossou, Guinea: a newly observed tool-using behaviour. *Primates*, *36*(4), 489–500. https://doi.org/10.1007/BF02382871

Yamamoto, S., Humle, T., & Tanaka, M. (2013). Basis for cumulative cultural evolution in chimpanzees: social learning of a more efficient tool-use technique. *PLoS ONE*, *8*(1), e55768. https://doi.org/10.1371/journal.pone.0055768

Yi, Y., Kim, Y., Hikmat, A., & Choe, J. C. (2020). Information transfer through food from parents to offspring in wild Javan gibbons. *Scientific Reports*, *10*(1), 714. https://doi.org/10.1038/s41598-019-57021-6

Young, N. M., Capellini, T. D., Roach, N. T., Alemseged, Z., & Klein, R. G. (2015). Fossil hominin shoulders support an African ape-like last common ancestor of humans and chimpanzees. *Proceedings of the National Academy of Sciences*, *112*(38), 11829–11834. https://doi.org/10.1073/pnas.1511220112

Zajonc, R. B. (1965). Social faciliation. *Science*, *149*(3681), 269–274. https://doi.org/10.1126/science.149.3681.269

Zefferman, M. R. (2016). Mothers teach daughters because daughters teach granddaughters: the evolution of sex-biased transmission. *Behavioral Ecology*, *27*(4), 1172–1181. https://doi.org/10.1093/beheco/arw022

APPENDICES

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A

Automated Audiovisual Behavior Recognition in Wild Primates

Published in *Science Advances*

ORGANISMAL BIOLOGY

Automated audiovisual behavior recognition in wild primates

Max Bain[1]*, Arsha Nagrani[1]†, Daniel Schofield[2], Sophie Berdugo[2,3], Joana Bessa[4], Jake Owen[4], Kimberley J. Hockings[5], Tetsuro Matsuzawa[6], Misato Hayashi‡§, Dora Biro[4,7], Susana Carvalho[2,8,9,10], Andrew Zisserman[1]

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Large video datasets of wild animal behavior are crucial to produce longitudinal research and accelerate conservation efforts; however, large-scale behavior analyses continue to be severely constrained by time and resources. We present a deep convolutional neural network approach and fully automated pipeline to detect and track two audiovisually distinctive actions in wild chimpanzees: buttress drumming and nut cracking. Using camera trap and direct video recordings, we train action recognition models using audio and visual signatures of both behaviors, attaining high average precision (buttress drumming: 0.87 and nut cracking: 0.85), and demonstrate the potential for behavioral analysis using the automatically parsed video. Our approach produces the first automated audiovisual action recognition of wild primate behavior, setting a milestone for exploiting large datasets in ethology and conservation.

INTRODUCTION

The field of ethology seeks to understand animal behavior from both mechanistic and functional perspectives and to identify the various genetic, developmental, ecological, and social drivers of behavioral variation in the wild (*1*). It is increasingly becoming a data-rich science: Technological advances in data collection, including biologgers, camera traps, and audio recorders, now allow us to capture animal behavior in an unprecedented level of detail (*2*). In particular, large data archives including both audio and visual information have immense potential to measure individual- and population-level variation as well as ontogenetic and cultural changes in behavior that may span large temporal and spatial scales. However, this potential often goes untapped: The training and human effort required to process large volumes of video data continue to limit the scale and depth at which behavior can be analyzed. Automating the measurement of behavior can transform ethological research, open up large-scale video archives for detailed interrogation, and be a powerful tool to monitor and protect threatened species in the wild. With rapid advances in deep learning, the novel field of computational ethology is quickly emerging at the intersection of computer science, engineering, and biology, using computer vision algorithms to process large volumes of data (*3*).

The aim of this paper is to automate animal behavior recognition in wild footage. Deep learning–based behavior recognition has thus far been shown in constrained laboratory settings (*4*, *5*) or using still images (*6*) and has yet to be effectively demonstrated on unconstrained video footage recorded in the wild. Measuring animal behavior from wild footage presents substantial challenges—often, behaviors are hard to detect, obscured by motion blur, occlusion, vegetation, poor resolution, or lighting. If successful, then the tools would enable exploration of a multitude of research questions in ethology and conservation. Increasingly, research is revealing fine-scale variation between individuals and populations of wild animals (*7*); however, capturing this variation is often laborious and not feasible on the large scale through manual annotation. Automated approaches allow us to examine in more detail the variation, through cross comparison of animal groups in a wide variety of contexts. Detailed time series data of individual behavior enables integration of time depth perspectives into field research to more comprehensively reconstruct how behavior develops across the life span (ontogenetically) as well as examine how other processes such as social transmission, demography, and ecology interact to drive behavior change over time (*8*). These detailed behavioral data are also a crucial component of conservation research: They enable us to investigate how anthropogenic pressures such as climate change and habitat fragmentation disrupt animal behavior (*9*) (migratory patterns, foraging, reproduction, etc.) and to develop novel behavioral metrics to monitor the risks to and viability of threatened populations (*10*, *11*). Here, we demonstrate the potential of such an approach by developing a system for the automated classification of two distinct wild chimpanzee behaviors with idiosyncratic audiovisual features: nut cracking and buttress drumming. We also analyze pilot data of sex and age differences in percussive behaviors (nut cracking and drumming) from longitudinal archive and camera trap datasets. Chimpanzees are an ideal species for testing behavioral recognition; owing to their large fission-fusion societies, complex sociality, and behavioral flexibility, they exhibit exceptionally rich behavioral repertoires (*12*). Our target behaviors, nut cracking and buttress drumming, differ in their function—extractive tool use versus long-distance communication, respectively—but both involve

[1]Visual Geometry Group, Department of Engineering Science, University of Oxford, Oxford, UK. [2]Primate Models for Behavioural Evolution Lab, Institute of Human Sciences, School of Anthropology and Museum Ethnography, University of Oxford, Oxford, UK. [3]Social Body Lab, Institute of Human Sciences, School of Anthropology and Museum Ethnography, University of Oxford, Oxford, UK. [4]Department of Zoology, University of Oxford, Oxford, UK. [5]Centre for Ecology and Conservation, College of Life and Environmental Sciences, University of Exeter, Exeter, UK. [6]Division of the Humanities and Social Sciences, California Institute of Technology, 1200 E. California Blvd., MC 228-77, Pasadena, CA 91125, USA. [7]Department of Brain and Cognitive Sciences, University of Rochester, Rochester, NY, USA. [8]Gorongosa National Park, Sofala, Mozambique. [9]Centre for Functional Ecology, Department of Life Sciences, Coimbra University, Coimbra, Portugal. [10]Interdisciplinary Centre for Archaeology and Evolution of Human Behaviour, Algarve University, Faro, Portugal.
*Corresponding author. Email: maxbain@robots.ox.ac.uk
†Now at Google AI Research.
‡Present address: Chubu Gakuin University, 30-1 Naka Oida-cho, Kakamigahara, Gifu 504-0837, Japan.
§Present address: Japan Monkey Centre, Kanrin-26, Inuyama, Aichi 484-0081, Japan.

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percussive actions that produce distinctive sounds, i.e., the pounding of a hammer stone against a nut balanced on an anvil stone and the pounding of hands or feet against large buttress roots. Whereas nut cracking is limited to some West African and Cameroon chimpanzees (*Pan troglodytes verus* and *Pan troglodytes ellioti*), buttress drumming is a universal behavior across all chimpanzee communities (*12*).

In relation to previous works using deep learning, individual reidentification has been a critical first step toward full automation (*13*, *14*), but this alone cannot capture the full complexity of behaviors that animals perform in the wild across space and time. Existing methods have used deep learning for markerless pose estimation to track the movement of animal body parts (*15*), but pose estimation models perform poorly at recognizing actions using posture and limb movements alone (*16*). Other approaches have used single-image analysis to identify basic activities of wild animals using tagged information from camera traps, but these fail to capture the dynamic sequences of behavior required for detailed analysis (*17*). Recent advances in human action recognition in the field of computer vision have used three-dimensional (3D) convolutional neural networks (CNNs) (*18*), which incorporate spatiotemporal information across video frames (*19*), but thus far have only been applied to animal species to produce broad behavioral classification limited to the visual domain (*20*).

Given that both behaviors have strong audio and visual signatures, we recognize actions using both audio and visual streams. Our automatic framework consists of two stages: (i) body detection and tracking of individuals through the video (localization in space and time) and (ii) audiovisual action recognition (Fig. 1 and movie S1). Audio allows us to determine temporal segments where the nut cracking and buttress drumming occur ("scene level") but does not pinpoint the individual responsible. By visually detecting and tracking all chimpanzees that appear in the video, frame by frame, we are able to determine the spatial position of each individual present. The next stage of our framework uses both the scene level audio and the visual content of each track to specify which individual is performing the behavior ("individual level"). Both stages in our pipeline use a deep CNN model (see Materials and Methods).

The audio stream can also be used to provide a preview mechanism to filter out behavioral sequences for human annotators to label (*21*), substantially reducing the time required to collect annotations. This is achieved using an audio-only action recognition model (which operates at the scene level) and can identify "proposals" or short video sequences where the action is likely to occur. A human annotator then only verifies whether the sequence contains the action or not. This allows us to efficiently create a labeled action recognition dataset that can be used to train the second stage of our automatic pipeline.

Our method is able to identify where fine-grained movements such as striking and drumming are occurring in time and space automatically. It consists of a deep CNN model, which predicts actions using audio only, visual only, and both audio and visual modalities together. We demonstrate the use of our pipeline on two different data sources: For nut cracking, we use part of a longitudinal video archive recorded by human-operated camcorders at an "outdoor laboratory" in Bossou, Guinea (*14*, *22*); while for buttress drumming, data were collected between 2017 and 2019 by 25 motion triggered cameras in Cantanhez National Park, Guinea-Bissau (*23*). Last, we also demonstrate possible next steps in behavioral analysis enabled by the automatically parsed video. This approach represents the first automated audiovisual action recognition of species in the wild.

RESULTS

For nut cracking, we apply our pipeline to 40.2 hours of video containing 2448 nut cracking sequences (see Materials and Methods for definition of a sequence), resulting in a total of 24,700 individual body tracks (linked detections through video frames of the same

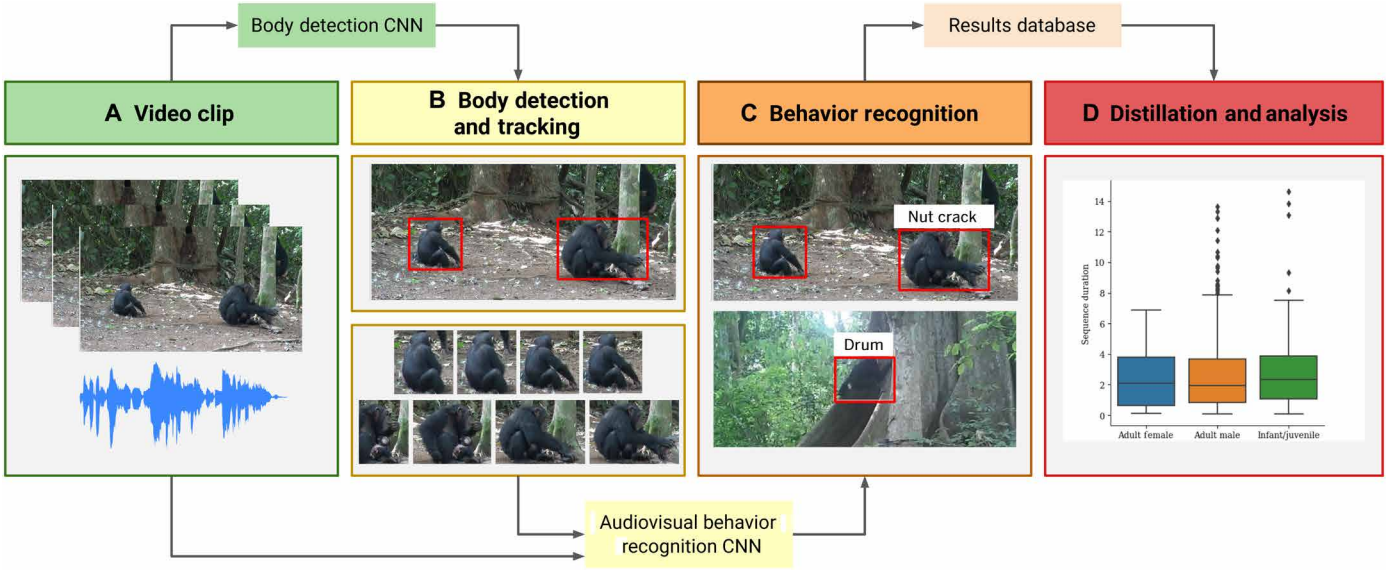


Fig. 1. Fully unified pipeline for wild chimpanzee behavior recognition and analysis from raw video footage. The pipeline consists of the following stages: (**A**) Frames and audio are extracted from raw video. (**B**) Body detection is performed over the video frames using a deep CNN single-shot detector (SSD) model, and the detections are tracked using a Siamese tracker. (**C**) The body tracks are classified (e.g., is this individual cracking nuts?) using the audio data and spatiotemporal visual information for the track by a deep CNN audiovisual behavior model. The system only requires the raw video as input and produces labeled body tracks and metadata as temporal and spatial information. This automated system can be used to perform large-scale analysis (**D**) of behavior. Photo credit: Kyoto University, Primate Research Institute.

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individual; Fig. 1C and fig. S1B). The training set for our model consists of data taken from three years (2004, 2008, and 2012), while we test the performance of our model entirely on data from a different year (2013) to demonstrate generalizability over time. Our audio-only nut cracking recognition CNN model obtains high average precision (85%; Table 1) at the scene level. Results at a scene level only detect time periods where nut cracking is being performed in the video, but they do not isolate the nut cracker, given that multiple individuals may be nut-cracking in the video at the same time (Fig. 2). We also predict results at an individual level, identifying whether a particular individual is nut-cracking or not. Our chimpanzee body detector achieved an average precision of 92% (fig. S1), and our nut cracking recognition model performed well on different poses and lighting conditions typical of videos recorded in the wild (Fig. 2 and movie S1), achieving an overall average precision of 77% at an individual level (Table 1 and Fig. 3).

For buttress drumming, 10.8 hours of camera trap footage are analyzed, resulting in a total of 1251 drumming sequences. We trained our model on data from two chimpanzee communities (Cabante and Caiquene-Cadique) and evaluated our model on manually labeled held-out test data from a third community (Lautchandé). Data from an additional community (Cambeque) are included in the analysis. Our drumming recognition CNN model achieved 87% average precision at a scene level (using audio only) and 86% average precision at an individual level (Table 1 and Fig. 3).

To demonstrate the potential applications of this framework, we used the output of our automatic pipeline to further characterize nut cracking and buttress drumming behaviors. For nut cracking, we trained a visual classifier to identify eating events: This model followed the protocols of the visual-only drumming and nut cracking classifiers and sought to identify instances when food was passed from hand to mouth (an indication of successful nut cracking). Given that an individual typically eats in conjunction with nut cracking, our audio prescreening narrowed down the search space, allowing us to efficiently label 896 body tracks of individuals consuming nuts. This enabled us to analyze, as a function of age/sex class, the average time spent nut cracking per eating event (a proxy for the number of nuts successfully cracked and consumed) (Fig. 4). For buttress drumming, we automatically detect the first and last beats of each drumming bout to precisely measure drumming bout length as a function of age/sex class, allowing us to map the distribution of drumming events throughout the day (Fig. 5; details of the automatic beat detection method are found in the "Analysis" section in Materials and Methods).

For Bossou chimpanzees, nut cracking bouts were predominantly performed by adult males (n = 4665 bouts) followed by adult females (n = 5485 bouts) and juveniles (n = 2134 bouts), while infants (n = 1) were not observed nut-cracking. The mean time spent nut-cracking and the proportion of time spent nut-cracking differed between age/sex groups. Adult males spent a greater proportion of their time nut-cracking than adult females (males, mean ± SD = 9.21 ± 9.49%; and females, mean ± SD = 7.97 ± 9.19%), while juveniles required longer nut cracking sequences per nut consumed than adult males and females (males, mean ± SD =16.8 ± 6.46 s; females, mean ± SD =15.7 ± 10.41 s; and juveniles/infants, mean ± SD = 43.4 ± 39.0 s) (Fig. 4C and table S3), confirming previous reports on the ontogeny of nut cracking (*24*). This suggests that adult males consumed the greatest number of nuts.

For buttress drumming, we analyzed 992 drumming bouts; the majority of bouts were performed by adult males (n = 845), confirming previous observations that this is a predominantly male activity (*25*), and occurred throughout the day, following a bimodal distribution with peaks in the morning and in the afternoon (Fig. 5B). When analyzing bout duration, adult males had, on average, shorter bouts (mean ± SD = 2.21 ± 1.80 s) than immature individuals (mean ± SD = 2.72 ± 2.39 s) and adult females (mean ± SD = 2.75 ± 1.79 s). There is a marked variation within each age/sex group, especially in adult males (min = 0.21 s and max = 19.48 s). In addition, drumming context (travel, feeding, and agonistic display) was analyzed for both adult males and adult females. In both groups drumming, during "travel" was the most common (509 bouts for males and 34 bouts for females), followed by "agonistic display" (225 bouts for males and 25 bouts for females), and lastly "feeding" (111 bouts for males and nine bouts for females). The proportion of drumming events for different contexts was approximately equal for both adult males and females (fig. S3). All drumming performed by immature individuals was done in a "play" context. Drumming bout duration varied between contexts in both adult males and adult females as well as between sexes. Feeding drumming bouts were, on average, shorter (males, mean ± SD = 1.74 ± 1.13 s; and females, mean ± SD = 2.17 ± 1.09 s) than agonistic display (males, mean ± SD = 2.31 ± 2.61 s; and females, mean ± SD = 2.78 ± 1.78 s) and travel drumming bouts (males, mean ± SD = 2.27 ± 1.35 s; and females, mean ± SD = 2.89 ± 1.97 s).

Table 1. Recognition results for both nut cracking and buttress drumming. We provide a baseline (random), which shows the chance performance of a random classifier. Bold indicates the highest performing method for the task.

Task	Method	Average precision	
		Nut cracking	Buttress drumming
I. Scene level	Random	0.09	0.11
	Audio	**0.85**	**0.87**
II. Individual level	Random	0.12	0.13
	Audio	0.30	0.81
	Visual	0.76	0.64
	Audiovisual	**0.77**	**0.86**

DISCUSSION

Overall, our model demonstrates the efficacy of using deep neural network architectures for a biological application: the automated recognition of percussive behaviors in a wild primate. Unlike older, rule-based automation methods, our method is entirely based on deep learning and is data-driven. It also improves on previous single-frame methods by being video-based: It uses 3D convolutions in time (*18*) to reason about temporal information, which is important for action detections, and exploits the multimodality of video to use the audio and visual streams jointly to classify behaviors.

Often, it is challenging to curate datasets large enough to train action recognition models without sifting through a significant amount of footage (20 and 4.1% of footage yielded our behaviors of interest for the nut cracking and buttress drumming data, respectively). A key aspect of our approach is the use of audio as a prescreening

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Fig. 2. Behavior recognition results demonstrate the CNN model's robustness to variations in pose, lighting, scale, and speed of action. Example of correctly labeled body tracks from unseen and unheard videos (nut cracking and drumming for the top two and bottom two rows, respectively). Middle two rows: Multiple individuals nut-cracking and buttress-drumming showing variations in lighting, pose, background, and number of chimpanzees. Photo credit: Kyoto University, Primate Research Institute; The Cantanhez Chimpanzee Project.

mechanism, which substantially cuts down the large search space of video for annotation.

Furthermore, we do not constrain the video data in any way, as is done commonly for deep learning methods applied to primate recognition and analysis by aligning individual detections or selecting for age, resolution, or lighting (*26*). Instead, we are able to perform the task "in the wild" and ensure an end-to-end pipeline that will work on raw video with minimum preprocessing (Fig. 2). We also demonstrate that our method is applicable to both long-term targeted field video recordings (including in a field experimental setting) and to

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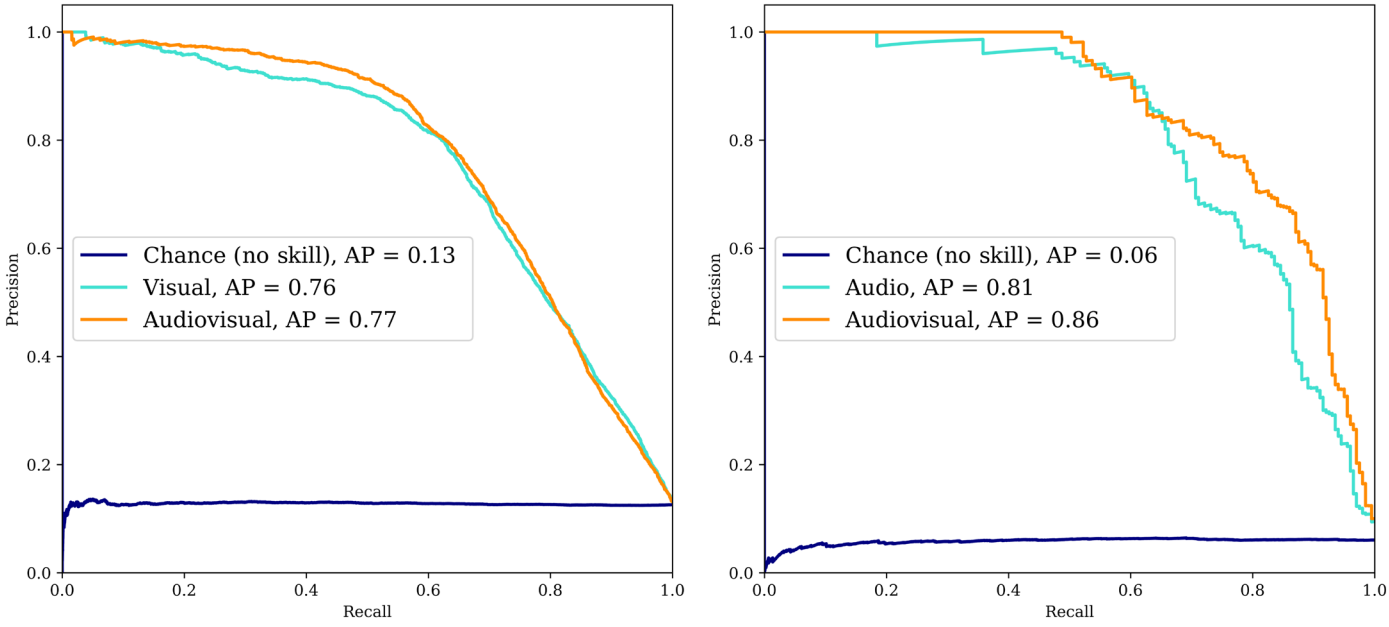


Fig. 3. Performance of the audio, visual, and audiovisual models for individual-level behavior classification. The curves for nut-cracking (**left**) and buttress-drumming (**right**) demonstrate that audiovisual outperforms single-modality methods. Instances where the behavior is either visually or audibly occluded can be compensated by using the other modality (AP: Average Precision).

remote monitoring camera trap datasets, demonstrating its usefulness across different data collection protocols.

The pipeline can be applied to data where only audio or only visual information is available (e.g., camera trap recordings where the behavior occurs off-screen, video recordings with noisy or corrupted audio, or microphone-only recordings). The benefits of our audio method are that it is not affected by visual distractors such as lighting, pose, size, and occlusion and is also computationally cheaper to run. Certain actions (such as buttress drumming) are also more discriminative in the audio space than the visual space (Table 1) and hence require less training data. Audio also allows greater coverage, by detecting actions beyond the field of view of the camera. Our visual-only method, on the other hand, provides the added benefit of allowing localization at an individual level, predicting which individuals are performing particular actions. This is a key advantage for potential future applications in, for example, the monitoring of individual behavior and welfare, both in the wild and in captive settings. Our audiovisual model combines the benefits of both modalities. For drumming, we demonstrate that our model works well even on camera trap data from locations unseen by our model during training (which therefore might contain different tree species) and communities of chimpanzees.

Our model's performance demonstrates the effectiveness of using multimodal deep learning for behavioral recognition of individual animals in longitudinal video archives and camera trap datasets in the wild. Using a novel combination of data collection methods (automated classifiers and manual annotations) and video datasets (archival footage and camera traps), we validate our approach by reproducing known findings on the ontogeny of nut cracking from the existing literature (*24*) and go further to gain preliminary insights into drumming behavior in unhabituated communities as well as revealing potential sex and age differences in different contexts (previously neglected in published work). Ultimately, the integration of computer vision and ethology using automated behavior recognition can aid behavioral research and conservation, moving beyond inferences of social structure and demographics that can be inferred using individual identification [e.g., (*14*)] to capturing the full complexity and dynamics of social interactions and behaviors. Typically, the time and resources required for manual data collection of multiple behaviors (either through in situ observation or retrospective video coding) prohibits analysis of large scale datasets. Adopting automated behavioral recognition is scalable, increasing the speed, quantity, and detail of data that can be collected and analyzed. Once classifiers have been trained, such work can move beyond broad classification of general behavioral states (eating, resting, etc.) to include fine-grained analysis at multiple layers/dimensions of behavior (*27*)—for example, using pose estimation to quantify postural kinematics or detect the number and order of elements in a behavioral sequence (e.g., nut cracking strikes) or investigating temporal co-occurrences between the behavior of individuals in the same group. We also envisage that our method could have a large impact in conservation science. Anthropogenic pressures are increasingly affecting animal behavior, with habitat fragmentation and population loss posing an imminent threat to "cultural species" through the erosion of behavioral diversity (*28*). Automating the measurement of behavioral diversity and activity budgets could be crucial for developing more sophisticated metrics to monitor the health and stability of wild populations (*10*).

There are some limitations to our study, notably that the audio preview step is limited to actions that contain a distinctive sound (such as percussion). Nonetheless, none of the pipeline steps are specific to primate behavior, and the method can be readily applied to other animal species and behaviors. Furthermore, behaviors that are audio distinctive exist in multiple domains, and we envisage possible applications for our pipeline in, for example, marine and terrestrial animal communication (vocalizations), movement (wing

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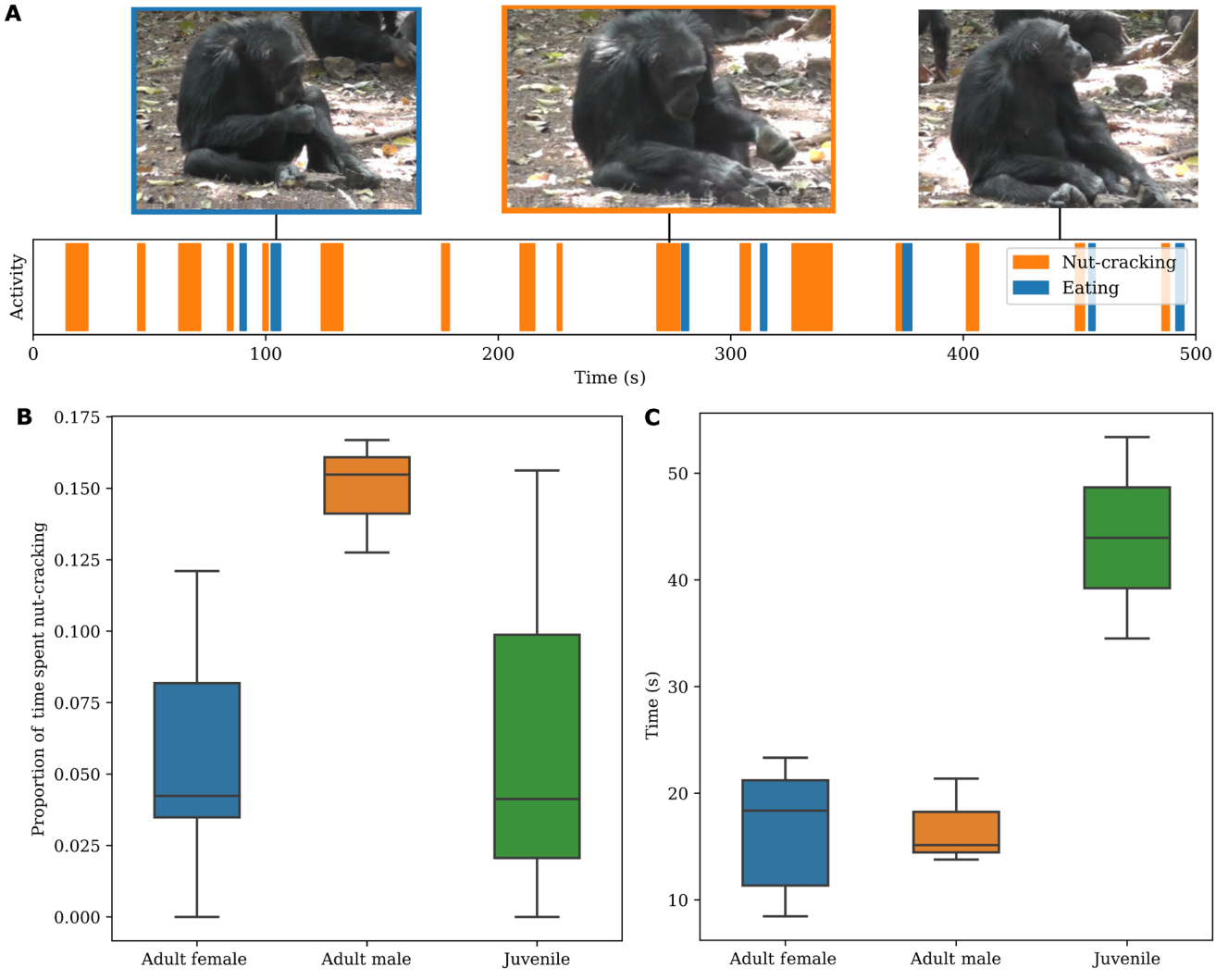


Fig. 4. Nut cracking analysis. (**A**) An example activity sequence following a single individual over the course of a video. The blank white spaces are any activities that are not nut cracking or eating. Note that eating typically follows nut cracking events. (**B**) Proportion of time spent nut cracking as a fraction of total time visible. (**C**) Average time spent nut cracking per eating event. Computed by dividing the cumulative time spent nut-cracking over the total number of eating events as a function of age and sex. Photo credit: Kyoto University, Primate Research Institute.

flapping and stepping), self-maintenance (scratching), aggression (hitting, slapping, and screaming), and foraging (tearing, smashing, and chewing). These analyses could be performed on data not only from remote sensors but also from animal-borne audio-only biologgers. Another limitation concerns the fact that, for individual-level recognition, our method is heavily reliant on the performance of the body detector: Individuals that are not detected or tracked cannot have their behavior classified. For example, the detector often fails to detect infants on their mother's backs, although for our present analyses, this poses no problem, because young chimpanzees do not nut-crack or buttress-drum while being carried. For behaviors that specifically require a visual classifier (such as successful nut cracking being identified through the hand-to-mouth motion of eating), visual occlusion or motion blur poses challenges. However, we note that the body detector has far fewer missed individual detections than other methods that are reliant on face detection (*14*, *22*). Future directions to improve our pipeline include adopting active learning, which minimizes annotator effort by automatically selecting informative samples from a pool of unannotated data for a human to annotate to retrain the network (*29*). In addition, self-supervised learning enables label-free pretraining, initializing the model in such a way that reduces the annotation requirement for training (*30*).

Our pipeline provides a critical first step in large-volume automated behavioral coding and represents a breakthrough in measuring behavior. It will permit detailed intraindividual, interindividual, and cross-site comparisons, automated collection of activity budgets, and longitudinal studies of behavior at individual and population levels, enabling detailed investigation into ontogeny, cultural evolution, and the persistence/decline of behavioral variation over time and how these relate to environmental change. It has transformative potential to science, setting a milestone for exploiting large datasets in ethology and conservation.

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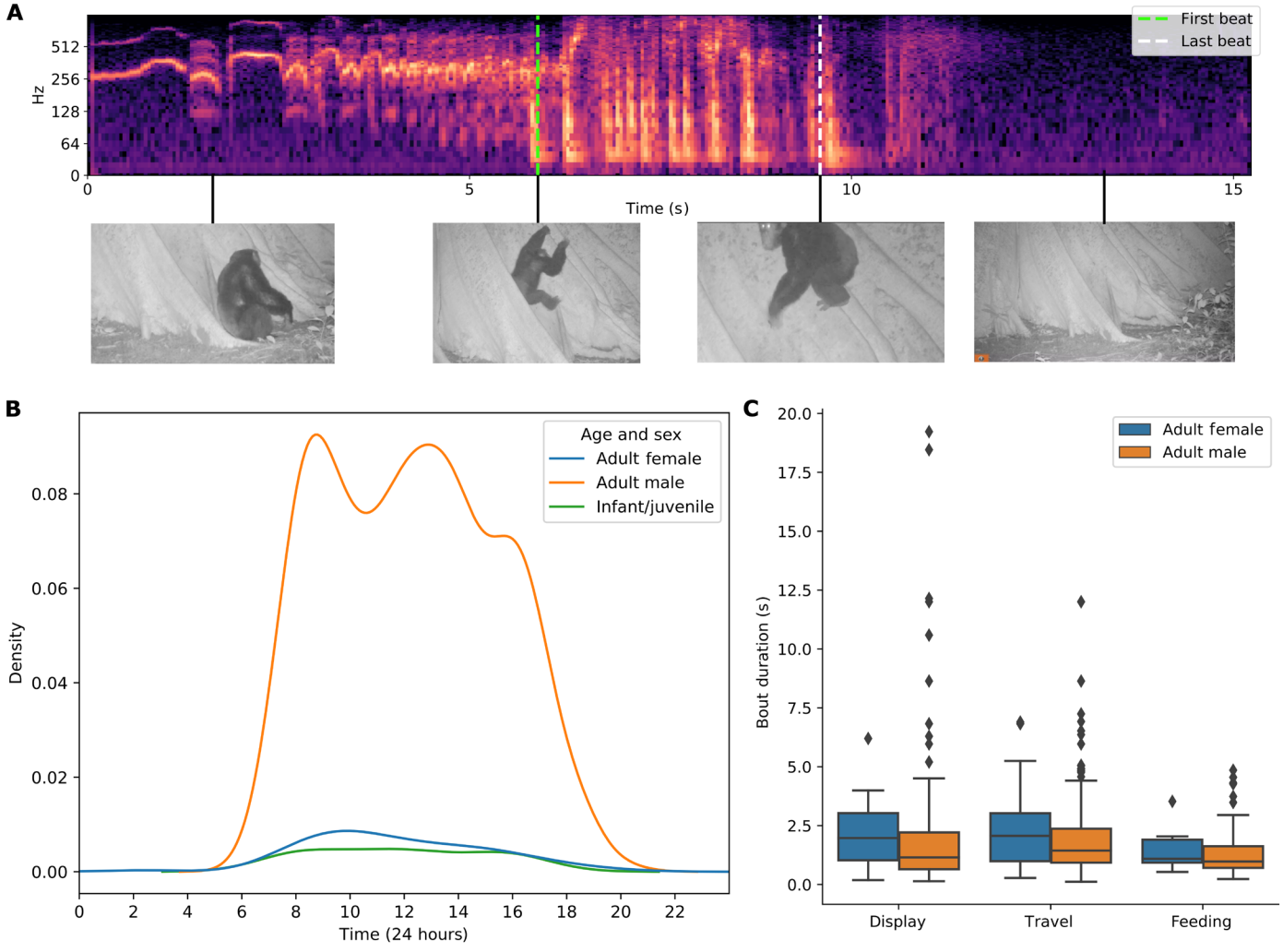


Fig. 5. Buttress drumming analysis. (**A**) Spectrogram showing a detected drumming bout delineated by the first and last beats, with video frames visualized. (**B**) Kernel density estimation plot showing the diel distribution of buttress drumming bouts, based on hh:mm:ss data captured by camera traps. (**C**) Duration (in seconds) of buttress drumming bouts by context (agonistic display, travel, and feeding) and by age/sex (adult females and adult males). Photo credit: The Cantanhez Chimpanzee Project.

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MATERIALS AND METHODS

Video archive

Description of actions

Nut cracking has been described as the most complex tool-use behavior in wild chimpanzees, with the nut cracker typically combining three objects (*31*, *32*). It involves placing a hard-shelled nut on an anvil and then using a hammer to pound the nut until the edible kernel is exposed—sometimes one or two wedges are used to stabilize the anvil. We defined nut cracking "sequences" as beginning when the hammer is raised before the initial strike of a nut and ending when the hammer makes contact with the nut or anvil for the final time before the nut is consumed or abandoned or the camera is moved away. Sequences often included multiple strikes for a single nut.

Buttress drumming is a universal and frequent behavior across all chimpanzee communities, but there is much left to understand about its functions and potential cross-community variation. Drumming occurs when a chimpanzee slaps or stamps rhythmically on the buttress of a tree, often accompanied by a distinct vocalization called a pant hoot. Multiple functions of drumming have been proposed, including long-distance communication (*25*, *33*) and intimidation accompanying agonistic displays (*34*). Distinctive individual drumming patterns and pant hoot vocalizations are thought to act as signals that coordinate group movement and distribution when traveling, as well as containing information about the individual's identity (*35*). These distinct drumming patterns have been described for both males and females (*36*), but male chimpanzees appear to drum more frequently when traveling (*35*). We defined buttress drumming sequences as beginning when the first beat was detected and ending with the last beat; any behavior, such as pant hoots, occurring immediately before the first beat or immediately after the last beat were not included. Beats were detected visually, when at least one hand or foot was in contact with the buttress, and auditorily, when the distinct beat sound was heard.

Structure of the data

Nut cracking at Bossou, Guinea. Data used were collected in the Bossou forest, southeastern Guinea, West Africa, a long-term chimpanzee field site established by Kyoto University in 1976 (*14*). Bossou is home to an outdoor laboratory: A natural forest clearing (7 m by 20 m)

located in the core of the Bossou chimpanzees' home range (07°39′N and 008°30′W) where raw materials for tool use—stones and nuts—are provisioned, and the same group has been recorded since 1988 (*14*, *22*). The use of standardized video recording over many field seasons has led to the accumulation of more than 30 years of video data, providing unique opportunities to analyze chimpanzee behavior over multiple generations. In total, we analyzed 43.1 hours of video footage.

Buttress drumming in Cantanhez National Park, Guinea-Bissau. Data used were collected by camera traps ($n = 25$) deployed in the home ranges of four different communities (Caiquene-Cadique, Lautchandé, Cambeque, and Cabante) in Cantanhez National Park, Southern Guinea-Bissau, West Africa (11°14′17.2″N and 15°02′16.9″W) between February 2017 and December 2018. Chimpanzees in Cantanhez National Park inhabit an agroforest landscape and are not habituated to researchers. The camera traps were set up in areas that chimpanzees' frequented and pointed to trees with large buttress roots with clear signs of wear from chimpanzee buttress drumming. Some cameras were moved during the study period to account for seasonal changes in chimpanzee ranging patterns and when a new area of interest was located. Cameras were motion sensitive and were set to record 1-min video clips when triggered. Approximately 41,000 video clips were collected over the study period, of which 4745 contained footage of chimpanzees, spanning a total of 47.2 hours of video footage.

Dataset splits: Training, testing, and analysis. We divide the dataset into different sections. Part of the data is manually annotated by human annotators, which provides data for training and testing our automated framework (described in the "Methods" section). The remaining data are unlabeled by humans. Our framework is applied to these unlabeled data automatically (this stage is referred to as inference) for analysis (described in the "Analysis" section). Dataset statistics are provided in table S1.

Methods

Our pipeline for the detection of audio-discriminative percussive behaviors consists of the following two stages: (i) chimpanzee detection and tracking and (ii) audiovisual action recognition (Fig. 1).

To efficiently collect annotations for the second stage (ii) audiovisual action recognition, we also use an additional "audio preview stage" (described below in the "Audio action recognition" section) only when collecting training data. This optional audio preview stage uses audio only to determine temporal segments where the behaviors (nut cracking and drumming) occur at a scene level. This markedly reduces the total search space of the video, allowing for efficient annotations, used to train a model on both scene-level audio and the visual content of each track to determine which individual is carrying out the behavior.

With this trained model, our pipeline can then be applied directly to previously unseen videos without any human input. At this point, we do not require the audio preview stage and only use (i) detection and tracking and (ii) audiovisual action recognition.

All stages in the method are implemented using deep CNNs. For audio previewing, we train a CNN on the spectrogram image of the audio. For detection, we use a single-shot detector (SSD) object category detector (*37*) to detect individuals. The detections for an individual are then grouped across frames (time) using a pretrained tracker. The final audiovisual action recognition stage involves a spatiotemporal CNN for the visual features and a spectrogram CNN for the audio. The training data were obtained by using the VGG Image Annotator (VIA) annotation tool (*38*). We provide a detailed description for each stage of the pipeline in the following sections and then describe how the analysis is carried out given the detected behaviors.

Audio action recognition

With the audio data alone, our framework is able to classify actions at the scene level. The nut cracking and buttress drumming audio classifier achieved 85 and 87% average precision, respectively, on unseen test data (Table 1).

Network architecture. For the audio model, we use a 2D CNN (ResNet-18), pretrained on VGGSound (*39*). The output is passed through two linear layers and then a final predictive layer with two neurons and a softmax activation function, resulting in a binary classifier for each target action.

Inputs. We use short-term magnitude spectrograms as input to a ResNet-18 model. All audio is first converted to single-channel, 16-bit streams at a 16-kHz sampling rate for consistency. Spectrograms are then generated in a sliding window fashion using a hamming window with a width of 32 ms and a hop of 10 ms, with a 512-point fast Fourier transform. This gives spectrograms a size of 257 × 201 for 3 s of audio. The resulting spectrogram is integrated into 64 mel-spaced frequency bins with a minimum frequency of 125 Hz and a maximum frequency of 7.5 kHz, and the magnitude of each bin is log-transformed. This gives log mel spectrogram patches of 64 × 201 bins, used as input to the CNN.

Augmentations. Temporal jittering of 0.5 s is used as well as augmentation to positive samples by randomly adding background audio samples (audio that does not contain nut cracking and buttress drumming).

Training. Binary cross-entropy is used as the training objective, along with an Adam optimizer with a learning rate of 5×10^{-3}.

Audio preview for manual annotation. Videos in the wild (including from camera traps) contain a lot of dead footage, where the actions of interest may be captured rarely. Manually searching through all this footage is a labor-intensive task. Hence, we use an inexpensive and computationally efficient prescreening method to automatically sift through many hours of footage, proposing short videos that contain the action and discarding the rest. This is done using the audio alone, because our actions of interest are all percussive and make a distinct sound.

The audio model is applied using a sliding window of size 3 s, with a stride of 0.5 s over the raw video footage. This produces a probability score P(action) of the action of interest being present within each temporal window. We then use the most confident 7% of windows (using the probability score as the confidence) for discrete video labeling, resulting in 2418 discrete, 3-s long video proposals to be annotated. The more expensive body detection and tracking is performed only on these "audio proposals." The body tracks are visualized on the proposals, allowing the annotators to label each actor in the proposal with a binary label denoting whether or not they are performing the action. Given that the drumming video footage is already segmented into short clips and annotated, the audio preview step was not required for the buttress drumming data at training time, so it was only used for nut cracking here.

At inference time, the audio preview can be used as a filtering step first before the full framework, providing computation savings. Because audio is much cheaper computationally than the full framework (detection, tracking, and audiovisual classification), this can be useful in resource-constrained environments such as running

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the framework on the camera traps themselves. Because this work was not constrained in terms of compute, we did not use the audio preview step at inference. For buttress drumming, the trade-off is minimal; a computation saving of 64% still captures 97% of drumming events. For nut cracking, the trade-off is greater; a computation saving of 64% captures 70% of nut cracking events. As there are many off-screen nut cracking events, the sound of nut cracking is not definitively on-screen.

Visual detection and tracking

A prerequisite for our method of automated detection of primate behavior is the detection and tracking of the target animal, producing spatiotemporal tracks following individuals through time. Deep learning has proved to be highly successful at object detection and tracking, and previous works describe the protocol and results of this applied to footage of wild animals (*13*, *14*, *40*, *41*).

In more detail, we follow the same protocol as in (*13*), which involves fine-tuning an SSD object detector (*37*) on bounding box annotations of chimpanzee bodies. Because the two datasets contain very different sources of footage, including camera traps for drumming and direct longitudinal recordings for nut cracking (the former containing night vision, varied lighting, and out of focus blur; with the latter having higher quality video but consisting of close-ups as well as medium shots), we separately fine-tune the two object detectors, one for each dataset.

For the nut cracking dataset, we fine-tune on 16,000 bounding box annotations across 5513 video frames. For the buttress drumming dataset, we fine-tune on 2200 bounding box annotations across 2137 video frames. All video frames were sampled every 10 s.

Tracking. The object tracker used to link the resulting detections through time is a pretrained Siamese network. Pairs of detections in consecutive frames with a Jaccard overlap greater than 0.5 are given as input to the network. Detection pairs with a similarity score greater than 0.5 are deemed to be from the same track.

Evaluation for the detectors. Evaluation is performed on a held-out test set using the standard protocol outlined in (*42*). The precision-recall curve is computed from a method's ranked output. Recall is defined as the proportion of all positive examples above a given rank, while precision is the proportion of all examples above that rank, which are from the positive class. For the purpose of our task, high recall is more important than high precision (i.e., false positives are less dangerous than false negatives) to ensure that no chimpanzees are missed. The Bossou and Cantanhez detectors achieved average precision scores of 0.92 and 0.91 on their respective test sets. Precision-recall curves for both detectors are shown in fig. S1A.

Programming implementation details. The detector was implemented using the machine learning library PyTorch and trained on two Titan X Graphical Processing Units (GPUs) for 20 epochs (where 1 epoch consists of an entire pass through the training set) using a batch size of 32 and two subbatches. Flip, zoom, path, and distort augmentation was used during preprocessing with a zoom factor of 4. The ratio of negatives to positives while training was 3, and the overlap threshold was 0.5. The detector was trained without batch normalization. The tracker was also implemented in PyTorch.

Audio-visual action recognition

Network architecture. For the visual stream, we use a 3D ResNet-18, with 3D convolutions (*30*). The output is passed through two linear layers and then a final predictive layer, with two neurons and a softmax activation function. For the audiovisual fusion model, 512 dimensional embeddings from the ResNet backbone in each stream are concatenated and then passed to the final predictive layer, with two neurons and a softmax activation function.

Inputs. For the audio stream, the preprocessing is identical to the "Audio action recognition" stage. Video frames are sampled at 25 frames per second, and all detections are resized to 128 × 128—we feed in 40 frames over 2.5 s, with three red-green-blue channels each, sampled randomly during training and uniformly during inference. This gives final inputs of size 40 × 128 × 128 × 3.

Augmentations. Standard augmentation techniques are applied to the visual inputs: color jittering, random cropping, and horizontal flipping. For the audio, we repeat the augmentations in the "Audio action recognition" section.

Training. All models are trained with a binary cross-entropy loss. In this stage, we use the annotations obtained from the "Audio action recognition" stage of the pipeline to train the model.

Evaluation. Evaluation for the action recognition models is performed on a held-out test set, the statistics of which are supplied in Table 1. The audiovisual fusion model performed the best at the individual level for both nut cracking and buttress drumming (77 and 86%, respectively), demonstrating its robustness across domains and actions and demonstrating its efficacy over audio or vision alone.

The models are evaluated on their precision recall at either the scene level or individual level. For the scene level, we evaluate the audio-only model with a stride of 0.5 s and a forgiveness collar of 0.5 s. For the individual level, we evaluate the audio, visual, and audiovisual models with a stride of 0.5 s per track and a forgiveness collar of 0.5 s.

Implementation details. The networks for action recognition were trained on four Titan X GPUs for 20 epochs using a batch size of 16. We trained both models end to end via stochastic gradient descent with momentum (0.9) weight decay (5×10^{-4}) and a logarithmically decaying learning rate (initialized to 10^{-2} and decaying to 10^{-8}). The visual stream is initialized with weights from (*30*), and the audio model is initialized with weights pretrained on VGG-Sound (*39*).

Action-specific implementation details

Nut cracking analysis: Success detection. To further analyze nut cracking behaviors, we additionally measure another action: passing food from hand to mouth, which is an indication of successful nut cracking. Here, the shell has been successfully cracked and the individual passes the kernel to their mouth using their hand; henceforth, this action is referred to as "eating." Because this behavior has a strong visual signature, we train a visual classifier to determine this. This model follows the protocol of the visual-only drumming and nut cracking classifiers. The training labels for eating events were gathered from the audio preview proposals, totaling 896 tracklets of individuals eating. While the audio preview searches for nut cracking, eating is often found shortly after successful nut cracking events, so the short audio proposals often contain this action as well. Furthermore, individuals often nut-crack together, resulting in multiple individuals in a video proposal. Training the model on data from 2004 and 2008 results in 89% accuracy in classifying eating on unseen tracks from 2012.

Buttress drumming duration analysis. We investigate the duration of drumming bouts by determining the start and the end beat in a drumming bout using audio-based beat detection. Beat detection is performed in an automated fashion by using low-pass filtering

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and onset detection to the audio signal of the drumming bout. The audio sequence is first low pass–filtered using a Butterworth filter with a cutoff frequency of 800 Hz. Onset detection is then performed on the filtered audio waveform. We use the onset detection method provided by the Librosa Python toolbox. The hyperparameters were chosen to achieve the best beat counting accuracy on 30 drumming bouts hand-labeled with the number of beats. During evaluation, we apply a forgiveness collar of 0.25 s on either side of the drumming event boundaries to be more lenient toward imprecise boundary annotation. From the beat detections, we define the duration of a drumming bouts to be the interval between the first and last beats. This beat detection method predicts drumming duration with a mean and median error of 0.205 and 0.131 s, respectively.

SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at https://science.org/doi/10.1126/sciadv.abi4883

View/request a protocol for this paper from *Bio-protocol*.

REFERENCES AND NOTES

1. N. Tinbergen, On aims and methods of ethology. *Z. Tierpsychol.* **20**, 410–433 (1963).
2. J. Krause, S. Krause, R. Arlinghaus, I. Psorakis, S. Roberts, C. Rutz, Reality mining of animal social systems. *Trends Ecol. Evol.* **28**, 541–551 (2013).
3. D. J. Anderson, P. Perona, Toward a science of computational ethology. *Neuron* **84**, 18–31 (2014).
4. O. Sturman, L. von Ziegler, C. Schläppi, F. Akyol, M. Privitera, D. Slominski, C. Grimm, L. Thieren, V. Zerbi, B. Grewe, J. Bohacek, Deep learning-based behavioral analysis reaches human accuracy and is capable of outperforming commercial solutions. *Neuropsychopharmacology* **45**, 1942–1952 (2020).
5. E. A. van Dam, L. P. J. J. Noldus, M. A. J. van Gerven, Deep learning improves automated rodent behavior recognition within a specific experimental setup. *J. Neurosci. Methods* **332**, 108536 (2020).
6. P. Swarup, P. Chen, R. Hou, P. Que, P. Liu, A. W. K. Kong, Giant panda behaviour recognition using images. *Glob. Ecol. Conserv.* **26**, e01510 (2021).
7. S. P. Kaufhold, E. J. C. van Leeuwen, Why intergroup variation matters for understanding behaviour. *Biol. Lett.* **15**, 20190695 (2019).
8. M. Cantor, A. A. Maldonado-Chaparro, K. B. Beck, H. B. Brandl, G. G. Carter, P. He, F. Hillemann, J. A. Klarevas-Irby, M. Ogino, D. Papageorgiou, L. Prox, D. R. Farine, The importance of individual-to-society feedbacks in animal ecology and evolution. *J. Anim. Ecol.* **90**, 27–44 (2021).
9. D. M. Dominoni, W. Halfwerk, E. Baird, R. T. Buxton, E. Fernández-Juricic, K. M. Fristrup, M. F. McKenna, D. J. Mennitt, E. K. Perkin, B. M. Seymoure, D. C. Stoner, J. B. Tennessen, C. A. Toth, L. P. Tyrrell, A. Wilson, C. D. Francis, N. H. Carter, J. R. Barber, Why conservation biology can benefit from sensory ecology. *Nat. Ecol. Evol.* **4**, 502–511 (2020).
10. F. Christiansen, M. H. Rasmussen, D. Lusseau, Inferring activity budgets in wild animals to estimate the consequences of disturbances. *Behav. Ecol.* **24**, 1415–1425 (2013).
11. A. Caravaggi, P. B. Banks, A. C. Burton, C. M. V. Finlay, P. M. Haswell, M. W. Hayward, M. J. Rowcliffe, M. D. Wood, A review of camera trapping for conservation behaviour research. *Remote Sens. Ecol. Conserv.* **3**, 109–122 (2017).
12. A. Whiten, J. Goodall, W. C. McGrew, T. Nishida, V. S. Reynolds, Y. Sugiyama, C. E. G. Tutin, R. W. Wrangham, C. Boesch, Charting cultural variation in chimpanzees. *Behaviour* **138**, 1481–1516 (2001).
13. M. Bain, A. Nagrani, D. Schofield, A. Zisserman, in *Workshop on Computer Vision for Wildlife Conservation, ICCV* (IEEE, 2019).
14. D. Schofield, A. Nagrani, A. Zisserman, M. Hayashi, T. Matsuzawa, D. Biro, S. Carvalho, Chimpanzee face recognition from videos in the wild using deep learning. *Sci. Adv.* **5**, eaaw0736 (2019).
15. A. Mathis, P. Mamidanna, K. M. Cury, T. Abe, V. N. Murthy, M. W. Mathis, M. Bethge, DeepLabCut: Markerless pose estimation of user-defined body parts with deep learning. *Nat. Neurosci.* **21**, 1281–1289 (2018).
16. D. Shao, Y. Zhao, B. Dai, D. Lin, FineGym: A hierarchical video dataset for fine-grained action understanding, in *Proceedings of the IEEE/CVF Conference on Computer Vision and Pattern Recognition* (IEEE, 2020), pp. 2616–2625.
17. M. S. Norouzzadeh, A. Nguyen, M. Kosmala, A. Swanson, M. S. Palmer, C. Packer, J. Clune, Automatically identifying, counting, and describing wild animals in camera-trap images with deep learning. *Proc. Natl. Acad. Sci. U.S.A.* **115**, E5716–E5725 (2018).
18. S. Ji, W. Xu, M. Yang, K. Yu, 3D convolutional neural networks for human action recognition. *IEEE Trans. Pattern Anal. Mach. Intell.* **35**, 221–231 (2013).
19. J. Carreira, A. Zisserman, Quo Vadis, action recognition? A new model and the kinetics dataset, in *Proceedings of the IEEE Conference on Computer Vision and Pattern Recognition* (IEEE, 2017), pp. 6299–6308.
20. F. Sakib, T. Burghardt, Visual recognition of great ape behaviours in the wild. arXiv:2011.10759 [cs.CV] (21 November 2020); http://arxiv.org/abs/2011.10759.
21. R. Gao, T.-H. Oh, K. Grauman, L. Torresani, Listen to Look: Action recognition by previewing audio, in *Proceedings of the IEEE/CVF Conference on Computer Vision and Pattern Recognition* (IEEE, 2020), pp. 10457–10467.
22. T. Matsuzawa, Field experiments on use of stone tools by chimpanzees in the wild, in *Chimpanzee Cultures*, R. W. Wrangham, W. C. McGrew, F. B. M. de Wall, P. G. Heltne, Eds. (Harvard Univ. Press, 1994), pp. 351–370.
23. J. Bessa, K. Hockings, D. Biro, First evidence of chimpanzee extractive tool use in Cantanhez, Guinea-Bissau: Cross-community variation in honey dipping. *Front. Ecol.* **9**, 625303 (2021).
24. D. Biro, N. Inoue-Nakamura, R. Tonooka, G. Yamakoshi, C. Sousa, T. Matsuzawa, Cultural innovation and transmission of tool use in wild chimpanzees: Evidence from field experiments. *Anim. Cogn.* **6**, 213–223 (2003).
25. A. C. Arcadi, D. Robert, C. Boesch, Buttress drumming by wild chimpanzees: Temporal patterning, phrase integration into loud calls, and preliminary evidence for individual distinctiveness. *Primates* **39**, 505–518 (1998).
26. D. Deb, S. Wiper, A. Russo, S. Gong, Y. Shi, C. Tymoszek, A. Jain, Face recognition: Primates in the wild, arXiv:1804.08790 [cs.CV] (24 April 2018); http://arxiv.org/abs/1804.08790.
27. K. Huang, Y. Han, K. Chen, H. Pan, G. Zhao, W. Yi, X. Li, S. Liu, P. Wei, L. Wang, A hierarchical 3D-motion learning framework for animal spontaneous behavior mapping. *Nat. Commun.* **12**, 2784 (2021).
28. H. S. Kühl, C. Boesch, L. Kulik, F. Haas, M. Arandjelovic, P. Dieguez, G. Bocksberger, M. B. McElreath, A. Agbor, S. Angedakin, E. A. Ayimisin, E. Bailey, D. Barubiyo, M. Bessone, G. Brazzola, R. Chancellor, H. Cohen, C. Coupland, E. Danquah, T. Deschner, D. Dowd, A. Dunn, V. E. Egbe, H. Eshuis, A. Goedmakers, A.-C. Granjon, J. Head, D. Hedwig, V. Hermans, I. Imong, K. J. Jeffery, S. Jones, J. Junker, P. Kadam, M. Kambere, M. Kambi, I. Kienast, D. Kujirakwinja, K. E. Langergraber, J. Lapuente, B. Larson, K. Lee, V. Leinert, M. Llana, G. Maretti, S. Marrocoli, R. Martin, T. J. Mbi, A. C. Meier, B. Morgan, D. Morgan, F. Mulindahabi, M. Murai, E. Neil, P. Niyigaba, L. J. Ormsby, R. Orume, L. Pacheco, A. Piel, J. Preece, S. Regnaut, A. Rundus, C. Sanz, J. van Schijndel, V. Sommer, F. Stewart, N. Tagg, E. Vendras, V. Vergnes, A. Welsh, E. G. Wessling, J. Willie, R. M. Wittig, Y. G. Yuh, K. Yurkiw, K. Zuberbühler, A. K. Kalan, Human impact erodes chimpanzee behavioral diversity. *Science* **363**, 1453–1455 (2019).
29. M. S. Norouzzadeh, D. Morris, S. Beery, N. Joshi, N. Jojic, J. Clune, A deep active learning system for species identification and counting in camera trap images. *Methods Ecol. Evol.* **12**, 150–161 (2021).
30. T. Han, W. Xie, A. Zisserman, Video representation learning by dese predictive coding, in *Proceedings of the IEEE International Conference on Computer Vision Workshops* (IEEE, 2019), pp. 1483–1492.
31. T. Matsuzawa, T. Humle, Y. Sugiyama, *The Chimpanzees of Bossou and Nimba* (Springer Science & Business Media, 2011).
32. S. Carvalho, E. Cunha, C. Sousa, T. Matsuzawa, Chaînes opératoires and resource-exploitation strategies in chimpanzee (Pan troglodytes) nut cracking. *J. Hum. Evol.* **55**, 148–163 (2008).
33. C. Boesch, Symbolic communication in wild chimpanzees? *Hum. Evol.* **6**, 81–89 (1991).
34. T. Nishida, *Chimpanzees of the Lakeshore: Natural History and Culture at Mahale* (Cambridge Univ. Press, 2011).
35. M. Babiszewska, A. M. Schel, C. Wilke, K. E. Slocombe, Social, contextual, and individual factors affecting the occurrence and acoustic structure of drumming bouts in wild chimpanzees (Pan troglodytes). *Am. J. Phys. Anthropol.* **156**, 125–134 (2015).
36. V. Reynolds, *The Chimpanzees of the Budongo Forest: Ecology, Behaviour and Conservation* (OUP Oxford, 2005).
37. W. Liu, D. Anguelov, D. Erhan, C. Szegedy, S. Reed, C.-Y. Fu, A. C. Berg, *European Conference on Computer Vision* (Springer, 2016), pp. 21–37.
38. A. Dutta, A. Zisserman, in *Proceedings of the 27th ACM International Conference on Multimedia (MM '19)* (Association for Computing Machinery, 2019), pp. 2276–2279.
39. H. Chen, W. Xie, A. Vedaldi, A. Zisserman, Vggsound: A large-scale audio-visual dataset, in *Proceedings of ICASSP 2020–2020 IEEE International Conference on Acoustics, Speech and Signal Processing (ICASSP)* (IEEE, 2020), pp. 721–725.
40. J. Yu, H. Su, J. Liu, Z. Yang, Z. Zhang, Y. Zhu, L. Yang, B. Jiao, A Strong Baseline for Tiger Re-ID and its Bag of Tricks, in *Proceedings of the IEEE International Conference on Computer Vision Workshops* (IEEE, 2019), pp. 302–309.
41. P. Chen, P. Swarup, W. M. Matkowski, A. W. K. Kong, S. Han, Z. Zhang, H. Rong, A study on giant panda recognition based on images of a large proportion of captive pandas. *Ecol. Evol.* **10**, 3561–3573 (2020).
42. M. Everingham, L. Van Gool, C. K. I. Williams, J. Winn, A. Zisserman, The pascal visual object classes (voc) challenge. *Int. J. Comput. Vis.* **88**, 303–338 (2010).

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Acknowledgments: We are grateful to Kyoto University's Primate Research Institute for leading the Bossou Archive Project and supporting the research presented here and to the IREB and DNRSIT of Guinea. This study is dedicated to all the researchers and field assistants who have collected data in Bossou since 1988. We thank the Instituto da Biodiversidade e das Áreas Protegidas (IBAP) for their permission to conduct research in Guinea-Bissau and for logistical support, research assistants and local guides for assisting with data collection, and local leaders for granting us permission to conduct research. We thank M. Ramon for collecting camera trap data in Cabante, Guinea-Bissau. **Funding:** This study was supported by EPSRC Programme Grants Seebibyte EP/M013774/1 and Visual AI EP/T028572/1; Google PhD Fellowship (to A.N.); Clarendon Fund (to D.S. and S.B.); Boise Trust Fund (to D.S., S.B., and J.B.); Wolfson College, University of Oxford (to D.S.); Keble College Sloane-Robinson Clarendon Scholarship, University of Oxford (to S.B.); Fundação para a Ciência e a Tecnologia, Portugal SFRH/BD/108185/2015 (to J.B.); Templeton World Charity Foundation grant no. TWCF0316 (to D.B.); National Geographic Society (to S.C.); St Hugh's College, University of Oxford (to S.C.); Kyoto University Primate Research Institute for Cooperative Research Program (to M.H. and D.S.); MEXT-JSPS (no. 16H06283), LGP-U04, the Japan Society for the Promotion of Science (to T.M.); and Darwin Initiative funding grant number 26-018 (to K.J.H.). **Author contributions:** Conceptualization: D.S. Methodology: M.B., A.N., and A.Z. Data curation: M.B., D.S., J.B., S.B., and J.O. Data collection: D.B., S.C., T.M., M.H., K.J.H., and J.B. Software, formal analysis, and visualization: M.B. Supervision: A.Z., D.B., and S.C. Writing (original draft): M.B., A.N., D.S., and J.B. Writing (review and editing): A.Z., D.B., S.C., and K.J.H. **Competing interests:** The authors declare that they have no competing interests. **Data and materials availability:** All data needed to evaluate the conclusions in the paper are present in the paper and/or the Supplementary Materials and at the Dryad data repository (https://datadryad.org/stash/share/UUfSTzsL9eTbAo-78pdaXPdaIUJmdJzSuqhXcb48vHM).

Submitted 12 March 2021
Accepted 23 September 2021
Published 12 November 2021
10.1126/sciadv.abi4883

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Science Advances
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Supplementary Materials for

Automated audiovisual behavior recognition in wild primates

Max Bain*, Arsha Nagrani, Daniel Schofield, Sophie Berdugo, Joana Bessa, Jake Owen, Kimberley J. Hockings, Tetsuro Matsuzawa, Misato Hayashi, Dora Biro, Susana Carvalho, Andrew Zisserman

*Corresponding author. Email: maxbain@robots.ox.ac.uk

Published 12 November 2021, *Sci. Adv.* **7**, eabi4883 (2021)
DOI: 10.1126/sciadv.abi4883

The PDF file includes:

Supplementary Text
Figs. S1 to S3
Table S1
Legend for Movie S1

Other Supplementary Material for this manuscript includes the following:

Movie S1

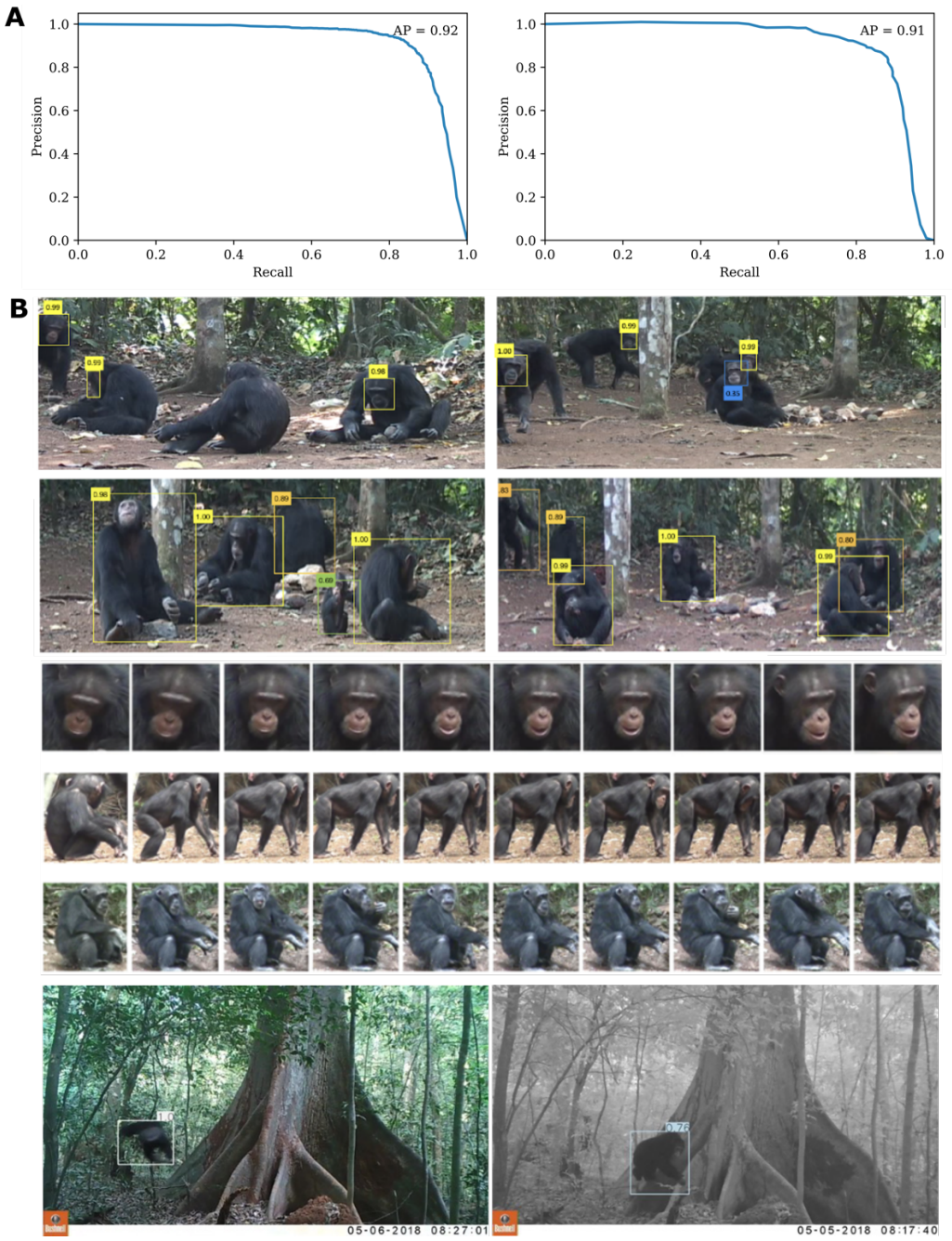


Fig. S1. Detection and Tracking Results: (A) Precision Recall Curves for the individual body detectors for Bossou (left) and Cantanhez (right), with their Average Precision (AP) scores labelled. (B) Qualitative examples of detections (detector confidences shown above each detection) and body tracks on both the Bossou and Cantanhez video footage. Photo credit: Kyoto University, Primate Research Institute; The Cantanhez Chimpanzee Project

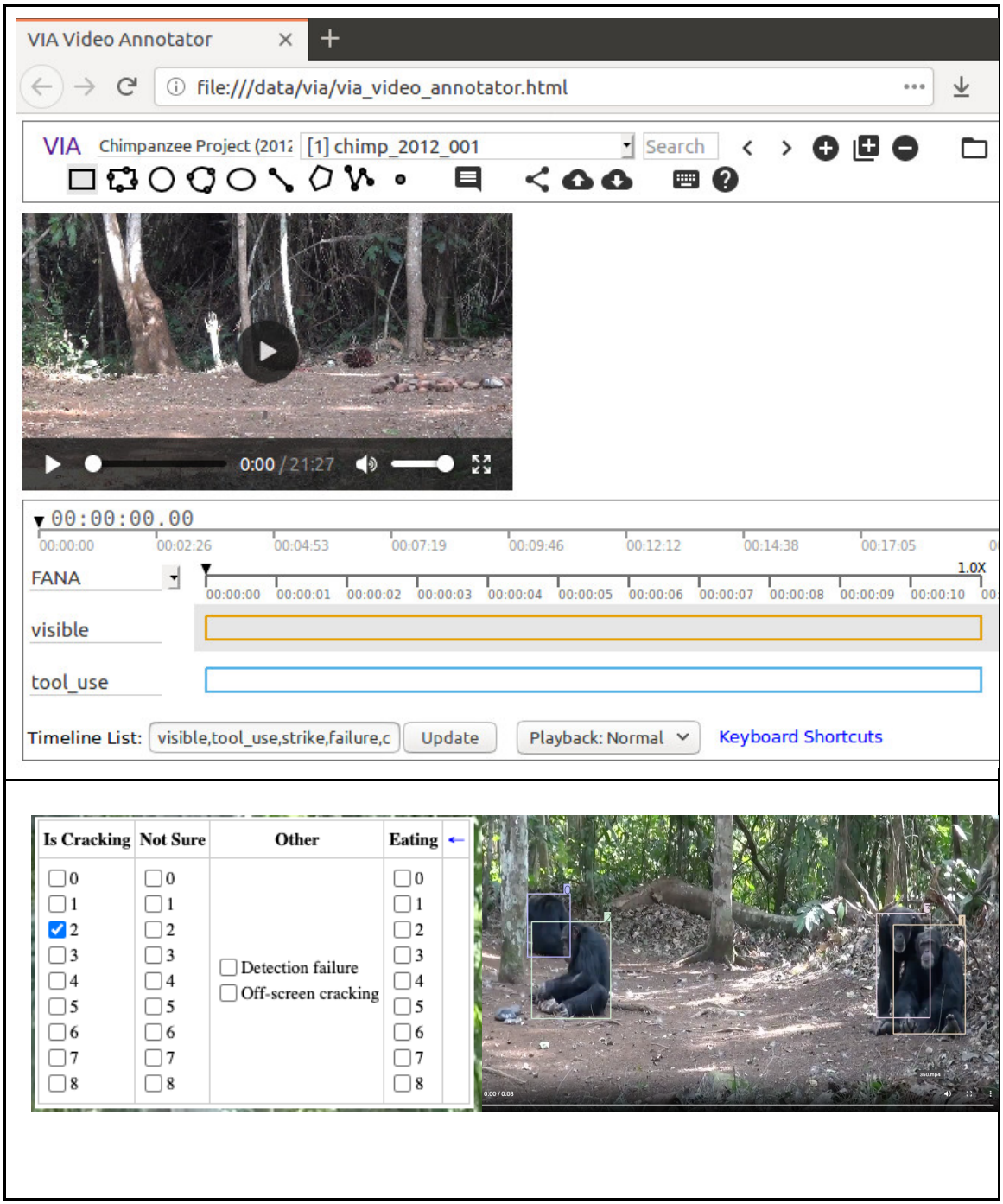


Fig. S2. Screenshots of the annotation tool, the VGG Image Annotator (VIA). VIA is a browser based, open-source annotation software which we modified for this purpose, facilitating temporal annotation of video.

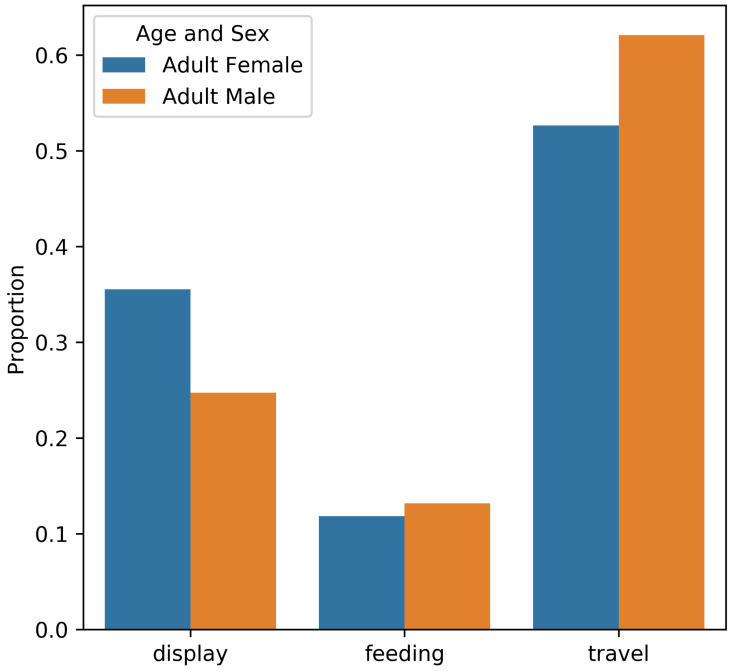


Fig. S3. Proportion of buttress-drumming bouts by context for Adult Males and Females. Context here consists of agnostic display, feeding and travel. Proportions for each context are approximately equal for both males and females.

Table S1. Training and Testing Data Statistics for (A) Nut-Cracking and (B) Buttress-Drumming for the Bossou and Cantahez video footage respectively.

(A)	Split	Sampled Years	Duration of video (hours)	# Nut-cracking Sequences	# Tracklets	# Tracklets containing *nut-cracking*
	Training	2012	10.5	864	11,400	508
	Training (Audio proposals)	2004, 2008, 2012	1.9	1,455	9,564	1,786
	Testing	2013	2.6	417	3,699	154
	Analysis	2012, 2013	13.1	1,281	15,099	662
(B)	**Split**	**Sampled Communities**	**Duration of video (hours)**	**# Drumming Bouts**	**# Tracklets**	**# Tracklets containing *drumming***
	Training	Cabante, Caiquene-Cadique	32.8	778	2,526	1,249
	Testing	Lautchande	1.7	166	521	191
	Analysis	Cabante, Caiquene-Cadique, Lautchande, Cambeque	10.8	1,251	-	-

Movie. S1. Demonstration of automatic behaviour classification pipeline to example videos. Videos are first processed by the body detection tracking stage, followed by audiovisual behaviour classification.

B

PILOT RESEARCH

Preliminary observations made during pilot research are critical when measuring animal behaviour (Martin & Bateson, 2007). Setchell (2019) recommends the use of pilot studies in primatological research to assess the logistical and practical elements of the project, and to troubleshoot any issues prior to the main body of research is conducted. Pilot research allows the measures, equipment, and methods to be tested on a smaller-scale, and provides an opportunity to ensure the data complies with the assumptions of the tests planned to be employed during the main data analysis (Setchell, 2019). This early testing also allows methods to be refined, ensuring they are replicable and consistent. Moreover, this practise period improves intra-observer reliability, whereby observer errors stemming from inexperience, which creates variation in the measures, are reduced (Setchell, 2019). This point was reiterated by Martin & Bateson (2007), who explained that coding experience ultimately leads to more accurate results.

Testing Measurements

The nut-cracking efficiency pilot study involved testing the measurement of adult efficiency in one video from the archive. A video from 2009 (Video UID: d3e88f7f-4d56-4cfd-83b1-ba2a4a2760a2; date: 2009-12-19) was selected given that there were multiple nut-cracking adults present. Having multiple adults in the video meant that the reliability of the measure could be established across individuals, and to preliminary assess inter-individual variability in nut-cracking efficiency. This video will be excluded from the main data collection.

A BORIS (v. 7.9.24) project was created, and the variables and ethogram were inputted. The nut-cracking adults present in the video were Jeje, Peley, Tua, and Fanle. The relevant behaviour patterns were measured in each subject according to the coding scheme. Once all data had been collected, the project was exported as aggregated events to a csv file.

Analysis

There was a total of 00:13:07:848 (hh:mm:ss:msms) observation time in the efficiency pilot study, with n = 198 nut-cracking bouts across the four focal subjects. Data cleaning was conducted using Python 3.8 and Jupyter Notebook (*Jupyter*, 2021). Descriptive statistics for the efficiency pilot study can be found in Table S1, below.

Table A1. Descriptive statistics for the efficiency pilot study.

	Bouts			Strikes				
Subject	***n***	**Duration mean**	**Duration SD**	***n***	**Duration mean**	**Duration SD**	**Displacements**	**Tool Switches**
Jeje	91	4.932	7.211	273	0.753	0.127	42	8
Peley	23	2.345	3.368	46	0.626	0.101	4	1
Tua	16	2.883	2.508	41	0.615	0.089	7	1
Fanle	68	3.016	4.255	129	0.705	0.168	27	13

Note: All duration units are in seconds.

Discussion

Conducting a pilot study for this research highlighted issues with the coding scheme and data collection protocol. As a result, the key outcome of the pilot study was the redesign of the following points:

1. Strike duration will no longer be collected. The pilot study demonstrated the considerable time investment to annotate the start and end of each strike, and there is no precedent in the literature to record the duration of each hammer strike.
2. Each video will be recorded as one observation, rather than creating a new observation in BORIS for each nut-cracking bout. This will increase the efficiency of data collection.
3. Modifiers will be used rather than independent variables, as the attributes can be assigned to each event as it occurs. This will also complement the previous research design alteration as individual bouts will no longer have to be new observations.

C

RESEARCH ASSISTANT BEHAVIOURAL CODING TRAINING DOCUMENTATION

This document outlines the training process for coding adult chimpanzee nut-cracking behaviour from video footage. Familiarise yourself with this document and install BORIS onto your machine before we meet.

BORIS

Installing BORIS

Firstly, go to the *Behavioural Observation Research Interactive Software* (BORIS) website and visit the 'Download' page (http://www.boris.unito.it/?page=download). Download the most up-to-date version of BORIS (v. 7.10.2 as of 19th April 2021) available using the hyperlink called "Link". Download the BORIS which is appropriate for your machine's operating system (GNU/Linux, Microsoft Windows, or MacOS). There are videos on YouTube to assist with the download and launch of BORIS:

Windows 10:

https://www.youtube.com/watch?v=oWs4e7iPy6I&t=160s&ab_channel=Borisbehavobs

MacOS:

https://www.youtube.com/watch?v=GcISDpjLwF8&t=86s&ab_channel=Borisbehavobs

Opening the Project

A BORIS project will be shared with you. Save this file to your machine. Open the BORIS application and go to *File > Open project* and find the saved project file. This project will have all the information (Ethogram, Subjects, Independent Variables) already inputted. Take time to familiarise yourself with the BORIS environment. Going to *File > Edit project* allows you to see all the information about the project. Do not change any of this information.

Coding Scheme

You have been provided with the coding scheme. It provides background information on the behaviours of interest, assistance on chimpanzee identification, details on how to code in BORIS and what behavioural patterns are to be recorded. Take time to familiarise yourself with the coding scheme. If any aspect of the coding scheme is unclear, alert me at the earliest opportunity so any ambiguities or queries can be addressed.

Demonstration of Behavioural Coding

I will then demonstrate the process of behavioural coding in BORIS using the coding scheme. This demonstration of the behavioural coding process will use the following video from 2012:

Video UID	Date and time	Tape set ID	Comments
4abd5840-4875-4672-ad61-7e02348fd08a	2012-01-30 16:15:14	dbd68e70-d952-4175-b047-f4b5b53d1ac1	Jeje cracking at 00:01:56, 00:09:52

Practise Behavioural Coding

You will then be provided with some pre-selected training observations to code which cover all of the behaviours described in the coding scheme. This will provide you with an opportunity to practise the process of behavioural coding in BORIS with another coder present. The coding scheme provides instructions on creating observations in BORIS. Ensure the hard drive with the video footage is plugged in to your machine and give BORIS permission to access the footage if a message appears.

The practice behavioural coding footage will be from the following 2012 video:

Video UID	Date and time	Tape set ID	Comments
357b79c7-9ce6-42a8-81f1-2a732dc483c5	2012-02-06	fa083253-7510-4bb0-919e-90903c6a9409	Foaf: 00:09 Jeje: 00:13 Jire: 00:54 [Peley peering] and 02:40

Training Footage

You will then be provided with some training footage for you to go through independently. At the end, we will go through our respective coding of the footage and determine if there are any irregularities or disagreements. These discrepancies will be clarified, and any ambiguities in the instructions corrected.

The training footage will be taken from the following 2012 year:

Video UID	Time and Date	Tape set ID	Comments
f1acdcbb-c0d2-4a5d-98e4-e6d5986f15e1	2012-02-02 15:58:34	dbd68e70-d952-4175-b047-f4b5b53d1ac1	Jire: 00:01:30, 00:04:11, 00:10:27, 00:23:49 Fanle: 00:30:36, 00:48:34 Jeje: 00:16:57, 00:19:01

D

INTER-RATER RELIABILITY TRAINING DATA

Each independent, hypothesis-blind coder received an extensive training period prior to the main data collection (as recommended by Setchell, 2019), which allowed them to familiarise themselves with the BORIS software, practise the measurement techniques and gain experience with behavioural coding, and check the adequacy of the definitions in the coding scheme. These factors were identified by Martin & Bateson (2007) as 'the most important factors influencing reliability' (p. 80), and so addressing these in the training phase aimed to increase the reliability of measurements made. The full instructions provided to each research assistant regarding the behavioural coding training can be found in Appendix C.

The videos selected for the training phase were specifically selected to ensure that the behaviours of interest occurred in the footage, allowing the elements of the coding scheme to be practised. The information on the videos used in the training phase for each independent coder can be found in Table A3, below.

Table A3. Details of the videos used for research assistant training.

Coder	Video UID	Video Date (YYYY-MM-DD)	Video Time	Video Length (HH:MM:SS)
1	f1acdcbb-c0d2-4a5d-98e4-e6d5986f15e1	2012-02-02	15:58:34	00:51:21
2	8cd3b20b-f527-4092-907c-0311c8f3cfa6	2010-01-03	08:05:33	00:25:31
3	77ca7933-9dcd-4ca1-a34e-b3fe25837dcc	2002-12-16	15:44:27	01:22:14

All data analysis was performed with R 4.0.3 (R Core Team, 2020) on RStudio 1.3.1093 for MacOS using the irr (Gamer et al., 2019) and tidyverse (Wickham et al., 2019) packages. Unweighted Cohen's κ scores were calculated using the function *kappa2*. For bout outcome, the agreement between the two coders (SB and coder_1) was substantial, $\kappa = 0.73$, and

greater than what would be expected by chance, $z = 5.81$, $p < .001$. All ICC scores to assess the reliability between two raters (k = 2, SB and coder_1) were calculated using the *icc* function, and can be found in found in Table A4 and Table A5, below.

Table A4. ICC calculation using single-rating, absolute agreement, two-way mixed-effects model.

		95% Confidence Interval		F Test with True Value 0			
	ICC	Lower bound	Upper bound	Value	*df1*	*df*2	Sig.
Strikes per nut	0.946	0.909	0.968	35.8	53	54	<0.00
Displacement rate	0.692	0.52	0.809	5.76	53	49.1	<0.00
Tool switch rate	NaN	NaN	NaN	NaN	53	NaN	NaN

Table A5. ICC calculation using single-rating, consistency, two-way mixed-effects model.

		95% Confidence Interval		F Test with True Value 0			
	ICC	Lower bound	Upper bound	Value	*df1*	*df*2	Sig.
Bout duration	0.86	0.771	0.916	13.3	53	53	<0.00
Mean strike duration	0.559	0.345	0.718	3.54	53	53	<0.00

Given the training nature of this behavioural coding, the raters met to discuss discrepancies in coding that fell below the 0.7 benchmark, namely the coding of displacements and mean strike duration. Clarifications to the coding scheme were made to reduce ambiguity in definitions. In order to assess whether observations of displacement had increased improved agreement between coders, exact time stamps of point events were compared rather than a binary yes/no of whether it had been recorded. For this, a single-rating, consistency, two-way model ICC analysis found $ICC(C,1) = 1$, $F(8,8) = 5595226$, $1 < ICC < 1$, $p < 0.000$, indicating perfect consistency.

The second RA was trained using earlier footage from the archive to test reliability across varying camera and lighting qualities. The same coding scheme and analyses were run to

determine inter-rater reliability between myself and this second independent coder. There were no instances of learning behaviour in the video, so inter-rater reliability was established for the variables bout outcome, strikes per nut, displacement rate, tool switch rate, and bout duration. For bout outcome, the agreement between the two coders (SB and coder_2) was moderate, $\kappa = 0.502$, and greater than what would be expected by chance, $z = 3.93$, $p < .001$. ICC scores to assess the absolute agreement between two raters (k = 2) can be found in Table A6. For bout duration, a single-rating, consistency, two-way model ICC analysis found ICC(C,1) = 0.922, F(52,52) = 24.6, 0.868 < ICC < 0.954, $p < 0.000$, indicating excellent consistency.

Table A6. ICC calculation using single-rating, absolute agreement, two-way mixed-effects model.

		95% Confidence Interval		F Test with True Value 0			
	ICC	Lower bound	Upper bound	Value	*df1*	*df2*	Sig.
Strikes per nut	0.969	0.947	0.982	64	52	53	<0.00
Displacement rate	0.693	0.521	0.81	5.45	52	52.4	<0.00
Tool switch rate	1	NaN	NaN	Inf	52	NaN	NaN

Notes: ICC scores for two raters: SB and coder_2.

As above, where scores fell below the 0.7 threshold the coders met to discuss the discrepancies. Following consultation on displacement rate and bout outcome, the videos were re-coded to account for clarifications. Displacement time stamps were compared to determine whether consistency had been improved. For this, a single-rating, consistency, two-way model ICC analysis found ICC(C,1) = 1, F(22,22) = 34891071, 1 < ICC < 1, $p < 0.000$, indicating perfect consistency. For bout outcome, the agreement between the two coders (SB and coder_2) following the consultation was almost perfect, $\kappa = 0.937$, and greater than what would be expected by chance, $z = 7.955$, $p < .001$.

E

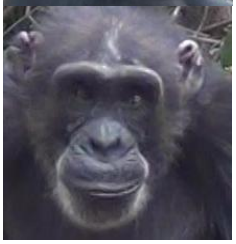
EFFICIENCY CODING SCHEME

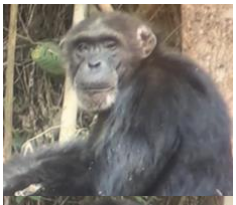
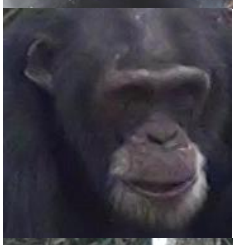
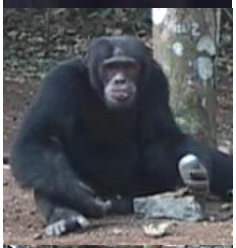
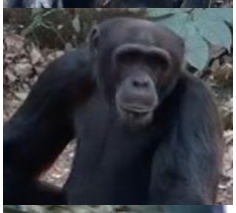
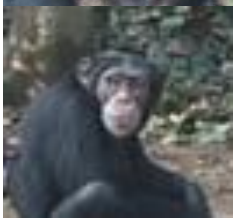
This coding scheme provides instructions on how to code chimpanzee nut-cracking behaviour using the *Behavioural Observation Research Interactive Software* (BORIS; Friard & Gamba, 2016). The purpose of the coding is to quantify the efficiency of nut-cracking bouts and the tolerance of nut-cracking models using a series of measures. The behaviours to be coded are related specifically to nut-cracking and are described below.

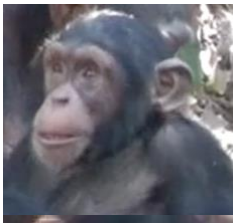
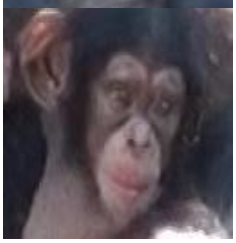
Chimpanzee Identification

Table A7 lists all individuals who appear in the archive in 2008 and 2012, the field season years you will be coding. You should learn the names and faces of each group member. Information is provided on their nut-cracking hand, sex, and some defining characteristics to aid with identification during behavioural annotation. You should be completely certain of identity when making annotations. Where there is confusion, consult with another coder.

Table A7. Identification information for the Bossou chimpanzees.

Individual	Sex	Laterality	Key characteristics	Image
Fana	F	Right	Left arm paralysed	
Jire	F	Left	Black face with white around mouth.	
Velu	F	Right	Large stomach. Dark face, white around mouth	
Pama	F	N/A	Dark face, white around mouth. Cauliflower ears. Does not crack nuts	

Yo	F	Left	Very dark face. Quite round head and prominent ridge above eyes	
Tua	M	Left	Lack of hair, big missing patch on right forearm. Left ear flat on side. Old. Dark but reddish face.	
Foaf	M	Right	Right ear ripped at top. White beard but otherwise dark face.	
Yolo	M	Left	Alpha male in 2008. Light face and flat top of head. Not present in 2012.	
Jeje	M	Left	Alpha male in 2012. Young adult. Lighter face and bigger body than Peley.	
Peley	M	Left	Young adult male. Dark face, slim.	
Joya	F	Left	Adolescent female. Only adolescent in the group. Prominent sexual swelling.	
Fanle	F	Right	Light face. Always with juvenile son Flanle and carrying infant son Fanwa	

Flanle	M	Only juvenile in group. Always with mother Fanle	
Fanwa	M	Only infant in group. Always with mother Fanle	

Coding in BORIS

The BORIS user guide can be found here: https://boris.readthedocs.io/en/latest/, and within the BORIS application itself (*Help* > *User Guide*). When you launch BORIS, you will see the display window (see Figure A1, top). Click *File* > *Open Project* to open the coding project (see Figure A1, bottom). You can resize any aspect of the display (i.e., Ethogram and Subject bars).

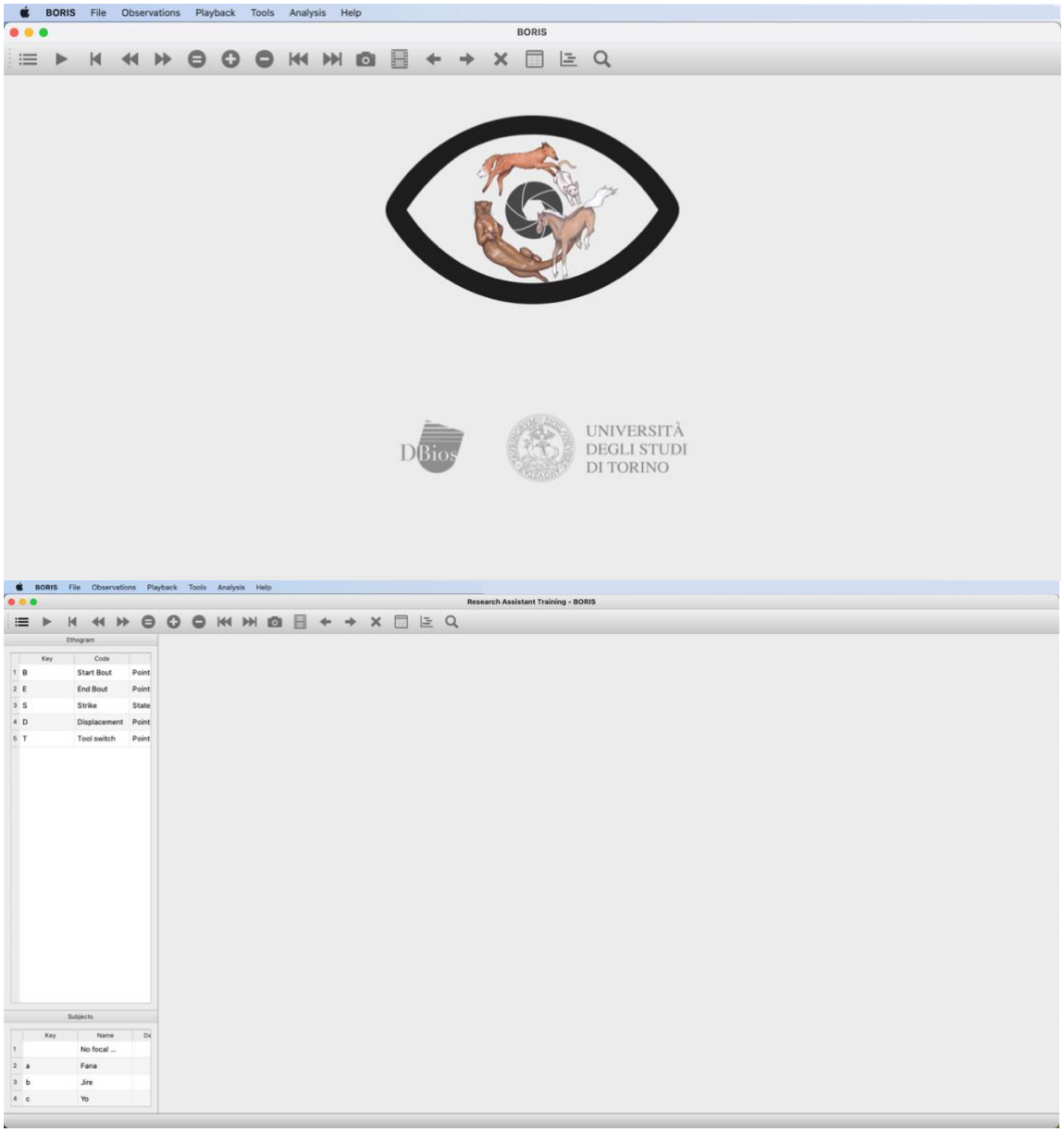


Figure A1. Top: BORIS launch window. Bottom: BORIS project display.

Observations

After you open the project in BORIS you will need to create a new observation for each bout you code. For this, go to *Observations* > *New observation*. The *Observation id* will be the unique identifier (UID) of the video and must be made each time you create a new observation (see Figure A2). Each new video is a new observation. Change *date and time* to be the date (YY-MM-DD) and time (HH-MM-SS) of the original video. Click the *Add media*

button under the *Media* tab to upload the video from the archive onto BORIS. Make sure *hh:mm:ss* is selected before clicking *Start*. Save each new observation as you go.

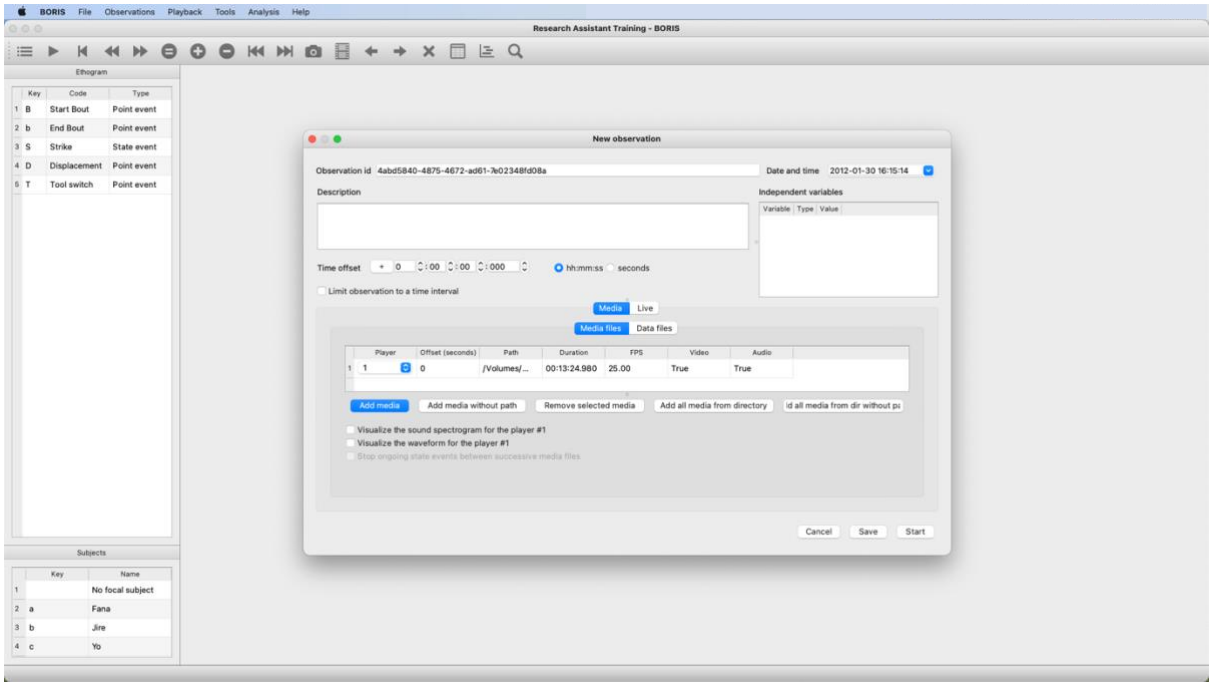


Figure A2. New observation window in BORIS.

Key for toolbar symbols



Symbols from left to right:

- Observation list
- Play/pause button
- Restarts video from beginning
- Fast backward by a predetermined number of seconds (set in *File* > *Preferences* > *Fast forward/backward speed (seconds)*)
- Fast forward by a predetermined number of seconds (set in *File* > *Preferences* > *Fast forward/backward speed (seconds)*)
- Return playback speed to 1x
- Increase playback speed (set in *File* > *Preferences* > *Playback speed step value*)
- Decrease playback speed (set in *File* > *Preferences* > *Playback speed step value*)

- Go to previous video file
- Go to next video file
- Takes a photo of current frame
- Change between VLC and frame-by-frame mode
- In frame-by-frame mode, goes backwards one frame
- In frame-by-frame mode, goes forwards one frame
- Close observation
- Plotting function for events coded in current observation
- Find event

Keyboard shortcuts

- *Page up:* Go to next video file
- *Page down:* Go to previous video file
- *Up arrow:* Go forwards in video
- *Down arrow:* Go backwards in video
- *Esc:* Change between VLC and frame-by-frame modes
- *Home:* Increase video playback speed
- *End:* Decrease video playback speed
- *Backspace:* Return playback speed to 1x
- *Left arrow:* In frame-by-frame mode, move back one frame
- *Right arrow:* In frame-by-frame mode, move forward one frame

Ethogram

The ethogram for the project will be found on the left-hand side of the main BORIS window. Each row of the ethogram comprises a behaviour to be coded. Each behavioural code has a case-sensitive keyboard shortcut to assist coding (found in the "Key" column of ethogram). Behaviours which require a calculation of duration will be recorded as "state events" on BORIS and behaviours which require frequency measurement will be recorded as "point events".

To record a behaviour *either*:

- Double click on the behaviour in the ethogram in the main BORIS window; *or*
- Press the keyboard shortcut assigned to the behavioural code.

To edit an event:

- Right click on the event in the "Events" widget on the right-hand side of the BORIS display and select what you wish to edit (for example, the time stamp).

Subjects

The list of individual chimpanzees (see table above) can be found in the Subjects display on the bottom left-hand side of the main BORIS window. Each individual has a case-sensitive keyboard shortcut to assist coding (found in the "Key" column of subject table).

To select a focal individual for coding:

- Double click on that individual's row in the Subject table in the main BORIS window.
- Press the keyboard shortcut assigned to the focal subject.

What to Record

Below are the definitions and instructions for recording each behaviour in the ethogram, and how to select the modifiers (attributes) of the behaviours. Routinely save the project (*File > Save project*) so no observations are lost.

Visibility of Behaviours

In video footage taken of species in the wild, factors such as different poses, light quality and image quality impact the ability to observe behaviours (Schofield et al., 2019). You should only record bouts (defined below) which are clearly visible (i.e., observable) in the footage.

Record a bout if:

- The focal individual is facing the camera, and you can see the nut, hammer, and anvil during the bout. If any of these three elements becomes obscured during the bout (for example, if a conspecific is between the focal individual and the

camera), stop recording the bout at the last point that the bout is clearly visible and select "No" for the *Complete bout* modifier (see below).

- The individual is not directly facing the camera, but you can see the nut, hammer and anvil and you can identify the individual from contextual footage (for example, you previously watched them move to the nut-cracking location) or by the researchers in the video audibly identifying the specific individual (e.g., 'Jire moved to nut matrix' or 'Jeje cracking with hammer D5').

<u>Do not record a bout if:</u>

- The focal individual is nut-cracking but has their back to the camera and you cannot see the tool composite and nut (i.e., you would not be able to see a displacement or tool switch event even if you can hear the individual strikes).
- There is a conspecific positioned between the camera and the focal individual meaning you cannot see the tool composite and nut.
- The quality of the video footage too low to clearly observe nut-cracking behaviour (for example, in wide shots where the individual is too far away for the hand, nut and stones to be clearly visible, or if the video is too low definition to clearly observe the nut-cracking behaviour).
- The nut-cracking individual cannot be identified, even following consultation with another coder or from contextual footage.

Behaviours

A **bout** is a continuous period (in seconds) of nut-cracking whereby the individual strikes a nut on an anvil with a hammer stone involving the same hand, bodily posture, hand grip, and nut. *Record the start and end point event of each bout as separate point events.*

Start bout. The start of the continuous nut-cracking period. A bout will start soon after a new nut is placed on the anvil.

Start recording a bout when:

- The hammer starts to be lifted from the ground for first strike of the nut on an anvil; *or*
- In the video frame when the nut-cracking arm or wrist is visibly higher than the proceeding frame, in instances where the hammer does not start on the ground (for example, when there has just been a strike or bout and the individual is already holding the hammer, or when the individual has lifted the hammer, but the nut is yet to be positioned on the anvil)

Double click "Code" in the ethogram widget or press the keyboard shortcut "B". The point event will appear in the "type" column.

Do not record a bout if:

- The video starts, or the individual only becomes fully visible, part way into a bout. In this case, begin coding at the start of the next full bout.
- The nut has been part of a previously failed bout.
- There is more than one nut placed on the anvil to be openned. [But make a note of the video and time stamps if this occurs].
- The individual is being groomed by a conspecific during their nut-cracking bout.

End Bout. The point when the continuous nut-cracking period finishes.

Stop recording a bout when:

- The hammer makes contact with the nut for the final time before the shell is opened ready for the kernel to be extracted; *or*
- The hand, bodily posture/position or nut is changed before the shell is opened. Record this bout as **failed** when selecting the bout outcome modifier (see below) as soon as this occurs; *or*
- If the hand grip on the hammer is altered and this does not result in a change in the surface of the stone being used (i.e., if there was no rotation of the stone).

Record this bout as **failed** when selecting the bout outcome modifier (see below) as soon as this occurs; *or*

- If the nut is cracked open and manipulated or eaten, but then replaced on the anvil to continue to crack, end the bout when the nut is hit with the hammer for the final time. Record this bout as **smashed** when selecting the bout end modifier (see below); *or*
- The last contact with either the nut, hammer, or anvil if the individual stops nut-cracking for one minute or more (for example, gets up and leaves location, becomes distracted by researchers or conspecific, grooming) before the nut is opened. Record the bout outcome modifier as **failed**.

Double click "Code" in the ethogram widget or press the keyboard shortcut "E". The point event will appear in the "type" column.

<u>Do not stop recording a bout if:</u>

- The nut is displaced due to a hammer strike hitting the nut off the anvil and is then replaced on the anvil. In this case, continue recording the bout until the hammer makes contact with the nut for the final time before the shell is opened ready for the kernel to be extracted; *or*
- The individual gets distracted (for example, chases off a conspecific, looking at researchers or pant hooting) for less than one minute but resumes cracking the same nut with the same tool composite; *or*
- If the hand grip on the hammer is altered and this results in a change in the surface of the stone being used (i.e., there was a *tool switch*, see below). Continue to record this bout and record the tool switch event as soon as this occurs.

Strike. The action of using a hammer to hit a nut on an anvil. *Record each strike in a nut-cracking bout*.

Start recording a strike:

- In the frame when hammer is lifted from the ground before hitting the nut on the anvil; *or*
- In the frame when the nut-cracking arm or wrist is visibly higher than the proceeding frame, in instances where the hammer does not start on the ground (for example, when there has just been a strike and the individual is already holding the hammer)

Note: The first strike of the bout starts at the same time stamp as the start of the bout (above).

Double click "Code" in the ethogram widget or press the keyboard shortcut "S". START will appear in the "type" column.

Stop recording a strike:

- In the frame when the hammer makes contact with the nut.

Double click "Code" in the ethogram widget or press the keyboard shortcut "S". STOP will appear in the "type" column.

Do not record a strike if:

- There is no nut on the anvil.

Displacement. A hammer strike results in the nut being hit off the anvil. *Record each displacement event. The time stamp does not need to be precise to the exact moment of displacement.*

Record a *displacement* event when:

- The nut is hit off the anvil because of a hammer strike.

Double click "Code" in the ethogram widget or press the keyboard shortcut "D". The point event will appear in the "type" column.

Do not record a *displacement* event if:

- The nut is repositioned on the anvil following a strike, but the nut remains on the anvil.
- The nut rolls off the anvil after being placed back on.
- The nut falls off the anvil because the nut is handled by the individual rather than because of a hammer strike.

Tool switch. The focal individual changes one or both parts of the tool composite (hammer or anvil) to a new tool. *Record each tool switching event. The time stamp does not need to be precise to the exact moment of the tool switch.*

Record a *tool switch* if:

- The individual replaces the hammer and/or anvil stones with new stones. Regardless of whether the individual switches one or both parts of the tool composite, record this as just one tool switch event.
- The individual swaps the hammer and anvil stones (i.e., hammer becomes anvil and vice versa).
- The individual uses the same tool but rotates it or turns it over to use a different surface. Regardless of how many times the tool is rotated or turned over, record this as just one tool switch event. Record a new switch event if there is a nut strike between the tool being rotated or turned over again.
- The individual rotates or turns the same tool, but it ends in the original position.

Double click "Code" in the ethogram widget or press the keyboard shortcut "T". The point event will appear in the "type" column.

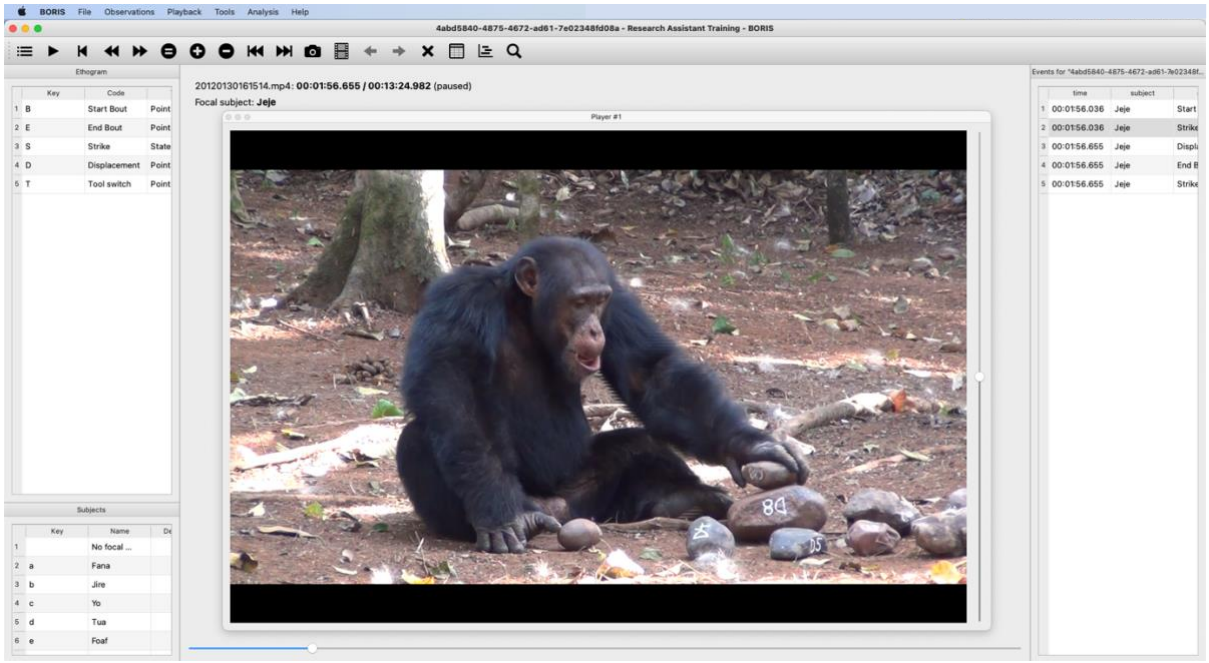


Figure A3. Screenshot of a complete bout observation in BORIS.

Modifiers

Modifiers are attributes of behaviours that must be inputted once the behaviour has been recorded. Here, you will only be required to select modifiers when a bout has started ("Start Bout") and ended ("End Bout"). A window will automatically appear for you to input these events, as outlined below.

Start Bout

Nut species. The nut species being cracked by the focal. Two nut-species are present in the video footage: coula nuts (*Coula edulis*) and oil palm nuts (*Elaeis guineensis*). Record *unknown* if the nut species is unclear (for example, due to low quality footage), or record:

- *Coula nut* - large and round nuts
- *Oil palm nut* - smaller and flatter than coula nuts

End Bout

Complete bout. Whether or not the full bout was able to be recorded or not because of the video footage itself.

Record *Yes* if:

- The full bout (from "Start Bout" to "End Bout") was recorded.

Record *No* if:

- If the bout was only partially recorded (for example, if the camera panned away from individual before the end of the bout, if the video ended before the end of a bout, if the bout becomes obscured by another individual).

*If you record "*No*", only record the remaining modifiers which are known from the footage available, for example if there was a learner or model tolerance or intolerance. Record "Number of strikes" as how many strikes were visible and "Bout outcome" as "None"*.

Number of strikes. The number of strikes performed by the focal individual on a nut in the whole nut-cracking bout. *The exact number must be manually inputted using your keyboard.*

- Remember that the START and STOP of strikes are for the same state event and constitute one strike.

Bout outcome. Outcome of the nut-cracking bout. *Select from list by clicking on the option.*

Record a bout outcome as *successful* if:

- The nut is cracked open using the hammer and anvil composite and the full kernel is retrieved and eaten by an individual (not necessarily by focal subject if kernel is scrounged).

Record a bout outcome as *smash* if:

- The nut is cracked open using hammer and anvil, but the kernel is smashed into multiple pieces (each piece may be eaten separately or only some of the kernel may be eaten. If no kernel is eaten after the nut is smashed, record as *failed*); *or*
- Kernel fragments are seen being dispersed because of strikes, and they are not

Record a *failed* bout if:

- A different nut is placed on the anvil following displacement of the original nut; *or*
- The nut is not retrieved or not eaten by any individual.

Learner. Whether or not there is a conspecific who is during their critical period (a "learner") present during the focal individual's nut-cracking bout. *Select from list by either clicking on the option or using the keyboard shortcut.*

Record a bout as having a learner *peering* if:

- There is a learner watching the focal subject during the nut-cracking bout, whereby the learner's face is oriented toward the model's hand or arm during the bout.

Record a bout as having a learner *interacting* if:

- There is a learner present, and they are interacting with the focal subject (for example, touching arm or body of model, climbing on model). If the learner is positioned behind the focal subject and is not clearly visible, record *present* and then *proximity* for the "Model Tolerance" modifier.

Record a bout as having a learner *clinging and peering* if:

- There is a learner present, and they are clinging to the focal subject or sat on the focal subject's lap and watching the nut-cracking bout. In this case, do not record the *Model Tolerance* modifiers of *model interaction* or *proximity*.

Record a bout as having a learner *clinging* if:

- There is a learner present, and they are clinging to the focal subject or sat on the focal subject's lap and not watching the nut-cracking bout. In this case, do not record the *Model Tolerance* modifiers of *model interaction* or *proximity*.

Record a bout as having a learner *present* if:

- There is a learner present, ≤ 1 metre (m) away from the focal subject during the bout, but they are not watching the bout or interacting with the model. In this case, record the model tolerance modifier of *proximity*.

Record a bout as *solo* if:

- There is no learner with the focal individual during their nut-cracking bout.

F

DEVELOPMENT CODING SCHEME

What to Record

Below are the definitions and instructions for recording each behaviour in the ethogram, and how to select the modifiers (attributes) of the behaviours. Routinely save the project (*File > Save project*) so no observations are lost.

Visibility of Behaviours

In video footage taken of species in the wild, factors such as different poses, light quality and image quality impact the ability to observe behaviours (Schofield et al., 2019). You should only record peering events, bouts, and behavioural episodes (defined below) which are clearly visible (i.e., observable) in the footage. Record all opportunity provision events that occur on screen (identifiable visually or audibly).

Peering

Record a peering event if:

- The focal individual is facing the camera, and you can see they are watching a nut-cracking conspecific; *or*
- The focal individual is not directly facing the camera, but you can clearly see the direction of their gaze due to positioning of the head.

Do not record a peering event if:

- The focal individual is not facing the camera for the duration of the event, so you cannot see clearly see the direction of the gaze from the position of the head; *or*
- There is a conspecific positioned between the camera and the focal individual during the whole peering event, meaning you cannot see the direction of the gaze; *or*
- The quality of the video footage is too low to clearly observe the peering event (for example, in wide shots where the individual is too far away for the gaze to be clearly visible, or if the video is too low definition to clearly observe the peering event); *or*

- The individual watching a conspecific's nut-cracking bout cannot be identified, even following consultation with another coder or from contextual footage.

Opportunity Provision

Record opportunity provision if:

- The maternal model is clearly visible (regardless of direction to the camera) cracking nuts whilst the focal subject is present in the outdoor laboratory.
- The maternal model is nut-cracking with their back to the camera and the focal subject is positioned behind them (relative to the camera). In this case, as it is not known whether the focal subject is peering at the nut-cracking or not, record as opportunity provision rather than peering.

Behaviours

Peering. When the focal subject's face is directly oriented towards a model's hand or arm or towards the nut and stone tool composite during a nut-cracking bout (see below). *Record the start and end point of each peering event as separate point events.*

Note: Peering events only occur when the model is in a nut-cracking bout (striking a nut on an anvil with a hammer stone). Record a new peering event for each new nut the model cracks.

Start Peering. The start of the period when the focal subject's gaze is directly oriented towards a model's hand, arm, nut, or stone tool composite during a nut-cracking bout.

Record the start of a peering event:

- In the frame where the learner orients their gaze towards the model's hand or arm or towards the nut and stone tool composite when the model in cracking; *or*
- In the frame when the model lifts the hammer for the first time to commence the nut-cracking bout if the learner begins observing prior to strikes.

Double click code in ethogram or press keyboard shortcut.

End Peering. When the focal subject's gaze is no longer oriented towards the model's hand or arm or towards the nut and stone tool composite.

Record the end of a peering event when:

- The subject ceases to look at the model's hand or arm or towards the nut and stone tool composite whilst the model in a nut-cracking bout; *or*
- The first point when an individual (the model, focal subject, or another conspecific) makes contact with the nut to pick it up to commence eating the extracted kernel, if the focal subject maintains their gaze after the nut has been opened; *or*
- The frame the model strikes the nut for the last time before they stop nut-cracking if they do not extract the kernel.
- The last point the subject is visible watching a nut-cracking model if the event is incomplete (for example, if the camera pans away, if the footage ends during an event). In this case, record "*No*" for the *Complete peering event* modifier (see below).

Double click code in ethogram or press keyboard shortcut.

Do not stop recording a peering event if:

- The focal subject moves their bodily position but continues to maintain their gaze on the model's hand or arm; *or*
- The focal subject momentarily looks away, but re-orients their gaze toward the nut-cracking model during the same bout.

Opportunity. The continuous period of when the focal subject's mother is on camera engaged in nut-cracking whilst the focal subject is present in the outdoor laboratory. *Record the opportunity event as separate start and stop opportunity point events.*

Start Opportunity. When the focal's mother commences nut-cracking whilst the focal subject is in the outdoor laboratory. *Select the learner as the focal subject, rather than the mother*.

Record a *start opportunity* event when:

- The hammer is lifted from the ground for the first strike of the nut on an anvil.

- The first time the mother is visible on camera cracking nuts, if the footage commences when the individual has already commenced to crack, or if the camera pans to the individual part way through a nut-cracking bout.

Double click code in ethogram or press keyboard shortcut.

End Opportunity. The focal's mother ceases to crack nuts whilst the focal subject is in the outdoor laboratory. *Select the infant as the focal subject, rather than the conspecific*.

Record an end opportunity event when:

- The hammer contacts the nut for the final time before the individual stops nut-cracking (i.e., does not start another nut-cracking bout or stops part way through a nut-cracking bout); *or*
- The point when the hammer contacts the nut for the final time before the individual gets distracted for ≥ 1 minute (for example). In this case, start a new opportunity event at the point when they lift the hammer to strike the nut again; *or*
- The point when the hammer contacts the nut for the final time before the individual is no longer on screen (for example, because the camera pans away). In this case, start a new opportunity event when they lift a hammer to strike a nut again when they are next on screen; *or*
- The focal subject walks out of shot from the camera and you are not certain they are still in the outdoor laboratory (for example, because they do not become visible again). In this case, stop recording the opportunity event at the last point the focal subject was visible in the outdoor laboratory whilst the mother was nut-cracking.

Double click code in ethogram or press keyboard shortcut.

Do not record an end opportunity event when:

- The maternal model is eating the extracted kernel between nut-cracking bouts.
- The maternal model gets distracted for < 1 minute.

- The focal subject walks out of shot from the camera but you are certain they are still in the outdoor laboratory (for example, because the camera pans to then shortly after, because they are an infant and so are always accompanied by their mother).

Total Visibility. The continuous period of when the focal subject's mother is on camera whilst the focal subject is in the outdoor laboratory. *Select the learner as the focal subject, rather than the mother. Record each total visibility event as a state event.*

Start recording a total visibility event:

- In the first frame the mother is visible on camera.

Double click code in ethogram or press keyboard shortcut. START will appear in the "type" column.

Stop recording a total visibility event:

- In the last frame the mother is visible on camera. Start recording a new total visibility event in the next frame the mother becomes visible on camera again.

Double click code in ethogram or press keyboard shortcut. STOP will appear in the "type" column.

Modifiers

Modifiers are attributes of behaviours that must be inputted once the behaviour has been recorded. Here, you will be required to select modifiers separately for peering events, opportunity events, bouts, and behavioural episodes. A window will automatically appear for you to input these events, as outlined below.

Start Peering

Model name. Record the name of the individual the focal subject was peering at during their nut-cracking bout. *Select from list by clicking on the option. Select "Unknown" where the nut-cracking model cannot be identified from the footage (for example, if they have their back*

to the camera and they cannot be identified from contextual footage). If the individual becomes identifiable throughout the course of the video, edit the previous "Start Peering" events to account for the updated information.

Maternal model. Record whether the model is the learner's mother or not. *Select from list by clicking on the option. Select "Unknown" where the nut-cracking model cannot be identified from the footage (for example, if they have their back to the camera and they cannot be identified from contextual footage). If the individual becomes identifiable throughout the course of the video, edit the previous "Start Peering" events to account for the updated information.*

- Yes
- No
- Unknown

End Peering

Complete peering event. Whether or not the full peering episode was able to be recorded or not because of the video footage itself.

Record *Yes* if:

- The full peering event was recorded.

Record *No* if:

- If the peering period was only partially recorded (for example, if the camera panned away from individual before the end of the peering event, if the video ended before the end of the peering event); *or*
- If the peering was only visible for part of the event because the individual becomes occulated part way through the event (for example, a conspecific moves in front of the focal subject; the focal subject repositions themselves to be behind an object, such as a tree).

*If you record "*No*", only record the remaining modifiers which are known from the footage available, for example if the model was the mother and the model's name. Record "Length" as "None" unless 3 seconds or more has already passed.*

Whole bout. Record whether the learner was peering for the whole nut-cracking bout or not. If the peering event is not complete (i.e., you recorded "*No*" to the modifier above) then record "*Unknown*".

Model name. Record the name of the individual the focal subject was peering at during their nut-cracking bout. *Select from list by clicking on the option. Select "Unknown" where the nut-cracking model cannot be identified from the footage (for example, if they have their back to the camera and they cannot be identified from contextual footage). If the individual becomes identifiable throughout the course of the video, edit the previous "Start Peering" events to account for the updated information.*

Maternal model. Record whether the model is the learner's mother or not. *Select from list by clicking on the option. Select "Unknown" where the nut-cracking model cannot be identified from the footage (for example, if they have their back to the camera and they cannot be identified from contextual footage). If the individual becomes identifiable throughout the course of the video, edit the previous "Start Peering" events to account for the updated information.*

- Yes
- No
- Unknown

Model tolerance. Record whether the model permitted any of the following learner behaviours within the nut-cracking bout. *Select <u>all</u> that apply from the list by clicking on the option(s).*

<u>Record *Not Applicable* if:</u>

- The learner did not attempt to scrounge the kernel, interact with the model or the model's tools or be proximate to the model during the nut-cracking bout.

Record *scrounge* if:

- The model permitted the learner to take the extracted kernel to eat themselves.

Record *tool interaction* if:

- The model permitted the learner to touch either one or both stones in the tool composite during the nut-cracking bout.

Record *model interaction* if:

- The model permitted the learner to interact with them (for example, touching arm or body of model, climbing on model) during their nut-cracking bout.

Record *proximity* if:

- The model permitted the learner to be ≤ 1 metre (m) away from them during the bout. In this case, the learner was not interacting with the model, but was merely close to the focal subject and peering at the nut-cracking bout.

Model intolerance. Record whether the model expressed intolerance towards the learner.

Select all that apply from the list by clicking on the option(s).

Record *Not Applicable* if:

- The model did not express intolerance towards the learner during the bout.

Record *physical* if:

- The model physically rejected or resisted a learner's attempts to scrounge, interact with the model or the tools, or be proximate whilst they were nut-cracking (for example, shoving, hitting, or chasing the learner; not allowing or resisting a scrounge attempt by continuing to eat the extracted kernel).

Record *vocal* if:

- The model vocally rejected or resisted a learner's attempts to scrounge, interact with the model or the tools, or be proximate whilst they are nut-cracking (for example, grunting, barking, or screaming). Barking sounds like 'waa,' 'waaoo' or 'aaoo,' and are shorter than screams (Crockford & Boesch, 2003, p. 117).

Nut-cracking conspecifics. Record the name of any other conspecific who was also engaged in a nut-cracking bout during the peering event. *Select all that apply from the list by clicking on the option(s). Record "Unknown offscreen" if you can hear nut-cracking off-camera during the peering event. Record 'None' if there were no other conspecifics nut-cracking at that time.*

End Opportunity

Complete opportunity. Whether or not the full opportunity was able to be recorded or not because of the video footage itself. *Select from list by clicking on the option.*

Record *Yes* if:

- The full opportunity was recorded.

Record *No* if:

- The opportunity was only partially recorded (for example, if the camera panned away from individual before the end of the opportunity, if the video ended before the end of the opportunity).

Learner behaviour. Which behaviour the infant is engaged in when their mother is cracking nuts. *Select all that apply from the list by clicking on the option(s).*

Record *Solitary Play* if:

- The focal subject is engaged in play by themselves.

Record *Social Play* if:

- The focal subject is engaging in non-aggressive behaviours such as wrestling, slapping, or chasing with at least one other individual.

Record *Object Play* if:

- The focal subject is, either independently or with at least one other individual, throwing or shaking objects available in the environment.

Record *Behavioural Episode* if:

- The focal subject is engaged in a behavioural episode, or multiple behavioural episodes.

Record *Bout* if:

- The focal subject is engaged in a nut-cracking bout, or multiple nut-cracking bouts.

Record *Feeding* if:

- The focal subject is eating whilst their mother is nut-cracking. This includes nursing from their mother.

Record *Drinking* if:

- The focal subject is drinking water whilst their mother is nut-cracking.

Record *Resting* if:

- The focal subject is resting, alone or with their mother, whilst their mother is nut-cracking.

Record *Peering* if:

- The focal subject is peering at *another individual* crack nuts whilst their mother is nut-cracking.

Record *Clinging* if:

- The focal subject is clinging to their mother whilst she is nut-cracking.

Record *Unknown* if:

- The focal subject is known to be in the outdoor laboratory, but their behaviour is not fully visible whilst their mother is nut-cracking.

Scrounge events. Record how many times the focal subject took the kernel extracted by the maternal model to eat themselves. Only record these scrounge events where the focal subject took the kernel but did not watch the nut-cracking bout. If the focal subject watched the bout (i.e., was peering) and then scrounged the kernel, record the episode using the *Model tolerance* modifier in the *End Peering* point event. *The exact number must be manually inputted using your keyboard. If there are no scrounge events, record the value as 0.*