Sequential Organization, Development, and Senescence of Stone-Tool Use Across Wild Chimpanzee Lifetimes



Elliot Howard-Spink

The Queens College and the Department of Biology
University of Oxford

A thesis submitted for the degree of Doctor of Philosophy
Trinity Term, 2023

In dedication to the four chimpanzees remaining at Bossou:
Jeje, Jire, Fanle and Fanwaa.

Abstract

Many behaviours of animals are comprised of individual units (such as actions, calls, or gestures), which are performed over space and time. These sequential behaviours can span vast temporospatial scales, and include the fast-paced movements of a fly's limbs when grooming its body, as well as the vast migrations of elephants with the turnover of seasons. To produce a sequential behaviour, animals are faced with making an extended number of decisions surrounding which behavioural units to elicit in relation to all others in the sequence. Thus, understanding how animals organize sequential behaviours offers a unique and valuable window into understanding their cognitive processes. Research into the organization of sequential behaviours often focuses on those which are considered to be in some way 'complex'; such as the highly flexible combinations of notes in birdsong, or the elaborate sequences of actions performed by humans during the production and use of highly technical tools. Among animals, humans are believed to possess a suite of particularly complex sequential behaviours, including language; musical abilities; and as mentioned, tool production and use. Nonhuman animal (henceforth animal) models serve as valuable systems for understanding the environmental contexts that select for the evolution of complexity within specific sequential behaviours; and of all animals, nonhuman primates (henceforth primates) offer a unique model for understanding the evolution of human behaviours, especially great-apes, given the likely homologous origins of behavioural similarities with humans. Thus, how great-apes organize, acquire, and retain sequential behaviours throughout their lives is a key question for understanding their cognition, and the evolutionary processes that shaped our own.

This thesis explores how wild West-African chimpanzees (*Pan troglodytes verus*) organize their actions during one of their most complex tool-use behaviours: the cracking of hard-shelled nuts using hammer and anvil stones (nut cracking). The data for this thesis are collected from a small population of chimpanzees living in the forests surrounding the village of Bossou, Guinea. The chimpanzees at Bossou have been studied for many decades, and perform a wide range of tool-use behaviours. Of these tool-use behaviours, nut cracking has been studied for over 30 years at Bossou through the use of an outdoor laboratory: a natural clearing in the forest where researchers deposit piles of nuts, and a selection of stone tools. Chimpanzees are free to visit the outdoor lab as part of their daily ranging behaviours, and when present, spontaneously engage in nut cracking, which is recorded by researchers using video cameras. Following the decades of data collection at Bossou, videos of chimpanzees engaging in nut cracking at the outdoor laboratory have been organized into a longitudinal video archive (the Bossou Archive). This data-rich video archive presents a unique opportunity to characterize the sequential behaviours of chimpanzees during tool-use, and allows for the behaviours of individual chimpanzees to be studied longitudinally, across extended periods of their lives.

This thesis interrogates three key questions: how do chimpanzees organize actions during their stone tool-use behaviours? How do chimpanzees acquire the repertoire of actions which allows for efficient stone-tool use? And finally, how do stone-tool use behaviours of chimpanzees change as they experience progressive old-age? In chapter 2, I coded over 8000 individual actions performed by chimpanzees during nut cracking, and draw upon the mutual information (MI) between actions in sequences to evidence that chimpanzees most likely structure sequences of actions hierarchically during tool-use behaviours, and produce nonadjacent dependencies between elements (a key property of human sequential action and language). In chapter 3, I developed upon this finding by programming a bespoke dictionary-based compression algorithm, which identified a number of candidate subroutines (shorter subsequences of actions) which are likely associated with this hierarchical organization. In chapter 4, I investigated how the repertoires of actions used by chimpanzees develops between one and eight years of age, and compared this developmental trajectory with the behaviours of adults, using over 24,000 coded actions. This chapter suggests that chimpanzees first explore many possible solutions to nut cracking, and once the skill is successfully acquired, refine their strategies across many years through pruning the action repertoire. In chapter 5, I investigated how the nut cracking behaviours of wild chimpanzees change as they experience progressive old-age, and report that tool-use behaviours of chimpanzees are subject to senescence, but, much like in humans, the extent and rate of senescence varies between individuals.

Ultimately, this thesis describes the structure of nut cracking behaviours of wild chimpanzees at an exceptional granularity, and traces how these behaviours change across individual lifetimes. Additionally, this thesis employs a number of highly computational methods for the study of sequential organization in animals, and provides several methodological considerations for further research in this field. The results of this thesis directly feed into a number of existing hypotheses surrounding the evolution of complex behaviours of humans, including early hominin stone-tool use; linguistic syntax, as well as processes of social learning, and the evolution of human culture.

Acknowledgements

At many points during my DPhil, I didn't expect to reach the point of writing a thesis. The summation of such a long period of work felt too intangibly vague, the obstacles too great, and the learning process too steep. Yet, at every moment when doubt reared its head, a kind voice would encourage me to keep going, and to see it through. I would like to take a short moment to thank the owners of these voices.

I would like to thank both of my supervisors, Dora Biro and Thibaud Gruber, who despite us being separated by great distances during the majority of my DPhil, consistently cheered me on. I have learnt so much during this process, about myself and science, and I appreciate the support you both offered throughout this journey.

Additionally, I would like to thank the wonderful members of different lab groups I have worked alongside during my DPhil. In particular, I would like to thank Tom Hart and Laure Cugnière for welcoming me into their lab group during the final years of my thesis. Also, I would like to thank all the members of Dora's and Tom's research groups, as well as all the members of OxNav, for making the department as fun and as welcoming as possible.

Thirdly, I would like to thank both of my examiners, Simon Townsend and Tim Guilford, for taking the time to assess my thesis, as well as for the enjoyable discussion that we shared during the viva. Similarly, I greatly appreciate the support and advice provided by Matthew Husband, who assessed my work at both transfer and confirmation of status, and provided useful insight which ultimately influenced the content of this thesis. I would also like to extend thanks to Victoria Forth, who provided support and encouragement throughout my studies on the NERC Doctoral Training Partnership.

I am grateful to so many people for providing me with the energy, love, and compassion to continue with this work. This includes all the various friends who supported me throughout this DPhil (I will not specify whether these names are in any particular order; instead, I will let them fight among themselves): Benedict, Lauren, Simona, Jonny, Alex, Alison, Jon, Nacho, Saran, Alice, Freya, James, Srishti, Stuart, Tamanna, Harriet, Eve, Bex, Rizwaan, Lizzy and Fergus. I would also like to thank my family (Heather, Colin, Ben and Frances), who even when unsure of precisely what I was doing in this 5-year long stint - "*it's on monkeys?*" - were unwaveringly supportive. Furthermore, I express my sincere gratitude for the support and guidance provided by Ellie Berthier and Jane Enticott, who helped be to find the skills and courage to believe in myself, and to persevere with my research.

I would like to thank all of my collaborators who provided data and advice during my DPhil. In particular, I would like to thank all the researchers who have been associated with data collection at Bossou, and the curation of this data into the Bossou archive.

Without this sustained effort, this thesis would not be possible. Additionally, I would like to thank everyone who welcomed me into the world of primate research, particularly when attending conferences. This includes Mael Leroux, Kirsty Graham, Alex Mielke, Alex Gergiev, Stuart Watson and Stuart Semple, as well as the wider research community at the Primate Society of Great Britain. Importantly, I would like to give a **massive** thank you to anyone who ever replied to one of my (many) tweets asking for help with statistics, R or Python. Whoever you are, you are my rock.

Now for a few more obscure ones! I'd like to thank Jat Hayer, my former driving instructor, for teaching me how to drive during my DPhil. This didn't directly link to my research, but he was a friendly face to see every week, and a great instructor (importantly, this is my acknowledgements section, and I will thank who I like). Likewise, I would like to thank all my school teachers. Going from a state school to university is tough, and going on to do a DPhil is even tougher. I wouldn't have had the skills or ambition to do either without their hard work. I therefore offer them all a sincere thank you.

Finally, I would like to thank Freddy Legg. For three years, Freddy bore the brunt of my emotions during this DPhil, and yet was an unstoppable force of positivity. At every moment I was overcome with stress, run down by failures, or apathetic to my own success, he helped me find solace, compassion and joy. His unbounded love and support during this difficult process have been a privilege, and I cannot imagine having finished it without him.

Author Contributions

All work presented in this thesis is primarily my own.

This thesis is comprised of an introduction, four data chapters, and a discussion chapter. Each of the data chapters (chapters 2-5) are presented in a standalone journal format.

My supervisors, Dora Biro and Thibaud Gruber, assisted in the conception of ideas for each chapter; provided advice during the collection and analysis of data; and supported my writing of this thesis with helpful feedback.

Tetsuro Matsuzawa and Misato Hayashi have conducted and overseen data collection at Bossou for many years, and during this time, many KUPRI researchers, as well as research assistants, have contributed to data collection. Additionally, Daniel Schofield contributed heavily to the curation of the Bossou archive, with support from Susana Carvalho. Without the hard work of these individuals, this thesis could not exist.

Tim Sainburg provided statistical advice for chapter 2.

Anna Ahlberg, Melissa Birtles, and James Hubbard assisted with data collection for chapter 4.

I would like to acknowledge the use of the University of Oxford Advanced Research Computing (ARC) facility in carrying out this work: http://dx.doi.org/10.5281/zenodo.22558.

Table of Contents

Chapter 1: General Introduction **9**

1.1.1 Sequential behaviours *10*

1.1.2 Organising a sequential behaviour *12*

1.1.3 Methods to characterise systems of sequential organization *16*

1.1.4 Sequential behaviours in primates: manual actions and tool-use. *20*

1.1.5 Tool-use at old-age: senescence in wild primates *23*

1.1.6 Nut cracking as a case study in the organisation, development, and senescence of primate tool-use *25*

1.1.7 The chimpanzees of the Bossou forest *28*

1.1.8 Thesis outline *30*

1.1.9 Figures *32*

1.2.0 References *34*

Chapter 2: Nonadjacent Dependencies and Syntactic Structure of Chimpanzee Action During a Natural Tool-Use Task **42**

2.1 Summary *44*

2.2 Introduction *44*

2.3 Results *50*

2.4 Discussion *57*

2.5 Figures *68*

2.6 Tables *71*

2.7 Methods *74*

2.8 References *83*

2.9 Supplementary Materials *88*

Chapter 3: Hierarchical Subroutines in Chimpanzee Nut Cracking are Identifiable Through Dictionary-Based Compression **102**

3.1 Abstract *103*

3.2 Introduction *104*

3.3 Methods *109*

3.4 Results *118*

3.5 Discussion *123*

3.6 Figures *134*

3.7 Tables *136*

3.8 References *139*

3.9 Supplementary Materials *143*

Chapter 4: Exploration and Pruning of Action Repertoires During the Development of Chimpanzee Tool-Use **155**

4.1 Abstract *156*

4.2 Introduction *157*

4.3 Methods *162*

4.4 Results *168*

4.5 Discussion *173*

4.6 Figures *181*

4.7 Tables *184*

4.8 References *186*

4.9 Supplementary Materials *190*

Chapter 5: The Impact of Old Age on Tool Using Abilities Varies in Wild Chimpanzees **214**

5.1 Abstract *215*

5.2 Introduction *216*

5.3 Methods *220*

5.4 Results *228*

5.5 Discussion *233*

5.6 Figures *242*

5.7 Tables *246*

5.8 References *249*

5.9 Supplementary Materials *255*

Chapter 6: General Discussion **265**

6.1.1 Summary of results *266*

6.1.2 Nut cracking as a sequential behaviour *268*

6.1.3 Nut cracking across lifetimes: development *271*

6.1.4 Nut cracking across lifetimes: senescence *274*

6.1.5 Implications for the evolution of human sequential behaviours *278*

6.1.6 Asocial learning of sequential manual actions and the evolution of cumulative culture *282*

6.1.7 Computational methods for characterizing sequential organization *285*

6.1.8 Study Limitations *286*

6.1.9 Concluding remarks *288*

6.2 References *288*

Chapter 1

General Introduction

1.1.1 Sequential behaviours

Many behaviours of animals are composed of discrete elements, which are organized into specific sequential orders. Some behaviours are highly conspicuous for their employment of sequential systems of organisation, such as the elaborate songs of cetaceans and songbirds (Allen, 2019; Berwick et al., 2011); the complex sequences of manual actions performed by apes during challenging foraging tasks (Byrne et al., 2001); or even the exceptionally sophisticated systems of human language, which vary around the world (Chomsky, 1995). Yet, sequential organisation is not just a feature of uniquely complex behavioural phenomena. The task of organising behaviours into sequences is just as apparent when a drosophila fly combines limb movements into stereotyped sequences of grooming behaviours (Dawkins, 1976; Dawkins and Dawkins, 1976), or when a roundworm navigates towards a stimulus by coordinating undulations of its body (Gomez-Marin et al., 2016).

Behaviours are 'sequential' if they require animals to make numerous decisions across a period of time, with these decisions resulting in the elicitation of one or multiple behavioural units (such as a call, or limb movement), all aimed towards a common goal (Dawkins, 1976). Arguably, the majority of animal behaviours involve some form of sequential organization (Jensen et al., 1986); however, the decision-making processes which generate such sequences may differ between species. These decision-making processes may be mentally explicit, like when a dancer learns the steps to a new dance; or mentally 'implicit', such as step-wise movements of one leg in front of another whilst walking through a field. These decisions can happen over small spatial scales during extremely short time frames; for example, during the production of human speech, speakers must precisely organize the movements of the lips, tongue and jaw across the scale of milliseconds (Ostry et al., 1996). Conversely, sequential behaviours can also span large spatiotemporal scales, such as when African Elephants (*Loxodonta africana*) flexibly organize routes across home ranges by planning a series of waypoints, and navigate to these waypoints using an extended number of steps and turns (Presotto et al., 2019).

Sequential behaviours include both those which are genetically innate to animals, such as the complementary movements of a spider's legs and thorax as it progresses through the stages of building a web (Corver et al., 2021; Simpson and De Bivort, 2021); however, they can also be acquired during the lifetime of an individual, either through processes of social or asocial learning. In contrast to a newly hatched spider possessing the ability to build a web, no human is born knowing how to play the violin, or dance the Fandango. Thus, the need to organise behaviours into sequences is a challenge which

faces many, if not all, animals, with these behaviours being performed across an array of spatiotemporal scales, and acquired through a number of different means.

Precisely how animals combine atomic units of behaviours to achieve their desired goals has been a focal point of scientific inquiry for many decades (Allen, 2019; Berwick et al., 2011; Byrne, 2007; Chomsky, 1956; Dawkins, 1976; Friederici, 2020; Genty and Byrne, 2010; Hauser et al., 2014; Lashley, 1951; Mielke and Carvalho, 2022). Sequential behaviours offer a valuable window through which we may understand the cognitive systems of animals (Byrne et al., 2001). Whilst generating the sequence of actions needed for a given behavioural goal, animals are required to incorporate information surrounding the steps previously taken to realise a goal (Seeds et al., 2014); the current organisation of their body plan (which is constantly changing over time; Corver et al., 2021; Simpson and De Bivort, 2021); and the state of the external environment (Corat et al., 2016; Dawkins, 1976; Simpson and De Bivort, 2021); and integrate this information into a course of goal-directed action. The organisation of sequential behaviours in space and time is therefore complex, and many questions persist surrounding the cognitive systems which underpin them (Petkov and ten Cate, 2020).

The sequential behaviours of animals are also important models for understanding the evolution of the highly complex sequential behaviours of humans, especially in the cases of human language (Arbib, 2005; Berwick et al., 2013; Fitch et al., 2005; Hauser et al., 2014, 2002) and technology (Bril, 2015; Bril et al., 2012; Carvalho et al., 2013; Meulman and Van Schaik, 2013; Nonaka et al., 2010; Stout et al., 2021, 2014; Stout and Chaminade, 2009) which are questions at the forefront of research in biological anthropology. Through studying the organisation of behaviours by taxonomic groups which are phylogenetically both proximate and distant to humans, scientists may uncover important clues surrounding the evolution of these highly generative behavioural systems (Aamodt et al., 2020; Berwick and Chomsky, 2013; Bril et al., 2012; Carvalho et al., 2013; Collier et al., 2014; Engesser et al., 2019; Hauser et al., 2002; Leroux and Townsend, 2020; Meulman and Van Schaik, 2013; Townsend et al., 2018). This includes the use of animal models of behaviours which likely share homologous origins with those of humans, such as the tool-use behaviours of humans and non-human primates (Bril et al., 2012; Carvalho et al., 2013; Meulman and Van Schaik, 2013) as well as behaviours which evolved separately to those of humans; for example, the use of birdsong as a comparative model for the evolution of complex communicative syntax (Berwick and Chomsky, 2013). These models are invaluable for understanding when, how, and why complex sequential behaviours evolve, and therefore have the

capacity to inform the formulation of likely models concerning the evolution of uniquely complex human behaviours.

1.1.2 Organising a sequential behaviour

The requirement for animals to make successive decisions when producing sequential behaviours invites the question: how is this decision-making process organized?

The simplest proposed model for the organisation of sequential behaviours is through **serial chaining** (Anderson and Matessa, 1997; Henson et al., 1996; Lashley, 1951; Terrace, 2005; Washburn, 1916; Watson, 1920). During serial chaining, the performance of one behavioural element leads to the elicitation of the next in a sequence. The performance of a second element then stimulates the production of a third, as so forth, ultimately producing an observed sequence of behaviours. Serial chaining is theorised to require minimal cognitive resources to produce a behaviour. Animals are not required to remember any elements of a behaviour which they have already produced except for the one which was performed most recently, thus greatly reducing requirements for working memory (Hauser et al., 2002; D. Isac and Reiss, 2013). For behaviours which are genetically wired into organisms, serial chains may emerge through the construction of a suppression hierarchy: a linear hierarchy where all possible actions are suppressed, and the performance of one action relieves suppression of the next in the sequence. Such linear suppression relationships are thought to be important for the execution of motor programs in invertebrates, and have been demonstrated as useful models for understanding the sequential manual actions used by *Drosophila* flies during grooming (Seeds et al., 2014; however, this system may be embedded within higher-order systems of action organization for *Drosophila* flies, see Berman et al., 2016; Dawkins and Dawkins, 1976). Theories of serial chaining have also been proposed for learnt behaviours, dating back to early work in the field of behaviourism (Washburn, 1916; Watson, 1920). For learnt behaviours, serial chaining is possible through the construction of chains of associatively learnt rules, such as '*If i have just performed action* X*, then perform action* Y' and '*if I have just performed action* Y*, perform action* Z*'* (Byrne, 2005; Terrace, 2005; Washburn, 1916; Watson, 1920).

Due to their inherent mechanistic simplicity, serial chaining continues to be considered a null model for the organization of both innate and learnt sequential behaviours in animals (Kershenbaum et al., 2014). Whilst serial chaining is a computationally simple system of producing a sequence (and is

therefore parsimonious), many have questioned the efficacy of serial chains when characterising the range of sequential behaviours observed in nature (Byrne et al., 2013; Dawkins, 1976; Lashley, 1951; Terrace, 2005). In particular, several criticisms have been raised surrounding the ability of serial chaining to support increasingly complex behaviours (Dawkins and Dawkins, 1976; Lashley, 1951; Terrace, 2005). Serial chains struggle to produce streamlined, goal-directed behaviours when multiple overlapping behavioural strategies exist for an individual (D. Isac and Reiss, 2013). For example, if a bird possesses two songs in its repertoire, both of which contain a common central note, structuring by serial chaining predicts that once reaching this central note, it is feasible that a bird may switch from singing the beginning of one song to the end of another, as its decision of how the song should progress after this central note has no bearing on the notes which came before it. Such an example may not appear detrimental in the case of a bird's song (which for several species are flexibly arranged, see Berwick et al., 2011); however, if taking the example of primate tool-use, the repeatability with which actions such as grasping, biting, peeling and striking are used across different contexts means that a system of organisation by serial chaining becomes theoretically less probable (Byrne and Russon, 1998; Terrace, 2005).

This issue stems from the 'memoryless' aspect of sequence production through serial chaining, and led to a seminal paper published by Karl Lashley in 1951 which argued that serial chaining would fail to explain the organization of sequential behaviours which exhibit nonadjacent dependencies between elements (Lashley, 1951). Taking an example from human language, case agreements would not be possible if structured through serial chains. For example, if the sentences '*the dog excitedly eats its dinner*' and '*the dogs excitedly eat their dinner*' were produced through learnt associative chains, this system would frequently produce the erroneous combinations, such as '*the dog excitedly eat their dinner*'; yet, examples of such errors are rare in conversation (Chomsky, 2002a; D. Isac and Reiss, 2013; Sainburg et al., 2019). The presence of nonadjacent dependencies between elements of a sequential behaviour are well documented for humans, including in language (Chomsky, 2002b; Isac and Reiss, 2013; Sainburg et al., 2019), manual actions (Greenfield, 1991; Lashley, 1951; Sainburg et al., 2020), and music (Asano and Boeckx, 2015; Cheung et al., 2018; Lerdahl, 2015), and Lashley drew upon examples from language and manual actions to argue that an alternative mechanism for the organization of human behaviour is required.

Thus, Lashley theorized that human sequential behaviours were **hierarchically organized** (Lashley, 1951), specifically that behaviours were organized using **branching hierarchies** (Dawkins, 1976). Branching hierarchies (henceforth 'hierarchies') organise behaviours through the division of wider goals into **subgoals**, which may themselves be split into smaller subgoals, and so on until reaching the atomic elements of a behaviour (Lashley, 1951). Hierarchies therefore structure behavioural elements into tightly linked **subroutines** (also sometimes referred to as 'motifs'), which may be combined with other subroutines to produce higher order structures (Byrne et al., 2013). This combinatorial process continues to ultimately produce a sequence which contains all required behavioural elements to address an individual's goal, with elements organised to address the constituent subgoals of a behaviour (Lashley, 1951).

Compared to serial chaining, the hierarchical organisation of behaviour requires the use of additional cognitive resources. When organizing behaviours hierarchically, an individual must possess some means to parse goals into subgoals, and also must recall and monitor the progression of a behaviour across more than one level of organisation simultaneously (Byrne et al., 2013; Dawkins and Dawkins, 1976; D. Isac and Reiss, 2013). Therefore, the hierarchical organisation of behaviour is theorised to place a greater burden on a number of systems of cognition, most notably on executive functioning and working memory (Read, 2008; Wilson et al., 2020). However, many researchers argue that through systems of hierarchical organisation, these cognitive burdens are offset through the ability to readily produce flexible, goal directed behaviours (Chomsky, 2002b; Dawkins, 1976; Fitch et al., 2005; D. Isac and Reiss, 2013; Lashley, 1951; Terrace, 2005). Repeatable subroutines may be recombined to confer flexibility, allowing for greater generativity, including the possibility for behaviours to be tailored to variations in environmental contexts (Byrne, 2005; Simpson and De Bivort, 2021). Most importantly, the hierarchical organization of behaviour permits the emergence of nonadjacent dependencies between sequence elements, where subroutines may be embedded within other subroutines. Taking another example from human language, the sentence '*the flower [that I placed in the vase] is yellow*' can be understood as two clauses. The clause 'the flower is yellow' spans one hierarchical level, and at a deeper, nested level is the relative clause 'that I placed in the vase'. As the relationship between the head noun phrase, 'the flower', and the verb phrase 'is yellow' are at the same hierarchical level, they are directly related in the sentence, and the reader intuitively grasps that it is in fact the flower which is yellow, and not the vase (which is closer to the adjective in the sentence in linear

space). Taking another example from the domain of manual actions, an actor may open a door by grasping and turning the handle, before pushing on the door. However, when approaching the same door, the actor may grasp a handle, then begin performing actions to open a lock (thus, embedding a subsequence within the sequence), before continuing to turn the handle, and push the door. In both examples, grasping and twisting a door handle share a dependency: a handle can only be twisted once it has been grasped. However, these two actions may be separated in time through the embedding of a number of additional actions.

Therefore, when considering highly flexible systems of behaviour, such as human language and tool-use behaviours, hierarchical models offer more likely explanations than those of serial chaining. Some of these behaviours can also be understood as profiting from a mixture of serial and hierarchical organization. One such aspect is the construction of phonemes (meaningless sounds) into words, where the combinations of phonemes which are permissible within a language can be successfully predicted by observing how they combine with neighbouring phonemes in words (Kaplan and Kay, 1994). Words are then hierarchically arranged using the rules of syntax (Chomsky, 2002b; Isac and Reiss, 2013). Therefore, human language exhibits a system of behavioural organisation which concurrently balances serial and hierarchical organisations of behaviour, a phenomenon named ‘duality of patterning’ (Hockett, 1960).

Despite rapid uptake in the use of hierarchical models to understand human behaviours, models surrounding the hierarchical organization of sequential behaviours in nonhuman animals progressed more slowly, in part due to the belief of some that animal behaviours were too simple to warrant the additional cognitive costs associated with hierarchical behavioural organization (Terrace, 2005). More recent research has demonstrated that hierarchical systems of organization are detectable within the behaviours of animals; however, the extent to which it is widespread across the animal kingdom is unclear. Many of the songs used by animals appear to contain some form of hierarchical organisation (Miksis-Olds et al., 2008; Sainburg et al., 2019; Suzuki et al., 2006), with the songs of birds possibly sharing a similar ‘duality of patterning’ as seen in human language (Sainburg et al., 2019). However, animal songs represent a form of behaviour which is restricted to a small number of taxonomic groups, so the extent to which the organisation of animal songs may be generalised across a broader range of species is limited. Moreover, the systems of organization employed by a particular species may vary across domains of behaviour. For example, many researchers have theorised that the manual

skills used by primates during foraging tasks should involve some form of hierarchical organisation (although further work is required in this area to assess the validity of such claims; Byrne et al., 2013; Byrne and Russon, 1998; Matsuzawa, 1996; Sanz and Morgan, 2010; Vereijken and Whiting, 1998). However, despite habitually producing sequences of gestures and vocalisations during communication, primates do not appear to produce communicative sequences which are more complex than can be expected under serial chaining (Fitch and Hauser, 2004; Hauser et al., 2002; ten Cate and Okanoya, 2012; although the comprehension of such units may involve the consideration of multiple units at a time; Leroux and Townsend, 2020; Watson et al., 2020). Therefore, structuring mechanisms may vary both between species and within a species' repertoire of behaviours.

Serial chaining and hierarchical structuring are not the only two possible mechanisms through which a sequence may be constructed (Sainburg et al., 2019); however, these two mechanisms are at the centre of an ongoing debate surrounding the complexity of systems of behavioural organization in animals. Understanding how animals generate sequences of behaviours is a central question for understanding their cognition; this includes the need to understand the taxonomic distribution of different structuring mechanisms, and also if and how structuring mechanisms vary between behaviours. These questions intersect with the intriguing puzzles of how and why humans have evolved so many hierarchically elaborate behaviours. For these questions, the hierarchical behaviours of animals offer key insight into the evolutionary scenarios that select for highly hierarchical organisations of behaviour.

1.1.3 Methods to characterise systems of sequential organization

Whether the combinatorial systems of nonhuman animals follow a process of serial chaining or hierarchical organisation is a challenging question, as in both instances behaviours are expressed element-by-element over the course of time.

Serial chains of behaviours may be understood within the framework of first order **Markov models**. In a Markov model, the elements of a behaviour can be represented as nodes of a network, and the likelihood of transitioning between different behavioural elements is modelled through the use of weighted edges (Gagniuc, 2017). Two positions in the network represent start and end points. When the model runs, it moves from the start point to a node connected to this start point, and once reaching that node, elicits the production of a behaviour. At each subsequent time-point, the model moves to a

new node, with the decision of which node to move to being determined by the weighted edges of the network (note: for some models, it is possible to stay at the same node over multiple time points, eliciting repetitions of the same behaviour). This process continues until the model reaches the end point, and the production of behavioural elements stops.

Markov models readily approximate the behaviour of serial chaining, as each element produced by the model is predicted by the element which precedes it. Markov models can be trained using the observed behaviours of animals, where the frequency with which an animal transitions from one type of behavioural element to another can be used to specify the model's transition matrix (a matrix which describes the probability that the model should transition between different nodes at any given timestep; Katahira et al., 2011; Kershenbaum et al., 2014; Sainburg et al., 2019; Yoon, 2009).

Whilst Markov models can, in theory, describe neighbouring transitions between elements of any sequential behaviour, Markov models are often not able to faithfully re-generate sequences which were produced hierarchically. As previously discussed, serial chaining (such as is performed in the case of Markov models) cannot balance flexibility and goal-directedness during sequence generation, and fail to account for nonadjacent dependencies during sequence generation (apart from certain circumstances where a highly stereotyped corpus is provided; see Chapter 2). Therefore, alternative models are required, both to determine whether a sequential behaviour contains hierarchical structuring (and therefore should not be modelled using Markov processes), and if so, how the hierarchical organisation of a behaviour takes place.

Through long-term observations of sequential behaviours, the **qualitative descriptions** of behaviours can offer indications of the presence of hierarchical relationships. Qualitative descriptions have been used to argue for the hierarchical organisation of manual actions in animal behaviours, particularly in the feeding and tool-use behaviours of great apes (Byrne et al., 2013; Byrne and Russon, 1998; Sanz and Morgan, 2010). These descriptions focus on the identification and description of frequently recurring **subroutines** of behaviour by observers (Byrne et al., 2013; Byrne and Russon, 1998). However, these descriptions are limited in the extent to which they may rule out simpler systems of sequential organisation. Many behaviours could be described as containing frequent repetitions of short subsequences, including those produced by highly directed systems of serial chaining, and therefore the hierarchical description of these sequences is not, in itself, sufficient to evidence hierarchy (Vereijken and Whiting, 1998).

A second method to characterise whether hierarchical relationships exist in sequential behaviours is through the use of a **clustering analysis** (Dawkins, 1976; Mielke and Carvalho, 2022)**.** During clustering analyses, networks reflecting the transition probabilities between different behavioural elements are constructed. This process is identical to the formation of Markov models; however, networks differ in that they are not used for generating sequences. Hierarchical systems of organisation produce networks with higher rates of clustering than is seen in serially ordered behaviours, as actions which reoccur in subroutines are closely linked (Mielke and Carvalho, 2022). However, clustering analyses have also received criticism for being limited in their ability to disentangle the formation of network clusters due to hierarchical organisations of behaviour from the presence of clusters merely through animals possessing multiple highly directed serial chains, which, when combined into a network, appear clustered (Dawkins and Dawkins, 1976).

In recent years, the use of **mutual information**, a mathematical property of sequences, has become an increasingly popular method for identifying signatures of hierarchical organisation from sequential behaviours (Miksis-Olds et al., 2008; Sainburg et al., 2022, 2020, 2019; Suzuki et al., 2006). Mutual information is a measure of how much the uncertainty surrounding the state of a particular element in a sequence (measured using entropy) is reduced by knowing the state of a previous element, including between possibly nonadjacent elements within sequences. As hierarchical systems of sequential organisation readily produce dependencies between nonadjacent sequence elements, mutual information scores between nonadjacent elements are higher than in serially chained behaviours. For serially chained behaviours, mutual information between elements separated by greater sequential distances rapidly decreases following an **exponential** decay dynamic (Lin and Tegmark, 2017; Sainburg et al., 2022, 2019), as serial chaining is limited in its ability to produce dependencies between nonadjacent sequence elements. This differs to hierarchical sequences, where the decay of mutual information is slower, following a **power-law** dynamic (Sainburg et al., 2020, 2019). In systems where both serial ordering and hierarchical organisation are employed, as I previously described for language, a **composite decay** dynamic is observed, where mutual information decays exponentially between elements which are chained together in close proximity (such as phonemes in words) and following a power-law decay between hierarchically organised elements (such as phonemes between words, which are hierarchically organised by the rules of syntax; Sainburg et al., 2022, 2019). In addition to human language, power-law decays are found in the relationships between nucleotides

in genomes (which are hierarchically arranged into codons, exons, and genes; Peng et al., 1992), as well as between notes in music (arranged into motives and phrases; Levitin et al., 2012), meaning that the decay of mutual information following a power-law is a signature of hierarchical organisation across many sequential phenomena. In the behaviours of animals, mutual information decay has been successful in revealing systems of hierarchical organisation within the communicative behaviours of birdsong (Sainburg et al., 2019) and whales (Miksis-Olds et al., 2008; Suzuki et al., 2006), suggesting that hierarchy is not an organisational property unique to the communication systems of humans.

Similarly to the recent uptake of mutual information as a signature of hierarchical organisation in animal behaviours, **compressibility** is another property of sequences which may be indicative of the processes through which they were generated (Gomez-Marin et al., 2016; Sainburg et al., 2022). Compressibility refers to the property of sequences where they may be represented using a minimal number of elements, but retain all previous information surrounding their structure (Larsson and Moffat, 2000; Nevill-Manning and Witten, 2000). Compressibility can be evaluated through the use of **dictionary-based compression algorithms**: computer programs which iteratively scan across sequences, identify frequently recurring motifs, and replace those motifs with non-terminal symbols. During replacement, the substituted subsequence is stored in a dictionary, alongside its corresponding symbol. As the algorithm passes iteratively across sequences, sequences become increasingly compressed, and a dictionary is built which documents all previous substitutions. The production of a dictionary allows for sequences to be converted back into their original form following compression, and so, this process does not lead to information being 'lost' from sequences (Nevill-Manning and Witten, 1997). Rather, compression allows for sequences to be represented as minimal descriptions of their repeating patterns of elements, which are indicators of recurrent subroutines.

During compression, hierarchical sequences often compress to a greater extent than sequences produced by serial chaining. This is because hierarchical sequences are characterised by recurring combinations of elements in the form of subroutines, which are readily selected for substitution by compression algorithms. Moreover, hierarchical sequences often also contain longer sequences of repeating elements, as animals generate actions which are directed at completing recurring, higher-order sub goals (e.g. a bird's song may contain similar combinations of notes in a phrase, but may also pass through similar combinations of phrases in a song). Thus, hierarchical behaviours readily compress due to the emergence of higher-order patterns-of-patterns (Dawkins and Dawkins, 1976;

Gomez-Marin et al., 2016). Sequences of human language (Sainburg et al., 2022), and locomotory behaviours of worms (Gomez-Marin et al., 2016) have been shown to compress to greater levels than comparable sequences generated by Markov models, suggesting that compression may be a useful diagnostic of animal sequences for uncovering systems of sequence generation.

1.1.4 Sequential behaviours in primates: manual actions and tool-use.

Primates habitually perform a wide array of sequential behaviours, including navigating between a series of resource patches during daily ranging (Janmaat et al., 2006); producing sequences of vocal and gestural signals (Clay and Zuberbühler, 2009; Genty and Byrne, 2010; Girard-Buttoz et al., 2022; Leroux and Townsend, 2020); and completing complex foraging tasks, of which many involve the use of tools (Byrne et al., 2013; Byrne and Russon, 1998; Carvalho et al., 2008; Martin-Ordas, 2020; Sanz and Morgan, 2010; Tonooka, 2001). The sequential behaviours of primates are of long-held scientific interest due to their potential to offer insight into the likely evolutionary pathways of complex human behaviours, such as language, and the production and use of highly technologically sophisticated tools. This is particularly true for primate communication (Arnold and Zuberbühler, 2012; Leroux and Townsend, 2020; Schlenker et al., 2016; Seyfarth and Cheney, 2008) and tool-use behaviours (Bril, 2015; Carvalho et al., 2013; Matsuzawa, 2001; Meulman and Van Schaik, 2013), given that they are homologues for such complex behaviours in humans. Among the primates, specific attention has been paid to the behaviours of nonhuman apes, given that their phylogenetic proximity to humans means that humans and apes diverged recently in evolutionary time, and therefore common behaviours between these two species are likely to stem from homologous evolutionary origins (Gruber and Clay, 2016).

Primates perform a wide range of tool-use behaviours (Shumaker et al., 2011); many of these behaviours are associated with **extractive foraging**, where individuals will use tools to access otherwise unobtainable food sources. Examples of extractive tool-use include long-tailed macaques using stone tools to crack open oysters (Tan et al., 2015) or chimpanzees using stick tools to perforate termite mounds before using flexible stems to “fish” out and consume termites (Boesch et al., 2020; Sanz and Morgan, 2010; Suzuki et al., 1995). However, primates also employ tools to meet several other ecological needs, including during social interactions (Boesch, 1991; Nishida, 1980), hunting (Pruetz et al., 2015), and self-care Kyes, 1988; O’Hara and Lee, 2006; see Shumaker et al., 2011, for

an extensive account of animal tool-use behaviours, including across primates). As well as using tools, some apes, including chimpanzees and orangutans, are documented producing tools from raw materials, through modifying objects prior to their use as tools to increase their efficiency (Boesch et al., 2020; Haslam, 2022; Sanz and Morgan, 2010; Tonooka, 2001). For example, chimpanzees produce "leaf-tools" for drinking by first tearing some leaves off a suitable plant, placing them inside their mouth where they are folded into a concertina-shape, and then submerging it into pools of water, before placing these leaves in the mouth to extract the collected fluid (Tonooka, 2001). In another example, chimpanzees have been documented stripping leaves off of stems, before modifying the end to produce 'brush tips' to increase the efficiency of termite fishing (Koops, 2020; Sanz and Morgan, 2010).

Tool-use behaviours by apes have been studied extensively, including their sequential organisation. Studying the sequential organisation of manual actions during tool-use is aided by the fact that tool objects offer a conspicuous means to observe the progression of a behaviour across space and time (Byrne et al., 2013). Stages of a behaviour may be readily categorised as individuals move through the process of acquiring raw materials, producing or modifying tools, combining tool-objects and substrates, and disposing of tools and waste materials. Thus, tools exist within an extended operation chain (the ***chaîne operatoire***) through which primates must organise their manual actions to achieve a number of subgoals (Carvalho et al., 2008; Sanz and Morgan, 2010; Sellet, 1993).

The organisation of actions into specific subgoals of behaviours means that primate tool use is a promising candidate for a hierarchically complex behaviour that can be studied in a taxonomic group closely related to humans. Theories surrounding the hierarchical organization of tool-use behaviours extend to both the organization of sequential actions (Byrne et al., 2013), as well as the relationships between the objects used in tool-use (Matsuzawa, 1996). Additionally, hierarchical organization has also been theorized to be central to the learning mechanisms which support the transmission of tool-use behaviours in apes (Byrne and Russon, 1998). Under **program-level imitation**, apes are theorized to observe the behaviours of knowledgeable individuals, and parse such behaviours into a hierarchically organized set of subgoals, which they then learn to address through sequences of actions generated via trial-and-error (Byrne and Russon, 1998). Such an explanation is supported through qualitative descriptions of the stages of great-ape tool use, where researchers are able to categorize stages of the *chaîne operatoire*. However, as previously mentioned, whilst these methods offer a useful model to consider how great-ape actions may be hierarchically organised, they may involve the subjective

inference of hierarchical organisation on highly serialised sequences by observers (Vereijken and Whiting, 1998). Thus, further examination is required to determine the extent to which great apes hierarchically organize their manual actions during tool-use.

Research into the tool-use behaviours of primates has also been driven by on-going debate surrounding the existence of nonhuman **animal cultures** (Biro et al., 2003; Boesch et al., 2020; Byrne, 2007; Meulman and Van Schaik, 2013; Tennie et al., 2020, 2009; Whiten et al., 1999). Several species of primates exhibit population-level differences in their repertoires of behaviours, including during social behaviours (Van Leeuwen et al., 2014), and foraging behaviours (Gruber et al., 2009; Schofield et al., 2018; Van De Waal et al., 2013; Whiten et al., 1999) including tool-use (Boesch et al., 2020; Falótico et al., 2019; Gruber et al., 2009; Van Schaik et al., 1999). Additionally, as well as populations differing in the types of tool-use behaviours that they perform, populations of chimpanzees have also been documented using different approaches to addressing seemingly identical tool-use tasks (cultural **techniques**; Boesch et al., 2020). Moreover, many of these behaviours - or at least certain aspects of them - appear to be passed between individuals through social observation, and therefore are inherited at least in part through **social learning**. However, understanding the precise mechanisms through which tool-use behaviours pass from knowledgeable to naive individuals – including what information is transmitted and how - is an ongoing challenge for scientific research. In the case of great apes, naive learners appear to pay specific attention to the end-states of behaviours, and therefore are theorised to acquire tool-use behaviours through the **emulation** of the goals of knowledgeable individuals (Call et al., 2005; Tennie et al., 2010; Tomasello, 1990) and as previously mentioned, this may also extend to emulation of subgoals prior to the end-state, through a process of program-level imitation (Byrne and Russon, 1998). The prevalence of emulation in apes is contrasted to that of human children, who during the acquisition of novel behaviours, will often pay additional specific attention to the fine-grained actions used by knowledgeable individuals, and thus are able to reproduce behaviours through the **imitation** of actions (Subiaul, 2016). Empirical investigation has yielded evidence both for (Bonnie et al., 2007; Fuhrmann et al., 2014; Hobaiter and Byrne, 2010; Horner and Whiten, 2005; Whiten et al., 2009) and against (Call et al., 2005; Subiaul, 2016; Tennie et al., 2012, 2010) claims that apes may also be able to imitate the fine-grained actions of other individuals, with the evidence supporting imitation in apes representing a much smaller body of literature than the evidence in favour of other mechanisms of social learning, such as emulation.

Thus, the current best model for understanding social learning in great ape tool use is that individuals emulate goals, and must innovate their own sequences of actions to meet these goals. However, such a mechanism for the socially mediated acquisition of tool use presents questions surrounding how observed heterogeneity in tool-use techniques emerges between great-ape populations (Byrne, 2005). Consequently, further examination of the social transmission of tool-use behaviours between knowledgeable and naive apes in the wild is required, particularly in the case of the development of fine-grained action sequences for tool use.

1.1.5 Tool-use at old-age: senescence in wild primates

Senescence is a by-product of selection (Medawar, 1951). If genes are able to increase an individual's fitness early on in their life history, they are likely to be passed on, even if they result in deleterious effects in later-life (Nussey et al., 2013). Thus, nearly all organisms senesce with old-age, yet even within species, the rate at which different organisms senesce is variable (Colchero et al., 2021; Lindenberger, 2014; Medawar, 1951; Nussey et al., 2013).

Studying the process of senescence in wild animals is extremely challenging (Nussey et al., 2013). Determining the precise ages of wild animals can be difficult, and many wild animals do not survive to the tail-ends of their lifespans. The reduced number of individuals that live to extreme old-age, and the difficulties associated with tracking animals to collect longitudinal data over many years, present barriers to the generation of robust models of ageing in wild animals, as often sample sizes do not permit the use of rigorous statistical analyses. Therefore, senescent ageing is an aspect of the lives of wild animals which holds many uncertainties (Nussey et al., 2013).

Of all animals, ageing in captive nonhuman primates has been researched extensively. Primates offer the most translatable models for understanding the human ageing process, and research into ageing in captive primates has often focussed on the use of short-lived species (most frequently rhesus monkeys, but also other short-living primates such as marmosets and mouse lemurs), which allow for senescence in primates to be observed over comparatively short timeframes compared to human lifetimes (Colman, 2018). This research has revealed a number of similarities in the ageing processes of humans and nonhuman primates, including increased social selectivity (Machanda and Rosati, 2020); reduced memory capacity (Lacreuse and Herndon, 2009); changes in a wide array of

physiological processes (Lowenstine et al., 2016); as well as similar hallmarks of neurological ageing as observed in human diseases, such as Alzheimer's disease (Edler et al., 2021).

The majority of research into primate ageing has been performed using **cross-sectional analyses of ageing**, where researchers exploit existing variation between the ages of individuals to infer the effects of old-age senescence on behaviour and cognition. However, such analyses are limited in how much information they can provide regarding the process of senescence over time, including the time of onset; the rate of senescence with increasing age; and the extent to which these factors vary between individuals (Nussey et al., 2013). Additionally, much of our understanding of primate ageing comes from experimental paradigms with captive individuals which, whilst highly informative for understanding the senescence of cognitive processes, do not closely reflect the behaviours which are habitually performed by primates in their natural habitats. In other words, we don't know how cognitive and physical ageing affects primates during their day-to-day lives in the wild. Hence, **longitudinal analyses** of ageing and senescence are required, and specifically, longitudinal analyses of wild behaviours.

Among the behaviours that primates perform, tool use presents an excellent candidate behaviour for the study of old-age senescence. Tool-use behaviours require planning, and part of this planning requires individuals to combine actions into sequences (Byrne et al., 2013; Call, 2013); and organizing objects into complex configurations (Matsuzawa, 1994; Sanz and Morgan, 2010). Many of the cognitive processes underlying tool-use have been identified as at risk of senescence as primates experience progressive old age in captivity, including executive functioning (Frye et al., 2022; Lacreuse et al., 2020), working memory (Frye et al., 2022; Languille et al., 2012) and fine-grained motor control (Lacreuse et al., 2014; Languille et al., 2012). Additionally, many tool-use behaviours require individuals to exert physical force using objects, particularly those which require the use of percussive actions (e.g. nut cracking, and pestle pounding), and so the efficiency of these behaviours may be expected to decline with age, as the gradual degradation of muscle tissue (sarcopenia) and bone density reduces strength and mobility within individuals (a facet of ageing that is well described in nonhuman primates; Lowenstine et al., 2016). Moreover, as previously discussed, many species of primates habitually perform tool-use behaviours in the wild, and do so throughout their lifetimes, allowing for the behaviours of individuals to be assessed longitudinally, and evaluated for changes with increasing old-age.

Despite tool-use representing a domain of behaviour which would likely be highly informative for understanding the effects of senescence in wild primates, I am currently aware of no existing literature on this topic. Therefore, how the tool-use behaviours of wild primates change with progressive old-age is an open question to science. This research not only has the potential to uncover further parallels in the ageing processes of humans and apes, but also may provide valuable information for the formation of effective enrichment strategies which support the captive care of old-age primates – an issue which is becoming increasingly pressing as the number of primates living to old-age in captivity is rapidly rising (Havercamp et al., 2019; Neal Webb et al., 2019), and many enrichment strategies in captivity involve the provisioning of primates with objects which simulate the manual tasks that they would face in the wild (Talbot et al., 2023). Understanding how old-aged apes engage in complex object manipulation tasks in the wild will therefore be highly informative to this issue.

1.1.6 Nut cracking as a case study in the organisation, development, and senescence of primate tool-use

The tool-use behaviours of primates offer an excellent opportunity to address a number of important questions in biology, including how seemingly complex sequential behaviours of animals are organised; what cognitive capacities scaffold such organisation; how learning processes underpin the emergence of cultural behaviours in animals; and how the senescence of biological systems leads to changes in an animal's behaviour as it experiences progressive old-age. This thesis aims to answer such questions by drawing on a specific, highly complex form of animal tool-use: **nut cracking**. Nut cracking is a tool-use behaviour which is habitually performed in the wild by a number of species of primates, including capuchin monkeys (*Sapajus* spp.; Fragaszy et al., 2023; Mangalam and Fragaszy, 2015), long-tailed macaques (*Macaca fascicularis*; Haslam et al., 2013; Luncz et al., 2019), and one species of ape: chimpanzees (*Pan troglodytes*; Boesch and Boesch, 1983; Carvalho and McGrew, 2012; Matsuzawa, 1994).

During nut cracking, primates use naturally occurring objects in their environment as **hammer and anvil** tools to crack open hard-shelled nuts. The process of nut cracking exists within a wider, describable operation chain, which includes the selection and acquisition of tool-objects and nuts; the combination of objects (i.e. the placement of the nut on the anvil, followed by striking the nut with the hammer); the processing of cracked nuts (e.g. peeling inedible shell away from edible kernels, and

consuming kernels); and the disposal of waste items (e.g. shell) as well as tools once individuals have finished performing the behaviour (Carvalho et al., 2008; Corat et al., 2016). The precise technique used to crack nuts varies between species. For example, capuchin monkeys in Brazil perform nut cracking using rocky outcrops, boulders or logs (which are generally immovable for capuchins) as anvils, and a separate stone to strike with as the hammer, where the hammer stone is held by both hands (Mangalam and Fragaszy, 2015). On the other hand, chimpanzees of the Bossou forest in Guinea crack nuts using portable hammer and anvil stones, and the majority of striking actions are performed using one hand, reflecting asymmetrical movement in the upper limbs during tool-use (see Fig. 1c for an illustration; Biro et al., 2006). Conversely, and demonstrating intra-species variation in technique, chimpanzees at the TaÏ forest, Ivory Coast, perform the majority of their nut cracking on immovable anvils (such as boulders embedded in the ground, or exposed tree roots), and utilise a much wider diversity of raw materials (including both stone and wood) as hammers, compared to chimpanzees at Bossou (likely reflecting variation in the local raw materials available at either site; Proffitt et al., 2022).

Nut cracking is a highly complex form of nonhuman primate tool-use. In fact, nut cracking has been argued to constitute one of the most complex forms of nonhuman animal tool-use, as it requires tool-users to orient multiple tool-objects (hammer and anvil) towards a specific target (the nut) simultaneously, in a highly specific spatiotemporal configuration (Matsuzawa, 1996). This contrasts with other tool-use behaviours of nonhuman primates, which often involve the combination of only a single tool with a target (e.g. chimpanzee ant-dipping, where a single stem is dipped into a column of marching army ants, before being withdrawn and the ants on the stem consumed; Humle and Matsuzawa, 2002), or the use of multiple tools but where each tool is used sequentially (e.g. during chimpanzee termite fishing for subterranean nests, where the nest is first perforated with a thick stick tool, before that tool is placed on the ground and a different stem is inserted into the opening to fish out termites; Sanz and Morgan, 2010). On rare occasions, chimpanzees at Bossou have also been observed using an additional, third stone tool - a **wedge stone** - which is placed underneath anvil stones to confer stability, representing a possible extended level of complexity which may be reached when chimpanzees crack nuts using stone tools at Bossou (Matsuzawa, 1991).

As well as the need for primates to effectively organise tools during nut cracking, this tool-use behaviour also requires individuals to be able to identify and evaluate the physical properties of objects,

including the hardness of nuts, and the suitability of stone tools (Bril et al., 2009; Carvalho et al., 2008; Proffitt et al., 2022). In extension, individuals must draw upon these properties when combining objects; for example, individuals must exert enough force with the hammer stone to crack open the outer shells of nuts, but not so much force that it smashes the inner edible inner kernel (Bril et al., 2009; Fragaszy et al., 2023; Mangalam and Fragaszy, 2015). Thus, the complexity of nut cracking as a technological behaviour is not only supported by its requirement for multiple tools to be simultaneously combined, but also in its requirement for tool-users to integrate information about the physical properties of tools, objects, and their combinations, to facilitate effective tool-use.

Nut cracking behaviours of primates are also a useful system for studying cultural evolutionary processes in nonhuman animal technology. For example, site-specific differences in the stone-tools used by capuchin monkeys persist despite raw materials at each site being highly similar, suggesting that stone-tool choice may represent a culturally transmitted tradition in capuchin monkeys (Falótico et al., 2019). In chimpanzees, nut cracking is a behaviour which does not appear to be readily innovated by naive individuals when presented with nuts and stone tools (Koops et al., 2023), highlighting that chimpanzees likely need observations of knowledgeable individuals performing nut cracking to acquire this behaviour. Moreover, chimpanzees struggle to acquire nut cracking behaviours if the behaviour is not learnt before adulthood - an observation which is supported by anecdotal reports of wild chimpanzees failing to acquire nut cracking after the age of seven years old, even when opportunities to observe conspecifics are frequent (Koops et al., 2023; Matsuzawa, 2011) as well as through experiments with captive chimpanzees, where naive adults struggle to successfully perform the necessary combination of actions and objects following demonstration (Hayashi et al., 2005). However, infant and juvenile chimpanzees readily acquire nut cracking in the wild, through a process of exploration of nuts and tool objects interspersed with frequent periods of observation of knowledgeable individuals, most often their mothers. Thus, infant and juvenile chimpanzees are theorised to acquire nut cracking during a sensitive developmental period, through a process of “Education by Master-Apprenticeship” (Matsuzawa, 2001). Education by master-apprenticeship predicts that young chimpanzees are motivated to learn how to perform nut cracking through the desire to reproduce the behaviours performed by their mothers, and that this desire accounts for the extended period through which young chimpanzees continue to engage with nuts and stone tools, and attempt to perform the correct sequences of actions through trail-and-error. This intrinsic motivation therefore explains why

chimpanzees continue to attempt to perform nut cracking even in the absence of any external reward, as no kernels are acquired through unsuccessful attempts. However, exactly what information is acquired through observations of knowledgeable individuals during this time remains to be fully characterised (see section 1.1.4).

Nut cracking is therefore an excellent candidate behaviour for research into the sequential structure of primate manual actions during tool-use. Nut cracking requires the organisation of actions into sequences which address specific sub-goals (as qualitatively described by the *chaine operatoîre* approach) and the use of multiple objects makes the performance of such actions highly conspicuous. Nut cracking is cognitively demanding, demonstrated by the requirement for individuals to understand complex spatial and cause-effect relationships between objects, or between actions and objects, as well as the physical properties and affordances of objects. Along with the physical demands of exerting sufficient percussive force to crack nuts, nut cracking is therefore a behaviour which will likely senesce with progressive old-age. Additionally, the argument that nut cracking represents a cultural behaviour in primates invites the question of how individuals learn and refine this behaviour in the wild. This thesis therefore aims to characterize the sequential structure, development, and possible senescence of nut cracking, through observations of stone tool use across the lifetimes of wild chimpanzees.

1.1.7 The chimpanzees of the Bossou forest

The village of Bossou is situated west of the Nimba mountains in the South-East of Guinea (07° 390' N; 008° 300' W), and the forests surrounding Bossou are home to a small community of chimpanzees (Matsuzawa et al., 2011). Research on the chimpanzees at Bossou began in 1976, and through the habituation efforts of researchers at Bossou, the behaviours of these chimpanzees have now been documented over close to five decades of research.

The Bossou chimpanzees inhabit a home range of 5-6 km^2. Until 2002, the community size at Bossou was stable at approximately 20 individuals, and contained individuals from a variety of demographic categories, ranging from a number of infants (below the age of five years), to several old-aged individuals, estimated to be between 40-60 years-old (see Fig. 1). However, following a flu-like epidemic in 2003 (Matsuzawa et al., 2004), which led to the death of five chimpanzees, community size at Bossou has slowly declined until the present day. This decline was not helped by the fact that, during the entire time research has been conducted at Bossou, no immigrants have ever remained

permanently (Matsuzawa et al., 2011). As of September 2023, there are currently four chimpanzees remaining at Bossou.

Research at Bossou has been transformative to scientific understanding of wild chimpanzees, including their sociality, demographic processes, interactions with human populations, and tool-use behaviours, including those which are culturally acquired (Matsuzawa et al., 2011). Chimpanzees at Bossou exhibit an extensive repertoire of tool-use behaviours (approximately 24 tool-use behaviours in total; Humle, 2011), many of which involve the production of tools from vegetation (usually sticks, stems and leaves), such as ant-dipping (Humle and Matsuzawa, 2002), leaf-folding (Tonooka, 2001), pestle-pounding (Yamakoshi and Sugiyama, 1995), and algae-scooping (Matsuzawa, 2019). The chimpanzees at Bossou have also been highly informative for understanding non-human lithic technology, through their habitual engagement in the cracking of naturally-occurring **oil-palm nuts** (*Elaeis guineensis*) using portable hammer and anvil stone tools (Biro et al., 2006, 2003; Carvalho et al., 2008; Inoue-Nakamura and Matsuzawa, 1997; Matsuzawa, 1996, 1994, 1991).

Research on the stone tool-use behaviours of chimpanzees at Bossou has been greatly aided through a longitudinal field experiment (Matsuzawa, 1994). Established in 1988, and located close to the peak of Mount Gban, a natural clearing in the forest has been used to set up an '**outdoor laboratory**' for the study of chimpanzee nut cracking (Matsuzawa, 1994). During the dry season of each year (approx. November - February), researchers position a selection of about 50 stone tools in the middle of the outdoor laboratory in a randomised matrix, and provide a number of piles of oil-palm nuts around the clearing (generally 40-60 in a pile; in some years, coula nuts, *Coula edulis,* and panda nuts*, Panda oleosa,* which are cracked by nearby communities of chimpanzees*,* were also provided as part of an experimental procedure; see Fig 2 and Biro et al., 2006, 2003). The clearing is open on three sides, and on the fourth side, an artificial wall is constructed using branches and palm fronds. Chimpanzees are free to enter the outdoor laboratory at any time as part of their daily ranging behaviours, and researchers, who are positioned behind the artificial screen and out of direct sight, record the chimpanzees using video cameras.

The several decades of recordings of chimpanzees engaging in nut cracking at Bossou have recently been collated into a longitudinal video archive ('**The Bossou Archive**'; Schofield et al., 2019, 2023). This video archive presents a novel opportunity to collect a large corpus of data on how chimpanzees organise actions during nut cracking, and also the ability to study how the behaviours of

individuals change over time. This includes the possibility of examining how the repertoire of actions used by chimpanzees during nut cracking develops throughout infancy and the juvenile stage - which may shed light on how individuals acquire tool-use behaviours during development - as well as the possible degradation of tool-use skills as chimpanzees experience progressive old-age in the wild.

1.1.8 Thesis outline

In addition to this introductory chapter, this thesis contains four studies focussed on the nut cracking tool-use behaviours of chimpanzees at Bossou (Chapters 2-5). Each of these studies can be read as an independent research paper.

In **Chapter 2,** I applied a model of mutual information (MI) decay to evaluate the likelihood that the action sequences produced by chimpanzees during nut cracking reflect serial chaining, hierarchical organization, or a composite of these two processes. Using a corpus of over 8000 coded actions, I determined that MI decay was best characterized by a composite model, reflecting that chimpanzees most likely used both processes when producing sequences of actions for nut cracking, a result which is similar to the organization of human language and birdsong. Additionally, through running our analysis on null Markov sequences, I illustrate the importance of using comparative, simulated data for MI decay analyses as biologically relevant controls.

In **Chapter 3**, I programmed a bespoke dictionary-compression algorithm to characterize the compressibility of observed action sequences during nut cracking, and compare this to sequences generated by Markov processes, as well as various randomization procedures. I also compared the compressibility of sequences between individuals, including the extent to which sequences compressed, and the nature of their compression by comparing individual dictionaries. Dictionary-based compression identified subroutines of actions which were performed disproportionately frequently by specific individuals, as well as several subroutines whose generation may be understood through processes of centre-embedding. The results of this chapter are discussed with relation to the utility of dictionary-based compression in characterizing flexibility in action sequence generation, both within and between individuals, as well as the compressibility of observed action sequences compared to those produced by Markov simulation and randomization.

In **Chapter 4**, I present a longitudinal analysis of how chimpanzees acquire the repertoire of actions used for nut cracking between the ages of one and eight years old, and compare repertoire

development to the repertoires of proficient nut crackers. I found that the repertoire of actions used by chimpanzees undergoes an expansion at ages prior to the successful acquisition of nut cracking, before gradually reducing across subsequent years (including into adolescence, past the age of eight years old). I discuss these results in relation to a likely model of 'exploration and pruning' used by chimpanzees during a highly asocial pathway of action repertoire development. However, the possibility of social acquisition of individual, highly frequent actions is discussed, in relation to the early emergence of a highly characteristic action of nut cracking: striking downwards on an object using one hand.

In **Chapter 5,** I report on a longitudinal analysis of the nut cracking behaviours of five individuals as they experience progressively extreme old-age. Using a number of metrics of engagement and efficiency in nut cracking, I demonstrate how the effects of old-age on nut cracking vary extensively between individuals, with some individuals showing no observable changes with extreme age, and others exhibiting profound changes in efficiency and engagement in stone-tool use.

Chapter 6 presents a general discussion. Chapters 2-5 are discussed jointly, with particular focus on the extent to with which these studies have improved our understanding of the sequential structure, development, and senescence of tool-use behaviours in great apes. The results of Chapters 2-5 are also discussed in the wider context of the sequential behaviours of nonhuman animals – including the methodologies used for evaluating the sequential structures of behaviours – as well as for understanding the evolution of complex sequential behaviours in humans, such as language and technologically complex tool-use.

1.1.9 Figures

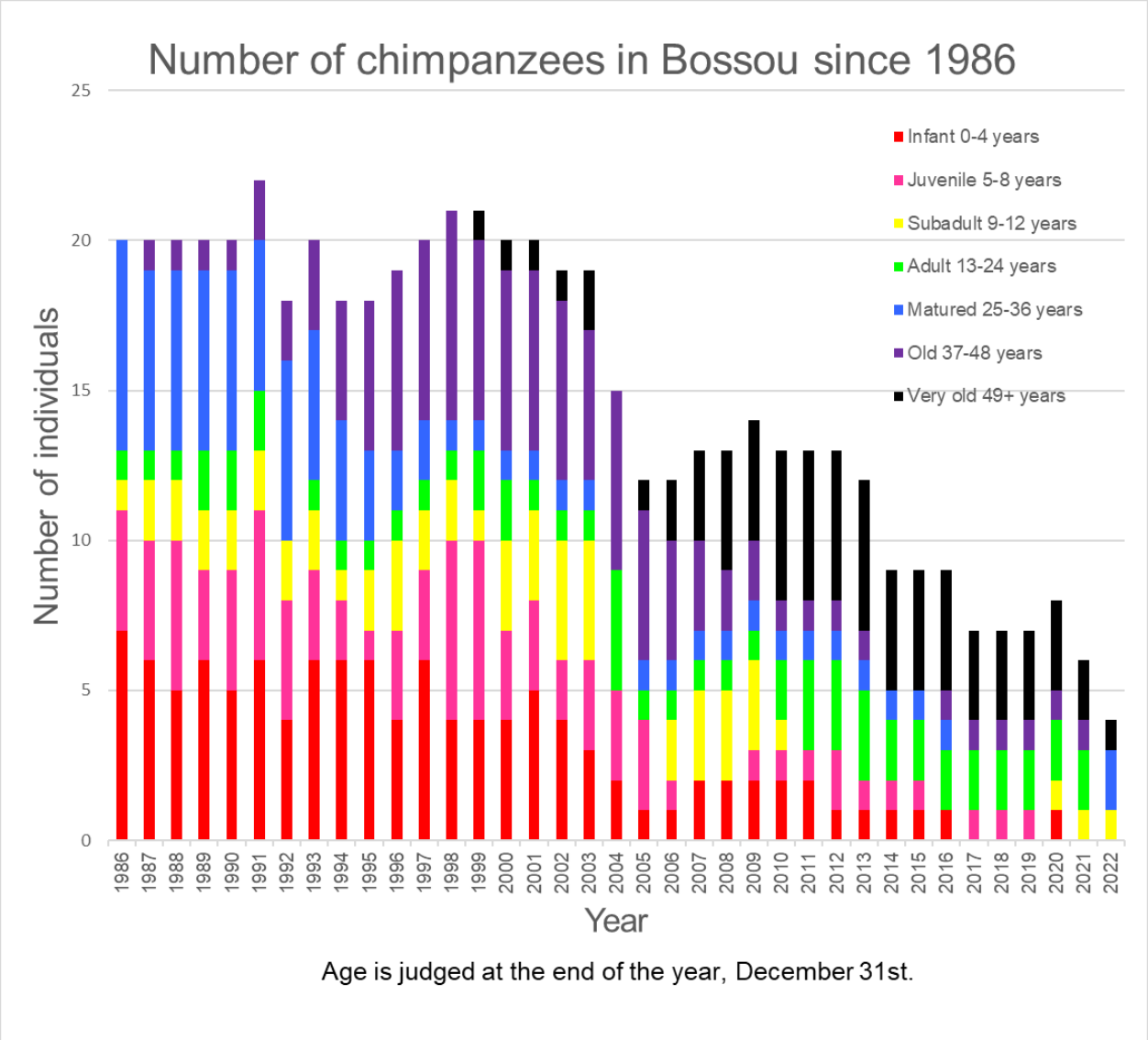


Fig 1. The Demographic Structure of the Bossou Community between 1986 and 2022. (Credit: T. Matsuzawa).



Fig 2. The 'Outdoor Laboratory' at Bossou. (a) The set-up of the outdoor laboratory: (1) two piles of nuts (more piles are present but are not indicated); (2) central stone-tool matrix; (3) a water point in the form of a large hole in a standing tree-trunk; (4) a raceme of oil-palm fruits. (b) The central stone-tool matrix. Each stone is uniquely numbered to aid identification from a distance. (c) Yo, an old-aged female (approx. 51 years old), has placed a coula nut (*Coula edulis*) on an anvil stone, and is preparing to strike with the hammer stone. Photo credits for 1b & 1c: D. Biro.

1.2.0 References

Aamodt, C.M., Farias-Virgens, M., White, S.A., 2020. Birdsong as a window into language origins and evolutionary neuroscience. Philos. Trans. R. Soc. B Biol. Sci. 375. https://doi.org/10.1098/rstb.2019.0060

Allen, J.A., 2019. Community through Culture: From Insects to Whales: How Social Learning and Culture Manifest across Diverse Animal Communities. BioEssays 41, 1–8. https://doi.org/10.1002/bies.201900060

Anderson, J.R., Matessa, M., 1997. A Production System Theory of Serial Memory. Psychol. Rev. 104, 728–748. https://doi.org/10.1037/0033-295X.104.4.728

Arbib, M.A., 2005. From monkey-like action recognition to human language: An evolutionary framework for neurolinguistics. Behav. Brain Sci. 28, 105–124. https://doi.org/10.1017/S0140525X05000038

Arnold, K., Zuberbühler, K., 2012. Call combinations in monkeys: Compositional or idiomatic expressions? Brain Lang. 120, 303–309. https://doi.org/10.1016/j.bandl.2011.10.001

Asano, R., Boeckx, C., 2015. Syntax in language and music: what is the right level of comparison? Front. Psychol. 6, 1–16. https://doi.org/10.3389/fpsyg.2015.00942

Berman, G.J., Bialek, W., Shaevitz, J.W., 2016. Predictability and hierarchy in *Drosophila* behavior. Proc. Natl. Acad. Sci. 113, 11943–11948. https://doi.org/10.1073/pnas.1607601113

Berwick, R.C., Chomsky, N., 2013. Foreword: A Bird's-Eye View of Human Language and Evolution. Birdsong Speech Languag Explor. Evol. Mind Brain ix–xii.

Berwick, R.C., Friederici, A.D., Chomsky, N., Bolhuis, J.J., 2013. Evolution, brain, and the nature of language. Trends Cogn. Sci. 17, 89. https://doi.org/10.1016/j.tics.2012.12.002

Berwick, R.C., Okanoya, K., Beckers, G.J.L., Bolhuis, J.J., 2011. Songs to syntax: The linguistics of birdsong. Trends Cogn. Sci. 15, 113–121. https://doi.org/10.1016/j.tics.2011.01.002

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. Anim. Cogn. 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. Cogn. Dev. Chimpanzees 476–508. https://doi.org/10.1007/4-431-30248-4_28

Boesch, C., 1991. Symbolic communication in wild chimpanzees? Hum. Evol. 6, 81–89. https://doi.org/10.1007/BF02435610

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

Boesch, C., Kalan, A.K., Mundry, R., Arandjelovic, M., Pika, S., Dieguez, P., Ayimisin, E.A., Barciela, A., Coupland, C., Egbe, V.E., Eno-Nku, M., Michael Fay, J., Fine, D., Adriana Hernandez-Aguilar, R., Hermans, V., Kadam, P., Kambi, M., Llana, M., Maretti, G., Morgan, D., Murai, M., Neil, E., Nicholl, S., Ormsby, L.J., Orume, R., Pacheco, L., Piel, A., Sanz, C., Sciaky, L., Stewart, F.A., Tagg, N., Wessling, E.G., Willie, J., Kühl, H.S., 2020. Chimpanzee ethnography reveals unexpected cultural diversity. Nat. Hum. Behav. 4, 910–916. https://doi.org/10.1038/s41562-020-0890-1

Bonnie, K.E., Horner, V., Whiten, A., De Waal, F.B.M., 2007. Spread of arbitrary conventions among chimpanzees: A controlled experiment. Proc. R. Soc. B Biol. Sci. 274, 367–372. https://doi.org/10.1098/rspb.2006.3733

Bril, B., 2015. Learning to Use Tools: A Functional Approach to Action, in: Francophone Perspectives of Learning Through Work. pp. 95–118. https://doi.org/10.1007/978-3-319-18669-6_5

Bril, B., Dietrich, G., Foucart, J., Fuwa, K., 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? Anim. Cogn. 12, 217–235. https://doi.org/10.1007/s10071-008-0184-x

Bril, B., Smaers, J., Steele, J., Rein, R., Nonaka, T., Dietrich, G., Biryukova, E., Hirata, S., Roux, V., 2012. Functional mastery of percussive technology in nut-cracking and stone-flaking actions: Experimental comparison and implications for the evolution of the human brain. Philos. Trans. R. Soc. B Biol. Sci. 367, 59–74. https://doi.org/10.1098/rstb.2011.0147

Byrne, R., 2005. Detecting, Understanding, and Explaining Imitation by Animals, in: Hurley, S.L., Chater, N. (Eds.), Perspectives on Imitation: From Neuroscience to Social Science. MIT Press, Cambridge, Mass, pp. 225–242.

Byrne, R.W., 2007. Culture in great apes: Using intricate complexity in feeding skills to trace the evolutionary origin of human technical prowess. Philos. Trans. R. Soc. B Biol. Sci. 362, 577–585. https://doi.org/10.1098/rstb.2006.1996

Byrne, R.W., Corp, N., Byrne, J.M.E., 2001. Estimating the complexity of animal behaviour: How mountain gorillas eat thistles. Behaviour 138, 525–557. https://doi.org/10.1163/156853901750382142

Byrne, R.W., Russon, A.E., 1998. Learning by imitation : A hierarchical approach. Behav. Brain Sci. 21, 667–721.

Byrne, R.W., Sanz, C.M., Morgan, D.B., 2013. Chimpanzees plan their tool use, in: Sanz, C.M., Call, J., Boesch, C. (Eds.), Tool Use in Animals. Cambridge University Press, pp. 48–64. https://doi.org/10.1017/CBO9780511894800.004

Call, J., 2013. Three ingredients for becoming a creative tool user, in: Sanz, C.M., Call, J., Boesch, C. (Eds.), Tool Use in Animals. Cambridge University Press, pp. 3–20. https://doi.org/10.1017/CBO9780511894800.002

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). Anim. Cogn. 8, 151–163. https://doi.org/10.1007/s10071-004-0237-8

Carvalho, S., Cunha, E., Sousa, C., Matsuzawa, T., 2008. Chaînes opératoires and resource-exploitation strategies in chimpanzee (Pan troglodytes) nut cracking. J. Hum. Evol. 55, 148–163. https://doi.org/10.1016/j.jhevol.2008.02.005

Carvalho, S., Matsuzawa, T., McGrew, W.C., 2013. From pounding to knapping: How chimpanzees can help us to model hominin lithics, in: Sanz, C.M., Call, J., Boesch, C. (Eds.), Tool Use in Animals. Cambridge University Press, pp. 225–241. https://doi.org/10.1017/CBO9780511894800.015

Carvalho, S., McGrew, W., 2012. The origins of the Oldowan: Why chimpanzees (Pan troglodytes) still are good models for technological evolution in Africa, in: Domínguez-Rodrigo, M. (Ed.), Stone Tools and Fossil Bones. Cambridge University Press, pp. 201–221. https://doi.org/10.1017/CBO9781139149327.010

Cheung, V.K.M., Meyer, L., Friederici, A.D., Koelsch, S., 2018. The right inferior frontal gyrus processes nested non-local dependencies in music. Sci. Rep. 8, 1–12. https://doi.org/10.1038/s41598-018-22144-9

Chomsky, N., 2002a. An Elementary Linguistic Theory, in: Syntactic Structures; Second Edition. Berlin ; New York : Mouton de Gruyter, pp. 18–25. https://doi.org/10.1515/9783110218329

Chomsky, N., 2002b. Phrase Structure, in: Syntactic Structures; Second Edition. Berlin ; New York : Mouton de Gruyter, pp. 26–33. https://doi.org/10.1515/9783110218329

Chomsky, N., 1995. Langage and Nature. Mind, New Series 104, 1–61.

Chomsky, N., 1956. Three models for the description of language. IRE Trans. Inf. Theory 2, 113–124.

Clay, Z., Zuberbühler, K., 2009. Food-associated calling sequences in bonobos. Anim. Behav. 77, 1387–1396. https://doi.org/10.1016/j.anbehav.2009.02.016

Colchero, F., Aburto, J.M., Archie, E.A., Boesch, C., Breuer, T., Campos, F.A., Collins, A., Conde, D.A., Cords, M., Crockford, C., Thompson, M.E., Fedigan, L.M., Fichtel, C., Groenenberg, M., Hobaiter, C., Kappeler, P.M., Lawler, R.R., Lewis, R.J., Machanda, Z.P., Manguette, M.L., Muller, M.N., Packer, C., Parnell, R.J., Perry, S., Pusey, A.E., Robbins, M.M., Seyfarth, R.M., Silk, J.B., Staerk, J., Stoinski, T.S., Stokes, E.J., Strier, K.B., Strum, S.C., Tung, J., Villavicencio, F., Wittig, R.M., Wrangham, R.W., Zuberbühler, K., Vaupel, J.W., Alberts, S.C., 2021. The long lives of primates and the 'invariant rate of ageing' hypothesis. Nat. Commun. 12, 3666. https://doi.org/10.1038/s41467-021-23894-3

Collier, K., Bickel, B., van Schaik, C.P., Manser, M.B., Townsend, S.W., 2014. Language evolution: Syntax before phonology? Proc. R. Soc. B Biol. Sci. 281. https://doi.org/10.1098/rspb.2014.0263

Colman, R.J., 2018. Non-human primates as a model for aging. Biochim. Biophys. Acta BBA - Mol. Basis Dis. 1864, 2733–2741. https://doi.org/10.1016/j.bbadis.2017.07.008

Corat, C., Siqueira, J., Ottoni, E.B., 2016. Sequential organization and optimization of the nut-cracking behavior of semi-free tufted capuchin monkeys (Sapajus sp.). Primates 57, 113–121. https://doi.org/10.1007/s10329-015-0491-1

Corver, A., Wilkerson, N., Miller, J., Gordus, A., 2021. Distinct movement patterns generate stages of spider web building. Curr. Biol. 31, 4983-4997.e5. https://doi.org/10.1016/j.cub.2021.09.030

Dawkins, R., 1976. Hierarchical organization: a candidate principle for ethology., in: Growing Points in Ethology. Cambridge University Press.

Dawkins, R., Dawkins, M., 1976. Hierarchical Organization and Postural Facilitation: Rules for Grooming in Flies. Anim. Behav. 24, 739–755. https://doi.org/10.1016/S0003-3472(76)80003-6

Edler, M.K., Munger, E.L., Groetz, H., Raghanti, M.A., 2021. Nonhuman primates as models for aging and Alzheimer's disease, in: Assessments, Treatments and Modeling in Aging and Neurological Disease. Elsevier, pp. 527–537. https://doi.org/10.1016/B978-0-12-818000-6.00047-0

Engesser, S., Holub, J.L., O'Neill, L.G., Russell, A.F., Townsend, S.W., 2019. Chestnut-crowned babbler calls are composed of meaningless shared building blocks. Proc. Natl. Acad. Sci. U. S. A. 116, 19579–19584. https://doi.org/10.1073/pnas.1819513116

Falótico, T., Proffitt, T., Ottoni, E.B., Staff, R.A., Haslam, M., 2019. Three thousand years of wild capuchin stone tool use. Nat. Ecol. Evol. 3, 1034–1038. https://doi.org/10.1038/s41559-019-0904-4

Fitch, W.T., Hauser, M.D., 2004. Computational Constraints on Syntactic Processing in a Nonhuman Primate. Science 303, 377–380. https://doi.org/10.1126/science.1089401

Fitch, W.T., Hauser, M.D., Chomsky, N., 2005. The evolution of the language faculty: Clarifications and implications. Cognition 97, 179–210. https://doi.org/10.1016/j.cognition.2005.02.005

Fragaszy, D.M., Aiempichitkijkarn, N., Eshchar, Y., Mangalam, M., Izar, P., Resende, B., Visalberghi, E., 2023. The development of expertise at cracking palm nuts by wild bearded capuchin monkeys, Sapajus libidinosus. Anim. Behav. 197, 1–14. https://doi.org/10.1016/j.anbehav.2022.12.008

Friederici, A.D., 2020. Hierarchy processing in human neurobiology: How specific is it? Philos. Trans. R. Soc. B Biol. Sci. 375, 1–9. https://doi.org/10.1098/rstb.2018.0391

Frye, B.M., Craft, S., Register, T.C., Kim, J., Whitlow, C.T., Barcus, R.A., Lockhart, S.N., Sai, K.K.S., Shively, C.A., 2022. Early Alzheimer's disease-like reductions in gray matter and cognitive function with aging in nonhuman primates. Alzheimers Dement. Transl. Res. Clin. Interv. 8. https://doi.org/10.1002/trc2.12284

Fuhrmann, D., Ravignani, A., Marshall-Pescini, S., Whiten, A., 2014. Synchrony and motor mimicking in chimpanzee observational learning. Sci. Rep. 4, 5283. https://doi.org/10.1038/srep05283

Gagniuc, P., 2017. Markov Chains: From Theory to Implementation and Experimentation. https://doi.org/10.1002/9781119387596

Genty, E., Byrne, R.W., 2010. Why do gorillas make sequences of gestures? Anim. Cogn. 13, 287–301. https://doi.org/10.1007/s10071-009-0266-4

Girard-Buttoz, C., Zaccarella, E., Bortolato, T., Friederici, A.D., Wittig, R.M., Crockford, C., 2022. Chimpanzees produce diverse vocal sequences with ordered and recombinatorial properties. Commun. Biol. 5, 410. https://doi.org/10.1038/s42003-022-03350-8

Gomez-Marin, A., Stephens, G.J., Brown, A.E.X., 2016. Hierarchical compression of *Caenorhabditis elegans* locomotion reveals phenotypic differences in the organization of behaviour. J. R. Soc. Interface 13, 20160466. https://doi.org/10.1098/rsif.2016.0466

Greenfield, P.M., 1991. Language, tools and brain: The ontogeny and phylogeny of hierarchically organized sequential behavior. Behav. Brain Sci. 531–595.

Gruber, T., Clay, Z., 2016. A Comparison Between Bonobos and Chimpanzees: A Review and Update. Evol. Anthropol. 25, 239–252. https://doi.org/10.1002/evan.21501

Gruber, T., Muller, M.N., Strimling, P., Wrangham, R., Zuberbühler, K., 2009. Wild Chimpanzees Rely on Cultural Knowledge to Solve an Experimental Honey Acquisition Task. Curr. Biol. 1806–1810. https://doi.org/10.1016/j.cub.2009.08.060

Haslam, M., 2022. Orangutan insights into the evolution of tool use. Nature 604, 427–428. https://doi.org/10.1038/d41586-022-00872-3

Haslam, M., Falótico, T., 2015. Nasal probe and toothpick tool use by a wild female bearded capuchin (Sapajus libidinosus). Primates 56, 211–214. https://doi.org/10.1007/s10329-015-0470-6

Haslam, M., Gumert, M.D., Biro, D., Carvalho, S., Malaivijitnond, S., 2013. Use-Wear Patterns on Wild Macaque Stone Tools Reveal Their Behavioural History. PLoS ONE 8, e72872. https://doi.org/10.1371/journal.pone.0072872

Hauser, M.D., Chomsky, N., Fitch, W.T., 2002. The faculty of language: What is it, who has it, and how did it evolve? Evol. Hum. Lang. Biolinguistic Perspect. 298, 14–42. https://doi.org/10.1017/CBO9780511817755.002

Hauser, M.D., Yang, C., Berwick, R.C., Tattersall, I., Ryan, M.J., Watumull, J., Chomsky, N., Lewontin, R.C., 2014. The mystery of language evolution. Front. Psychol. 5, 1–12. https://doi.org/10.3389/fpsyg.2014.00401

Havercamp, K., Watanuki, K., Tomonaga, M., Matsuzawa, T., Hirata, S., 2019. Longevity and mortality of captive chimpanzees in Japan from 1921 to 2018. Primates 60, 525–535. https://doi.org/10.1007/s10329-019-00755-8

Hayashi, M., Mizuno, Y., Matsuzawa, T., 2005. How does stone-tool use emerge? Introduction of stones and nuts to naïve chimpanzees in captivity. Primates 46, 91–102. https://doi.org/10.1007/s10329-004-0110-z

Henson, R.N.A., Norris, D.G., Page, M.P.A., Baddeley, A.D., 1996. Unchained Memory: Error Patterns Rule out Chaining Models of Immediate Serial Recall. Q. J. Exp. Psychol. Sect. Hum. Exp. Psychol. 49, 80–115. https://doi.org/10.1080/713755612

Hobaiter, C., Byrne, R.W., 2010. Able-Bodied Wild Chimpanzees Imitate a Motor Procedure Used by a Disabled Individual to Overcome Handicap. PLoS ONE 5, e11959. https://doi.org/10.1371/journal.pone.0011959

Hockett, C., 1960. The origin of speech. Sci. Am. 88–111.

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

Humle, T., 2011. The Tool Repertoire of Bossou Chimpanzees, in: The Chimpanzees of Bossou and Nimba. Springer Japan, Tokyo, Japan, pp. 61–72.

Humle, T., Matsuzawa, T., 2002. Ant-dipping among the chimpanzees of Bossou, Guinea, and some comparisons with other sites. Am. J. Primatol. 58, 133–148. https://doi.org/10.1002/ajp.10055

Inoue-Nakamura, N., Matsuzawa, T., 1997. Development of Stone Tool Use by Wild Chimpanzees (Pan troglodytes). J. Comp. Psychol. 111, 159–173. https://doi.org/10.1037/0735-7036.111.2.159

Isac, D., Reiss, C., 2013. Finite State Languages, in: I-Language: An Introduction to Linguistics as Cognitive Science. Oxford University Press, pp. 99–107.

Isac, Reiss, 2013. A syntactic theory that wont work, in: I-Language, An Introduction to Linguistics as Cognitive Science. Oxford University Press, pp. 91–113.

Janmaat, K.R.L., Byrne, R.W., Zuberbühler, K., 2006. Evidence for a spatial memory of fruiting states of rainforest trees in wild mangabeys. Anim. Behav. 72, 797–807. https://doi.org/10.1016/j.anbehav.2005.12.009

Jensen, P., Algers, B., Ekesbo, I., 1986. Methods in the Analysis of Behavioural Sequences, in: Methods of Sampling and Analysis of Data in Farm Animal Ethology. Birkhäuser Basel, Basel, pp. 59–74. https://doi.org/10.1007/978-3-0348-6614-9_5

Kaplan, R.M., Kay, M., 1994. Regular Models of Phonological Rule Systems. Comput. Linguist. 20, 331–378.

Katahira, K., Suzuki, K., Okanoya, K., Okada, M., 2011. Complex sequencing rules of birdsong can be explained by simple hidden Markov processes. PLoS ONE 6. https://doi.org/10.1371/journal.pone.0024516

Kershenbaum, A., Bowles, A.E., Freeberg, T.M., Jin, D.Z., Lameira, A.R., Bohn, K., 2014. Animal vocal sequences: not the Markov chains we thought they were. Proc. R. Soc. B Biol. Sci. 281, 20141370. https://doi.org/10.1098/rspb.2014.1370

Koops, K., 2020. Chimpanzee termite fishing etiquette. Nat. Hum. Behav. 4, 887–888. https://doi.org/10.1038/s41562-020-0895-9

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. Anim. Behav. Cogn. 10, 163–168. https://doi.org/10.26451/abc.10.02.05.2023

Kyes, R.C., 1988. Grooming with a stone in sooty mangabeys (Cercocebus atys). Am. J. Primatol. 16, 171–175. https://doi.org/10.1002/ajp.1350160208

Lacreuse, A., Herndon, J.G., 2009. Nonhuman Primate Models of Cognitive Aging, in: Bizon, J.L., Woods, A. (Eds.), Animal Models of Human Cognitive Aging. Humana Press, Totowa, NJ, pp. 1–30. https://doi.org/10.1007/978-1-59745-422-3_2

Lacreuse, A., Raz, N., Schmidtke, D., Hopkins, W.D., Herndon, J.G., 2020. Age-related decline in executive function as a hallmark of cognitive ageing in primates: an overview of cognitive and neurobiological studies. Philos. Trans. R. Soc. B Biol. Sci. 375, 20190618. https://doi.org/10.1098/rstb.2019.0618

Lacreuse, A., Russell, J.L., Hopkins, W.D., Herndon, J.G., 2014. Cognitive and motor aging in female chimpanzees. Neurobiol. Aging 35, 623–632. https://doi.org/10.1016/j.neurobiolaging.2013.08.036

Languille, S., Blanc, S., Blin, O., Canale, C.I., Dal-Pan, A., Devau, G., Dhenain, M., Dorieux, O., Epelbaum, J., Gomez, D., Hardy, I., Henry, P.-Y., Irving, E.A., Marchal, J., Mestre-Francés,

N., Perret, M., Picq, J.-L., Pifferi, F., Rahman, A., Schenker, E., Terrien, J., Théry, M., Verdier, J.-M., Aujard, F., 2012. The grey mouse lemur: A non-human primate model for ageing studies. Ageing Res. Rev. 11, 150–162. https://doi.org/10.1016/j.arr.2011.07.001
Larsson, N.J., Moffat, A., 2000. Off-Line Dictionary-Based Compression. Proc. IEEE 88.
Lashley, K., 1951. The problem of serial order in behavior. Cereb. Mech. Behav. 112–147.
Lerdahl, F., 2015. Musical Syntax and Its Relation to Linguistic Syntax. Lang. Music Brain 257–272. https://doi.org/10.7551/mitpress/9780262018104.003.0010
Leroux, M., Townsend, S.W., 2020. Call combinations in great apes and the evolution of syntax. Anim. Behav. Cogn. 7, 131–139. https://doi.org/10.26451/abc.07.02.07.2020
Levitin, D.J., Chordia, P., Menon, V., 2012. Musical rhythm spectra from Bach to Joplin obey a 1/ *f* power law. Proc. Natl. Acad. Sci. 109, 3716–3720. https://doi.org/10.1073/pnas.1113828109
Lin, H.W., Tegmark, M., 2017. Critical behavior in physics and probabilistic formal languages. Entropy 19, 1–25. https://doi.org/10.3390/e19070299
Lindenberger, U., 2014. Human cognitive aging: Corriger la fortune? Science 346, 572–578. https://doi.org/10.1126/science.1254403
Lowenstine, L.J., McManamon, R., Terio, K.A., 2016. Comparative Pathology of Aging Great Apes: Bonobos, Chimpanzees, Gorillas, and Orangutans. Vet. Pathol. 53, 250–276. https://doi.org/10.1177/0300985815612154
Luncz, L.V., Gill, M., Proffitt, T., Svensson, M.S., Kulik, L., Malaivijitnond, S., 2019. Group-specific archaeological signatures of stone tool use in wild macaques. eLife 8, e46961. https://doi.org/10.7554/eLife.46961
Machanda, Z.P., Rosati, A.G., 2020. Shifting sociality during primate ageing. Philos. Trans. R. Soc. B Biol. Sci. 375, 20190620. https://doi.org/10.1098/rstb.2019.0620
Mangalam, M., Fragaszy, D.M., 2015. Wild Bearded Capuchin Monkeys Crack Nuts Dexterously. Curr. Biol. 25, 1334–1339. https://doi.org/10.1016/j.cub.2015.03.035
Martin-Ordas, G., 2020. What Human Planning Can Tell Us About Animal Planning: An Empirical Case. Front. Psychol. 11, 1–11. https://doi.org/10.3389/fpsyg.2020.00635
Matsuzawa, T., 2019. Chimpanzees foraging on aquatic foods: algae scooping in Bossou. Primates 60, 317–319. https://doi.org/10.1007/s10329-019-00733-0
Matsuzawa, T., 2011. Stone Tools for Nut-Cracking, in: The Chimpanzees of Bossou and Nimba. Springer Japan, Tokyo, Japan, pp. 73–84.
Matsuzawa, T., 2001. Primate Foundations of Human Intelligence: A View of Tool Use in Nonhuman Primates and Fossil Hominids, in: Matsuzawa, T. (Ed.), Primate Origins of Human Cognition and Behavior. Springer Japan, Tokyo, pp. 3–25. https://doi.org/10.1007/978-4-431-09423-4_1
Matsuzawa, T., 1996. Chimpanzee intelligence in nature and in captivity: Isomorphism of symbol use and tool use, in: Great Ape Societies. pp. 196–212.
Matsuzawa, T., 1994. Field Experiments on use of Stone Tools in the wild, in: Chimpanzee Cultures. pp. 351–370.
Matsuzawa, T., 1991. Nesting cups and metatools in chimpanzees. Behav. Brain Sci. 14, 570–571. https://doi.org/10.1017/S0140525X00071417
Matsuzawa, T., Hulme, T., Sugiyama, Y., 2011. The Chimpanzees of Bossou and Nimba.
Matsuzawa, T., Humle, T., Koops, K., Biro, D., Hayashi, M., Sousa, C., Mizuno, Y., Kato, A., Yamakoshi, G., Ohashi, G., Sugiyama, Y., Kourouma, M., 2004. Wild chimpanzees at Bossou-Nimba: Deaths through a flu-like epidemic in 2003 and the green corridor project. Primate Res 20, 45–55.
Medawar, P., 1951. An Unsolved Problem of Biology: An Inaugural Lecture Delivered at University College, London, 6 December, 1951., Inaugural Lecture (University College, London); 1951. H.K. Lewis and Co., London.
Meulman, E.J.M., Van Schaik, C.P., 2013. Orangutan tool use and the evolution of technology, in: Sanz, C.M., Call, J., Boesch, C. (Eds.), Tool Use in Animals. Cambridge University Press, pp. 176–202. https://doi.org/10.1017/CBO9780511894800.012
Mielke, A., Carvalho, S., 2022. Chimpanzee play sequences are structured hierarchically as games. PeerJ 10, e14294. https://doi.org/10.7717/peerj.14294
Miksis-Olds, J.L., Buck, J.R., Noad, M.J., Cato, D.H., Stokes, M.D., 2008. Information theory analysis of Australian humpback whale song. J Acoust Soc Am 124, 2385–93. https://doi.org/10.1121/1.2967863
Neal Webb, S.J., Hau, J., Lambeth, S.P., Schapiro, S.J., 2019. Differences in Behavior Between Elderly and Nonelderly Captive Chimpanzees and the Effects of the Social Environment. J. Am. Assoc. Lab. Anim. Sci. 58, 783–789. https://doi.org/10.30802/AALAS-JAALAS-19-000019

Nevill-Manning, C., Witten, I., 1997. Identifying Hierarchical Structure in Sequences: A linear-time algorithm. J. Artif. Intell. Res. 7, 67–82.
Nevill-Manning, C.G., Witten, I.H., 2000. On-line and off-line heuristics for inferring hierarchies of repetitions in sequences. Proc. IEEE 88, 1745–1755. https://doi.org/10.1109/5.892710
Nishida, T., 1980. The leaf-clipping display: A newly-discovered expressive gesture in wild chimpanzees. J. Hum. Evol. 9, 117–128. https://doi.org/10.1016/0047-2484(80)90068-8
Nonaka, T., Bril, B., Rein, R., 2010. How do stone knappers predict and control the outcome of flaking? Implications for understanding early stone tool technology. J. Hum. Evol. 59, 155–167. https://doi.org/10.1016/j.jhevol.2010.04.006
Nussey, D.H., Froy, H., Lemaitre, J.-F., Gaillard, J.-M., Austad, S.N., 2013. Senescence in natural populations of animals: Widespread evidence and its implications for bio-gerontology. Ageing Res. Rev. 12, 214–225. https://doi.org/10.1016/j.arr.2012.07.004
O'Hara, S.J., Lee, P.C., 2006. High Frequency of Postcoital Penis Cleaning in Budongo Chimpanzees. Folia Primatol. (Basel) 77, 353–358. https://doi.org/10.1159/000093700
Ostry, D., Gribble, P., Gracco, V., 1996. Coarticulation of jaw movements in speech production: is context sensitivity in speech kinematics centrally planned? J. Neurosci. 16, 1570–1579. https://doi.org/10.1523/JNEUROSCI.16-04-01570.1996
Peng, C.-K., Buldyrev, S.V., Goldberger, A.L., Havlin, S., Sciortino, F., Simons, M., Stanley, H.E., 1992. Long-range correlations in nucleotide sequences. Nature 356, 168–170. https://doi.org/10.1038/356168a0
Petkov, C.I., ten Cate, C., 2020. Structured Sequence Learning: Animal Abilities, Cognitive Operations, and Language Evolution. Top. Cogn. Sci. 12, 828–842. https://doi.org/10.1111/tops.12444
Presotto, A., Fayrer-Hosken, R., Curry, C., Madden, M., 2019. Spatial mapping shows that some African elephants use cognitive maps to navigate the core but not the periphery of their home ranges. Anim. Cogn. 22, 251–263. https://doi.org/10.1007/s10071-019-01242-9
Proffitt, T., Reeves, Jonathan.S., Pacome, S.S., Luncz, Lydia.V., 2022. Identifying functional and regional differences in chimpanzee stone tool technology. R. Soc. Open Sci. 9, 220826. https://doi.org/10.1098/rsos.220826
Pruetz, J.D., Bertolani, P., Ontl, K.B., 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, Sénégal. R. Soc. Open Sci. 2, 140507. https://doi.org/10.1098/rsos.140507
Read, D.W., 2008. Working Memory: A Cognitive Limit to Non-Human Primate Recursive Thinking Prior to Hominid Evolution. Evol. Psychol. 6, 147470490800600. https://doi.org/10.1177/147470490800600413
Sainburg, T., Mai, A., Gentner, T.Q., 2022. Long-range sequential dependencies precede complex syntactic production in language acquisition. Proc R Soc B 289:, 2020.08.19.256792. https://doi.org/10.1098
Sainburg, T., Mai, A., Gentner, T.Q., 2020. Long-range sequential dependencies precede complex syntactic production in language acquisition. bioRxiv 2020.08.19.256792.
Sainburg, T., Theilman, B., Thielk, M., Gentner, T.Q., 2019. Parallels in the sequential organization of birdsong and human speech. Nat. Commun. 10, 1–11. https://doi.org/10.1038/s41467-019-11605-y
Sanz, C.M., Morgan, D.B., 2010. The Complexity of Chimpanzee Tool-Use Behaviors, in: The Mind of the Chimpanzee: Ecological and Experimental Perspectives. The University of Chicago Press, pp. 127–140.
Schlenker, P., Chemla, E., Schel, A.M., Fuller, J., Gautier, J.P., Kuhn, J., Veselinović, D., Arnold, K., Cäsar, C., Keenan, S., Lemasson, A., Ouattara, K., Ryder, R., Zuberbühler, K., 2016. Formal monkey linguistics: The debate. Theor. Linguist. 42, 173–201. https://doi.org/10.1515/tl-2016-0010
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. Sci. Adv. 5, 1–10. https://doi.org/10.1126/sciadv.aaw0736
Schofield, D.P., 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 Ecol. Evol. 14, 1937–1951. https://doi.org/10.1111/2041-210X.14181

Schofield, D.P., McGrew, W.C., Takahashi, A., Hirata, S., 2018. Cumulative culture in nonhumans: overlooked findings from Japanese monkeys? Primates 59, 113–122. https://doi.org/10.1007/s10329-017-0642-7

Seeds, A.M., Ravbar, P., Chung, P., Hampel, S., Midgley, F.M., Mensh, B.D., Simpson, J.H., 2014. A suppression hierarchy among competing motor programs drives sequential grooming in Drosophila. eLife 3, e02951. https://doi.org/10.7554/eLife.02951

Sellet, F., 1993. Chaine Operatoire; The Concept and Its Applications. Lithic Technol. 18, 106–112. https://doi.org/10.1080/01977261.1993.11720900

Seyfarth, R.M., Cheney, D.L., 2008. Primate social knowledge and the origins of language. Mind Soc. 7, 129–142. https://doi.org/10.1007/s11299-007-0038-2

Shumaker, R., Walkup, K., Beck, B., 2011. Animal Tool Behavior: The Use and Manufacture of Tools by Animals. The John Hopkins University Press, Baltimore, Maryland, USA.

Simpson, J.H., De Bivort, B.L., 2021. Orb weavers: Patterns in the movement sequences of spider web construction. Curr. Biol. 31, R1467–R1469. https://doi.org/10.1016/j.cub.2021.09.066

Stout, D., Apel, J., Commander, J., Roberts, M., 2014. Late Acheulean technology and cognition at Boxgrove, UK. J. Archaeol. Sci. 41, 576–590. https://doi.org/10.1016/j.jas.2013.10.001

Stout, D., Chaminade, T., 2009. Making tools and making sense: Complex, intentional behaviour in human evolution. Camb. Archaeol. J. 19, 85–96. https://doi.org/10.1017/S0959774309000055

Stout, D., Chaminade, T., Apel, J., Shafti, A., Faisal, A.A., 2021. The measurement, evolution, and neural representation of action grammars of human behavior. Sci. Rep. 11, 13720. https://doi.org/10.1038/s41598-021-92992-5

Subiaul, F., 2016. What's Special about Human Imitation? A Comparison with Enculturated Apes. Behav. Sci. 6, 13. https://doi.org/10.3390/bs6030013

Suzuki, R., Buck, J.R., Tyack, P.L., 2006. Information entropy of humpback whale songs. J. Acoust. Soc. Am. 119, 1849–1866. https://doi.org/10.1121/1.2161827

Suzuki, S., Kuroda, S., Nishihara, T., 1995. Tool-Set for Termite-Fishing By Chimpanzees in the Ndoki Forest, Congo. Behaviour 132, 219–235. https://doi.org/10.1163/156853995X00711

Talbot, C.F., Reamer, L.A., Lambeth, S.P., Schapiro, S.J., Brosnan, S.F., 2023. Meeting Cognitive, Behavioral, and Social Needs of Primates in Captivity, in: Robinson, L.M., Weiss, A. (Eds.), Nonhuman Primate Welfare. Springer International Publishing, Cham, pp. 267–305. https://doi.org/10.1007/978-3-030-82708-3_12

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, 1–25. https://doi.org/10.1371/journal.pone.0124733

ten Cate, C., Okanoya, K., 2012. Revisiting the syntactic abilities of nonhuman animals: Natural vocalizations and artificial grammar learning. Philos. Trans. R. Soc. B Biol. Sci. 367, 1984–1994. https://doi.org/10.1098/rstb.2012.0055

Tennie, C., Bandini, E., van Schaik, C.P., Hopper, L.M., 2020. The zone of latent solutions and its relevance to understanding ape cultures, Biology and Philosophy. Springer Netherlands. https://doi.org/10.1007/s10539-020-09769-9

Tennie, C., Call, J., Tomasello, M., 2012. Untrained Chimpanzees (Pan troglodytes schweinfurthii) Fail to Imitate Novel Actions. PLoS ONE 7, e41548. https://doi.org/10.1371/journal.pone.0041548

Tennie, C., Call, J., Tomasello, M., 2010. Evidence for Emulation in Chimpanzees in Social Settings Using the Floating Peanut Task. PLoS ONE 5, e10544. https://doi.org/10.1371/journal.pone.0010544

Tennie, C., Call, J., Tomasello, M., 2009. Ratcheting up the ratchet: on the evolution of cumulative culture. Philos. Trans. R. Soc. B Biol. Sci. 364, 2405–2415. https://doi.org/10.1098/rstb.2009.0052

Terrace, H.S., 2005. The simultaneous chain: a new approach to serial learning. Trends Cogn. Sci. 9, 202–210. https://doi.org/10.1016/j.tics.2005.02.003

Tomasello, M., 1990. Cultural transmission in the tool use and communicatory signaling of chimpanzees?, in: Parker, S.T., Gibson (Eds.), Language and Intelligence in Monkeys and Apes. Cambridge University Press, pp. 274–311.

Tonooka, R., 2001. Leaf-folding behavior for drinking water by wild chimpanzees (Pan troglodytes verus) at Bossou, Guinea. Anim. Cogn. 4, 325–334. https://doi.org/10.1007/s100710100110

Townsend, S.W., Engesser, S., Stoll, S., Zuberbühler, K., Bickel, B., 2018. Compositionality in animals and humans. PLoS Biol. 16, 1–7. https://doi.org/10.1371/journal.pbio.2006425

Van De Waal, E., Borgeaud, C., Whiten, A., 2013. Potent Social Learning and Conformity Shape a Wild Primate's Foraging Decisions. Science 340, 483–485. https://doi.org/10.1126/science.1232769

Van Leeuwen, E.J.C., Cronin, K.A., Haun, D.B.M., 2014. A group-specific arbitrary tradition in chimpanzees (Pan troglodytes). Anim. Cogn. 17, 1421–1425. https://doi.org/10.1007/s10071-014-0766-8

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. J. Hum. Evol. 36, 719–741. https://doi.org/10.1006/jhev.1999.0304

Vereijken, B., Whiting, H., 1998. Hoist by their own petard: The constraints of hierarchical models. Behav. Brain Sci. 21, 705–705. https://doi.org/10.1017/S0140525X98451744

Washburn, M., 1916. Movement and mental imagery. Hougon Mifflin, Boston.

Watson, J., 1920. Is thinking merely the action of the language mechanisms? Br. J. Psychol. 86–104.

Watson, S.K., Burkart, J.M., Schapiro, S.J., Lambeth, S.P., Mueller, J.L., Townsend, S.W., 2020. Nonadjacent dependency processing in monkeys, apes, and humans. Sci. Adv. 6. https://doi.org/10.1126/sciadv.abb0725

Whiten, A., Goodall, J., Mcgrew, W.C., Nishida, T., Reynoldsk, V., Sugiyama, Y., Tutin, C.E.G., Wrangham, R.W., Boesch, C., 1999. Cultures in chimpanzees. Nature 399, 682–685.

Whiten, A., McGuigan, N., Marshall-Pescini, S., Hopper, L.M., 2009. Emulation, imitation, over-imitation and the scope of culture for child and chimpanzee. Philos. Trans. R. Soc. B Biol. Sci. 364, 2417–2428. https://doi.org/10.1098/rstb.2009.0069

Wilson, B., Spierings, M., Ravignani, A., Mueller, J.L., Mintz, T.H., Wijnen, F., van der Kant, A., Smith, K., Rey, A., 2020. Non-adjacent Dependency Learning in Humans and Other Animals. Top. Cogn. Sci. 12, 843–858. https://doi.org/10.1111/tops.12381

Yamakoshi, G., Sugiyama, Y., 1995. Pestle-pounding behavior of wild chimpanzees at Bossou, Guinea: a newly observed tool-using behavior. Primates 36, 489–500.

Yoon, B.-J., 2009. Hidden Markov Models and their Applications in Biological Sequence Analysis. Curr. Genomics 10, 402–415. https://doi.org/10.2174/138920209789177575

Chapter 2

Nonadjacent Dependencies and Syntactic Structure of Chimpanzee Action During a Natural Tool-Use Task

This chapter has been submitted as a manuscript which is under review. The name of this manuscript, and its contents, are identical to this chapter. Elsewhere in this thesis, this chapter is referenced as: Howard-Spink et al., In Review.

Authors

Elliot Howard-Spink[1*], Misato Hayashi[2,3], Tetsuro Matsuzawa[2,4], Daniel Schofield[5], Thibaud Gruber[6§*], Dora Biro[1,7§]

[1] Department of Biology, University of Oxford, Oxford, UK, OX1 3SZ

[2] Chubu Gakuin University, 30-1 Naka Oida-cho, Kakamigahara, Gifu 504-0837, Japan.

[3] Japan Monkey Centre, Kanrin-26, Inuyama, Aichi 484-0081, Japan.

[4] Division of the Humanities and Social Sciences, California Institute of Technology, 1200 E. California Blvd., MC 228-77, Pasadena, CA 91125, USA.

[5] Primate Models for Behavioral Evolution Lab, Institute of Human Sciences, School of Anthropology and Museum Ethnography, University of Oxford, Oxford, UK, OX2 6PE

[6] Faculty of Psychology and Educational Sciences, and Swiss Center for Affective Sciences, University of Geneva, Chem. des Mines 9, 1202 Geneva, Switzerland

[7] Department of Brain and Cognitive Sciences, University of Rochester, Rochester, NY 14627, USA

* Corresponding Authors: Elliot Howard-Spink & Thibaud Gruber

§ Co-senior Authors: Thibaud Gruber & Dora Biro

Keywords: nonadjacent dependencies, hierarchical cognition, sequential action, syntax, mutual information, tool use

Author Contributions: E.H.S., D.B. and T.G. conceived and designed this project. D.B., M.H., and T.M. conducted and oversaw video data collection at Bossou. D.S. processed, cleaned and curated the archive. E.H.S. performed behaviour coding from video data, data analysis, and produced all figures. E.H.S., D.B. and T.G. discussed results and provided comments on the analysis. E.H.S. led the writing of this paper, with all authors contributing suggestions throughout drafting and revisions.

2.1 Summary

The hierarchical organisation of sequential behaviour, and the ability to compensate for nonadjacent sequential dependencies, are fundamental and interrelated abilities for producing complex human behaviours, including language and tool use. Tool use has been identified as a likely candidate behaviour for the existence of these structural properties in nonhuman primates, who appear to lack these same properties in their communication. Using estimations of mutual information (MI) - a measure of dependencies between sequence elements – we show that during a naturalistic tool-use task (nut cracking), chimpanzees produce nonadjacent sequential dependencies at distances exceeding what is expected from null Markov models. Optimal models of MI decay with increasing sequential distance included a power-law component for most individuals, a key indicator of hierarchical organisation of behaviour. We discuss these findings alongside hypotheses for the coevolution of complex syntax in language and tool-action, and methodological considerations for the use of MI decay models.

2.2 Introduction

Many behaviours of both humans and non-human animals (henceforth animals) can be considered sequences of discrete actions. Therefore, understanding how both humans and animals generate, store and retrieve such sequences is key to understanding the cognition supporting these serial behaviours. One simple way sequences may be produced is through associative chains, where the production of one action triggers the production of a subsequent action, which in turn predicts a further action, and so forth throughout sequence production. In such an instance, the rules of how elements are probabilistically related to their neighbours can be generalised as Markovian grammars - a finite-state grammar system which probabilistically predicts the occurrence of any element in a sequence, based on the element that precedes it (Gagniuc, 2017).

For a number of combinatorial systems, including the assembly of phonemes into words in human language (Kaplan and Kay, 1994), or the concatenation of animal calls into bouts of vocal communication (Fitch et al., 2005; Hauser et al., 2002; ten Cate and Okanoya, 2012, with the exception of bird/cetacean song – see below), generated sequences often possess the Markov property: each element in a sequence

is predictable by the element which precedes it, and this predictability rapidly decreases when consulting elements which are increasingly further away in a sequence. However, for more elaborate sequential behaviours, Markovian grammars are argued to be incapable of supporting the complexity of observed sequential dynamics, including in the sequences of actions in tool use (Fitch and Martins, 2014; Greenfield, 1991; Greenfield and Schneider, 1977; Lashley, 1951; Stout et al., 2021), syntax in human language (Chomsky, 1956, 2002a; Fitch et al., 2005; Jäger and Rogers, 2012; Lashley, 1951) and music (Asano and Boeckx, 2015; Cheung et al., 2018; Koelsch et al., 2013), and animal songs (Miksis-Olds et al., 2008; Sainburg et al., 2019; Suzuki et al., 2006). Markovian grammars lack the ability to simultaneously balance directedness and flexibility in sequence production, and therefore are unable to support highly flexible and generative behaviours such as sequential action and tool use, language, music and animal song (Byrne et al., 2013; Chomsky, 2002a; Dawkins, 1976; Isac and Reiss, 2013; Lashley, 1951). In addition, purely Markovian grammars for complex behaviours are argued to be evolutionarily unstable. Markovian grammars of action would require the use of uneconomical neural underpinnings to produce complex sequential behaviours; and, if used to generate sequences in their totality, Markovian grammars would be unable to produce the necessary subroutines required to confer stability in extended sequences (see the redundancy reduction advantage and evolutionary rate advantage in Dawkins, 1976). Importantly, Markovian grammars also fail to account for the presence of nonadjacent dependencies within many observed sequential behaviours, including human language (Chomsky, 2002a; Isac and Reiss, 2013; Sainburg et al., 2019), whale song (Miksis-Olds et al., 2008), birdsong (Sainburg et al., 2019), and the sequential action of humans and animals (Greenfield, 1991; Greenfield and Schneider, 1977; Sainburg et al., 2020).

Conversely, hierarchical structuring is believed to offer greater flexibility, generativity, and evolutionary stability for the production of complex sequential behaviours (Chomsky, 2002b; Dawkins, 1976; Fitch and Martins, 2014; Isac and Reiss, 2013; Lashley, 1951; Rosenbaum et al., 2007). Hierarchical sequencing allows for the combination of elements into short subroutines, which may then be themselves organised into longer sequences, which in turn may be combined, and so on to produce an extended bout of behaviour (Byrne et al., 2013; Dawkins, 1976; Fitch and Martins, 2014; Lashley, 1951). Therefore, hierarchical structuring allows for sequences to be produced from repeatable subroutines of behaviours at

multiple levels, and can facilitate the production of sequential behaviours which address nested sub-goals within a wider goal-directed behaviour (Fitch and Martins, 2014; Lashley, 1951). Hierarchical sequencing also readily generates nonadjacent dependencies within sequential behaviours. Nonadjacent dependencies can emerge during hierarchical structuring through the embedding of subroutines within other subroutines. Within language, this is reflected when a clause is embedded within another clause (Chomsky, 2002b, 1956; Fitch and Martins, 2014; Jäger and Rogers, 2012; Lashley, 1951; Sainburg et al., 2022, 2019); e.g. in the sentence "*The weather is horrible!*", a prepositional phrase may be embedded to produce the sentence "*The weather [outside the window] is horrible!"*. Such a sentence may then feature distant dependencies, where the verb 'is' and adjective 'horrible' both relate to the noun at the head of the phrase (the weather), despite being closer to the noun of 'the window' in space and time. Further long-distance dependencies in language include subject-verb agreements, where the nature of the subject (gender, number, etc.) may influence the morphology of its corresponding verb, irrespective of how far separated they are in linear space and/or time (Mel'čuk, 1988; Rispens and Soto de Amesti, 2017). Within sequential action, nonadjacent dependencies occur when a series of actions addressing one subgoal are embedded within a sequence of actions addressing another goal. For example, when opening a door an actor may grasp, turn, and push the handle. However, if the door is locked, the actor may grasp the handle, then begin eliciting a number of actions to open the lock (thus completing the embedded subgoal: undo the lock), before continuing to turn and push the handle to open the door (wider goal: open the door). In such an example, grasping a handle always precedes turning a handle; however, they may be separated by an embedded string of actions, producing a nonadjacent dependency similar to what is seen in language.

Whilst nonadjacent dependencies are the product of more flexible and goal-directed sequence generation, they present the need for individuals to remember, trace and match dependencies across sequences during online production (Fitch and Hauser, 2004; Wilson et al., 2020). Therefore, nonadjacent dependencies present a number of cognitive challenges to sequence production and interpretation, including challenges to planning and working memory (Fitch and Hauser, 2004; Wilson et al., 2020). Thus, despite the higher generativity of hierarchical sequencing, it comes at a greater cognitive cost than memoryless, Markovian systems of sequence production, which are able to operate using simpler computational resources. Consequently, the evolution of highly hierarchical organisations of behaviour can

only be expected when the fitness benefits of high generativity and flexibility in sequential organisation of a behaviour outweigh the costs of maintaining its underlying neural architecture.

Despite the adaptive utility of hierarchical structuring, its distribution across both behaviours and taxa presents an interesting evolutionary puzzle. This is especially true within the domain of communication. Among communication systems, strong evidence for hierarchical structuring is confined to human language (Chomsky, 2002b, 1956; Fitch and Martins, 2014; Jäger and Rogers, 2012; Sainburg et al., 2022), and the songs of birds and whales (Miksis-Olds et al., 2008; Sainburg et al., 2019). Given the lack of intermediary species also possessing hierarchical systems of communication, this shared property of human, bird and whale communication is likely a result of convergent evolution. Of these species, the evolution of hierarchical syntax in human language, as well as the processing of nonadjacent dependencies, is of particular interest, as human language is currently the only known semantically-meaningful communication system to possess these structural properties (Berwick et al., 2011; Rohrmeier et al., 2015). The evolution of hierarchical structuring in human language, and the abilities of humans for naturally producing and processing nonadjacent dependencies, therefore reflects an enduring open question (Fitch et al., 2005; Fitch and Martins, 2014; Hauser et al., 2002; Sainburg et al., 2019; Watson et al., 2020).

Using nonhuman primates as comparative models, it is possible to gain valuable insights into the phylogenetic breadth, adaptive utility, and possible homologous origins of human cognition for hierarchical organisation and nonadjacent-dependency processing. This is especially true for chimpanzees (P*an troglodytes*) and bonobos (*Pan paniscus*), where common behavioural traits across humans, chimpanzees and bonobos likely reflect a shared evolutionary origin (Gruber and Clay, 2016). Nonhuman primates habitually employ non-random sequences of calls (Arnold and Zuberbühler, 2012; Clay and Zuberbühler, 2009; Girard-Buttoz et al., 2022; Hedwig et al., 2015, 2014; Leroux et al., 2023, 2021; Leroux and Townsend, 2020; Schlenker et al., 2016a, 2016b) and gestures (Genty and Byrne, 2010; Hobaiter et al., 2017; Hobaiter and Byrne, 2011; Tanner and Perlman, 2017) within their natural communicative behaviours; however, there is little evidence that combinations reflect hierarchical structures (Fitch et al., 2005; Girard-Buttoz et al., 2022; Hauser et al., 2002; ten Cate and Okanoya, 2012; Traxler et al., 2012), and even less for the presence of nonadjacent dependencies. Despite scant evidence for hierarchical structuring and nonadjacent dependencies in the natural communicative repertoires of nonhuman primates,

artificial grammar experiments suggest that some primates are able to detect nonadjacent dependencies both in visual (Sonnweber et al., 2015) and auditory domains (Milne et al., 2016; Watson et al., 2021, 2020; Wilson et al., 2013); however, it is important to note that other primates have failed to learn auditory grammars containing nonadjacent dependencies when used in similar paradigms (Fitch and Hauser, 2004; Wilson et al., 2013). Given the tentative evidence that nonhuman primates can account for nonadjacent dependencies within experimental stimuli, it is possible that nonhuman primates have the cognitive capacity to trace nonadjacent sequential dependencies, despite not habitually employing such structuring during communication. Nonhuman primates may therefore naturally employ such structuring to produce complex, flexible strategies in other domains of behaviour, such as in sequential action and tool use.

Within the domain of action, tool use has been highlighted as a behaviour which likely possesses high hierarchical complexity (Byrne and Russon, 1998; Greenfield, 1991; Stout et al., 2021). The process of producing, using and disposing of a tool may be partitioned into stages with their own unique sub-goals (Byrne et al., 2013; Byrne and Russon, 1998; Lashley, 1951), and when using tools, hierarchical relationships may emerge between tool objects (Byrne et al., 2013; Greenfield, 1991; Hayashi, 2007; Hayashi and Takeshita, 2022; Matsuzawa, 1991; Sanz and Morgan, 2010). Both the presence of substages within tool production and use, and hierarchical relationships between tool objects, have been qualitatively described for great apes (Byrne and Russon, 1998; Hayashi, 2015; Hayashi and Takeshita, 2022; Matsuzawa, 1996, 1991; Sanz and Morgan, 2010; see Matsuzawa 1996 for tree-structure analysis of tool relationships, and Figure 1a. for a graphical representation of tool relationships during nut cracking), with a particular emphasis on the tool behaviours of chimpanzees (Boesch et al., 2020; Byrne et al., 2013; Carvalho et al., 2008; Estienne et al., 2017; Hayashi, 2015; Hayashi and Takeshita, 2022; Matsuzawa, 1996, 1991; Sanz and Morgan, 2010; Tonooka, 2001). However, relying on qualitative descriptions to characterize hierarchical structures in sequential action have received criticism: the description of a behaviour as hierarchical by human observers does not exclude the possibility that non-human apes are relying on Markovian generative grammars to produce complex sequences of action (Vereijken and Whiting, 1998). Furthermore, the extent to which apes produce and account for nonadjacent dependencies during sequential tool-use behaviours remains unknown. Therefore, there is a need for quantitatively powerful methodologies that can evaluate, verify, and exclude hypothesised grammars of action from

observed sequences of behaviours. Additionally, empirical investigation of possible nonadjacent dependencies within the sequential tool action of nonhuman primates will likely offer key insight into the ways in which they produce and compensate for nonlinear sequential dependencies during ecologically-relevant behaviours.

To better characterise the sequential organisation of actions during tool-use behaviours, and the extent to which such behaviours produce nonadjacent dependencies, we herein draw upon models of mutual information (MI) decay. Mutual information (MI) refers to the predictability of a given sequence element when the state of another element elsewhere in the sequence is known. MI often decreases between elements separated by greater distances; for example, looking out of a window at the weather one morning provides some information about the likely weather events that same afternoon. However, knowing the weather several days, or weeks prior would carry increasingly less information about the likely weather conditions in the upcoming afternoon. As Markovian grammar systems produce sequences based on neighbouring probabilistic dependencies, they exhibit exponential decreases in MI between elements separated by increasing sequential distances (Lin and Tegmark, 2017). Alternatively, hierarchical grammar systems are able to readily produce long-distance dependencies between elements, and as such, show higher MI scores between distantly separated elements, which decay following a power-law dynamic (Sainburg et al., 2022, 2019). Hierarchical and Markovian structuring mechanisms may also be combined to form a composite structure (Sainburg et al., 2022, 2019), where shorter, Markovian strings are hierarchically organised to produce longer sequences. Sequences produced by composite structuring may then display MI decay dynamics that are best approximated by exponential decay for sequential elements in close proximity, and power-law decays for elements separated further across sequences. MI decay dynamics have been used to evaluate corpora of human and non-human vocal behaviours (Sainburg et al., 2022, 2019), as well as the sequential actions of humans, zebrafish and fruitflies (Sainburg et al., 2020). In the present study, we employ MI decay models to investigate two overlapping research questions, concentrating on the sequential organisation of serial action in chimpanzee tool use:

[1] Do chimpanzees produce nonadjacent dependencies within their sequential actions during tool-use behaviours?

[2] What do the dynamics of MI decay in chimpanzee tool-action sequences suggest about their underlying grammars of production (Markovian, hierarchical, or a composite system)?

To answer these questions, we focus on the sequential organisation of actions used by wild West-African chimpanzees (*Pan troglodytes verus*) when engaging in one of their most complex natural tool-use behaviours: the cracking of hard-shelled nuts with hammer and anvil stones. Through MI estimations, we demonstrate that observed sequences of tool action possess sequential dependencies at significantly greater distances than those predicted by simulated Markov models. We also report that the sequences of actions used by chimpanzees during nut-cracking yield MI decay profiles that are concurrent with previous qualitative descriptions of hierarchical structuring in the tool action of apes. We compare this result to MI decay dynamics of sequences produced by simulated Markov models; we find that whilst models of MI decay have a moderate false-positive rate for identifying hierarchical decay types from Markovian sequences, MI decay from chimpanzee action sequences is identified as following a composite/power-law at much higher rates than can be expected by false identification of Markovian sequences alone. Thus, our findings provide novel insights into non-human apes' capacity to draw upon non-Markovian rules of sequence production, including nonadjacent dependencies, during a natural behaviour: tool use. In extension, our findings feed into the wider discussion surrounding the hierarchical abilities of animals, as well as possible homologous origins of hierarchical action processing between humans and our sister species.

2.3 Results

2.3.1 Sampled sequence data

We analysed a total of 251.85 min of video data from the 2011/2012 field season, yielding action sequences from nine individuals during their interactions with nuts, nut fragments or stone tools (see Table 1). Within our analyses, actions were compound descriptions of both the functional movement produced by an individual, and the focal object of the action (e.g., "Place Nut" = 1 element - see the methods section *behaviour coding* for further information). Of these nine individuals, one (Velu) had fewer than 200 actions coded throughout the entire series of sampled videos. As entropy estimation from small sample sizes can be subject to high levels of error (Grassberger, 2003), this individual was omitted from our MI analyses.

Subsequently, eight individuals (two adult females: Fanle & Jire; four adult males: Foaf, Jeje, Peley & Tua; one juvenile female: Joya; and one infant male: Flanle) were included in our MI analyses, as we had documented a corpus of over 200 actions for each individual.

Across the eight individuals in our dataset, we recorded action sequences for the cracking of 303 individual nuts, using 8,261 coded actions of 82 different action types (where action types are unique categories of actions, e.g. 'Touch Hammer', 'Touch Hammer' would represent two actions, but just one action type; however, 'Grasp Hammer', 'Drop Hammer' would represent two actions of two distinct action types). The number of action types per individual ranged from 18 (Foaf) to 59 (Flanle, the youngest individual, who engaged in multiple bouts of solo play with stone tools), with an average of 40 unique action types per individual. For the youngest individuals, Flanle and Joya, the extended number of action types employed included those associated with object exploration, such as 'Bite Hammer', and 'Kiss Nut'. Across action types, adult chimpanzees relied on a small subset of high-frequency actions to facilitate nut-cracking, with the five most common actions including 'Strikeonehand Hammer' (24.6%), 'Eat Kernel' (11.8%), 'Grasp Nut' (10.5%), 'Place Nut' (8.6%), and 'Grasp Kernel' (8%; in total, 63% of all actions within our dataset fell into one of these five action types). However, these highly frequent actions were supplemented by an extended number of less-frequent actions during observed sequences of behaviours, with observable variability in the diversity and frequency of supplementary actions used by different individuals (see Fig. 1b & 1c).

2.3.2 Maximum inter-element distance MI detected

To evaluate the maximum sequential distances over which dependencies occur, we identified the maximum inter-element distances where MI was greater than zero, using an MI metric that was adjusted to account for chance relationships in the data (MI_{Adj}). To determine whether the maximum sequential distances over which dependencies occurred was greater than what could be expected from equivalent Markovian sequences, Markov models were approximated for each individual using observed action sequences (see Fig. S3 for graphical depictions of Markov models). We simulated 100 sequences from each Markov model, and estimated the sequential distance at which MI_{Adj} fell to zero (see Fig. S4 for distributions). We then

constructed probability distributions for where MI_{Adj} should fall to zero for each individual, if their action sequences were produced by a Markovian grammar.

On average, the maximum sequential distances where MI_{Adj} remained above zero was 30.3 elements (N = 8, SD = 29.9; see table 3); for Flanle, MI_{Adj} did not fall to zero before the maximum distance of 100 sequence elements. When excluding Flanle from this average, for whom the maximum distance over which dependencies were detected was over two standard deviations higher than all other individuals, the mean maximum sequential distance at which MI_{Adj} was positive was 20.3 elements (N = 7, SD = 10.8). For six individuals (Fanle, Flanle, Jeje, Joya, Peley and Tua), MI_{Adj} was determined to be above zero for sequential distances that were significantly greater than those found in counterpart Markovian sequences (identified by a higher inter-element distance where MI_{Adj} was positive compared to the upper 95% CI of the Markov distribution; see Fig. 2a and Table S3). For two individuals, (Foaf & Jire), the inter-element distance at which MI_{Adj} fell to zero was within the 95% CI for the corresponding Markov distributions for each individual. Therefore, for these individuals, the inter-element distance at which MI_{Adj} fell to zero was not significantly different from Markov sequences.

To determine whether successive repeats of elements (e.g. repeatedly striking a hammer) influenced the maximum inter-element distance where MI_{Adj} was above zero, observed action sequences were passed through a condensing algorithm that removed repeated elements, and MI_{Adj} was estimated in the same way as before. Separate Markov models were also constructed from condensed data, and distributions describing the maximum distance at which MI_{Adj} was greater than zero were constructed for Markov sequences (see Fig. S5 for distributions). For the condensed action sequences, the mean sequential distances where MI_{Adj} was above zero was 13.3 elements (N = 8, SD = 5.9). Flanle showed the largest decrease in the maximum distance where MI_{Adj} was greater than zero, reducing from possibly over 100 elements, down to 9 sequence elements. For three individuals (Fanle, Peley and Tua), the distances at which MI_{Adj} were detected as above zero remained above the upper 95% CI for Markov sequences (see Fig. 2a and Table S3). Following sequence compression, three individuals (Flanle, Joya and Jeje) no longer showed a significantly greater inter-element distance where MI_{Adj} was above zero compared to Markov sequences; this was also the case for the two individuals where the maximum inter-element distances

where MI_{Adj} was positive previously showed no significant difference between observed and Markovian sequences (Foaf and Jire).

2.3.3 MI decay analysis: observed action sequences

For all individuals, we capped datasets at the maximum sequential distance MI_{Adj} was detected to be greater than zero. We then characterised the decay dynamics of MI_{Adj} as the inter-element distance increased from 1 to the maximum distance for each individual's MI_{Adj} dataset. Exponential, power-law, and composite decay models were all fitted to each decay profile (see Fig. 2b), and the performance of each model in characterising MI_{Adj} decay was evaluated using AICc (where lower values represent a better explanation of the data, relative to the number of model parameters).

For seven out of eight individuals, MI_{Adj} decay was best characterised by a model which included a power-law decay dynamic (see Fig. 2b and Table 3; see Table S4 for AICc values). The MI_{Adj} decay profiles of two individuals (Flanle and Jire) were best explained by a purely power-law model; while for five individuals (Flanle, Jeje, Joya, Peley and Tua), the optimal decay model was identified as the composite model, which combines periods of exponential and power-law decay. For one individual (Foaf), the exponential model was identified as the optimal model.

Similarly to the previous analysis on maximum inter-element distances where MI_{Adj} was greater than zero, we repeated the analysis above on condensed sequences to ensure power-law relationships were not simply a product of highly repetitive elements (see Table 2). For the condensed sequence data, the MI_{Adj} decay profiles of six individuals were still best explained by a single model. Five decay profiles were best explained by a model which included a period of power-law decay (two by a purely power-law, and three by a composite model). For two individuals (Jeje and Jire), multiple models offered competing explanations of decay dynamics; for sequence data collected from Jeje, the composite and exponential models offered competing explanations of the data; whereas for Jire, the power-law and exponential models exhibited similar explanatory power. For the MI_{Adj} decay profile for Foaf, the exponential model continued to offer the best explanation of the data following sequence compression.

2.3.4 Transition points for composite models

For each individual for whom our analysis showed a preference for the composite decay model, we also identified the transition point between primarily exponential and primarily power-law decay dynamics through the second differential of the curve in log-space (see Fig. 2c.; see Methods section *Estimating Transition Points in Composite Model*). The maximum sequential distance prior to the transition between exponential and power-law decay dynamics ranged from 2-8 elements (mean = 4.6 elements, N = 5; see Table 3; see Fig. S6 for transition point profiles for each individual whose MI_{Adj} is best explained by the composite model). This implies that for individuals whose sequence structure is best approximated by composite models, Markovian structuring dynamics most likely extend to elements 2-8 elements apart. These local associations may then be hierarchically combined, resulting in distant-dependencies across longer timescales.

2.3.5 MI decay analysis: markovian sequences

It is possible that highly-directed Markov models may reproduce sequences with regularities occurring between nonadjacent sequence elements. More numerous nonadjacent regularities would lead to higher MI_{Adj} estimates at greater sequential distances (and a subsequent bias towards erroneous identification of grammar models associated with power-law decays). Therefore, we created a number of 'community' Markov models (trained on action-sequences from all individuals) to act as a negative control, where we can estimate a false positive rate for the identification of power-law and composite decay dynamics from Markovian sequence data (see methods section *Markov Models and Simulated Sequences*). The four community Markov models include: (1) A Markov model trained on the entire corpus of action-sequence data; (2) a Markov model trained on a condensed version of all action-sequence data; (3) a Markov model trained on the entire corpus of action-sequence data, and then homogenised for all transition probabilities to be equal; and (4) a Markov model trained on a condensed version of the entire corpus of action-sequence data, and then homogenised for all transition probabilities to be equal (see Fig. S7 for graphical representations of community Markov models). For all of these models, 500 sequences were produced, each 1000 elements long, and MI_{Adj} was estimated between 0-100 elements.

For the 500 sequences produced by all four Markov models, a subset of MI_{Adj} decay datasets failed to fit all three models. We omitted these datasets from our comparisons, and evaluated the proportion of remaining MI_{Adj} decay datasets which were best characterised by exponential, power-law, and composite decay dynamics.

For the Markov model trained on the entire corpus of action-sequence data, including repeating elements (model 1), all three decay models were successfully fitted for 425 MI_{Adj} decay datasets. There was a significant positive relationship between the maximum sequential distance at which MI_{Adj} was above zero, and the likelihood of successfully fitting all three models (Binomial GLM with Logit Link: Success ~ Maximum Sequence Length, N = 425; Intercept: -9.25; Maximum Length: 1.53; Z = 8.96; $p < 0.001$; see Fig. 3a), and this relationship held for all four Markov models (see Table S5 for all model outputs.).

Of the 425 model comparisons, AICc identified a single best model for characterising MI_{Adj} decay for 340 datasets (80% of all model comparisons). 52.5% of model comparisons identified the exponential model as highly competitive. In 37.6% of model comparisons the exponential model was identified as the sole best performing model, and in 14.3% of comparisons the exponential model was identified as one of multiple equally optimal models (see Fig. 3c). 16.5% of comparisons showed a sole preference for the power-law model, and 25.9% of comparisons showed a sole preference for the composite model.

Of the 500 sequences produced by a Markov model trained on the condensed version of the total corpus of action sequences (model 2), 442 datasets permitted three-way model comparisons (see Fig. 3c). 59% of comparisons identified the exponential model as highly competitive (53.4% as the sole model preference, and 5.7% tied with other models). 0.68% of comparisons identified the power-law model as the sole optimal model, and 40% of comparisons identified the composite model as the sole optimal model.

For the Markov model that was trained on action sequences with repeating elements, and had transition probabilities homogenised (model 3), 456 datasets permitted model fitting. 63.4% of comparisons identified the exponential model as highly competitive (26.5% as the sole model preference, and 36.8% tied with the power-law model). 30.4% of comparisons identified the composite model as the sole preference, and the 6.1% of comparisons identified the power-law. Similar selection rates for each model type were observed when analysing sequences from the homogenised Markov model trained on condensed sequences (model 4). From 468 datasets, 71.4% of comparisons identified the exponential model as highly

competitive (32.3% as the sole model preference, and 39.1% tied with the power-law model). 26.1% of comparisons identified the composite model as the sole preference, and the 2.6% of comparisons identified the power-law as the sole optimal model (see Fig. S8 for pie-charts of both datasets from homogenised Markov models).

For the corpus of datasets produced by each Markov model, where a preference was found for solely one candidate decay model, we investigated whether this was related to the maximum sequential distance over which MI_{Adj} was positive in the provided datasets. For all community Markov models, we found a significant difference in the mean maximum sequential distance MI_{Adj} was positive for datasets which showed a sole preference for each type of decay model (see Table S6 for all model summaries); however, the order in which model preference varied with data-set size differed between the different community Markov models. For the Markov model that was trained on observed action sequences, and included repeating actions (model 1), exponential decay models were more commonly preferred in MI_{Adj} datasets with shorter maximum sequential distances; whereas power-law decay models were preferred when maximum sequential distances were intermediary, and composite decay preferred with greater maximum sequential distances (Output of GLM fit to data from Community Markov model 1: Max Sequence Length ~ Model Preference; Intercept: coefficient = 2.12, SE = 0.027, Z = 77.3, $p < 0.001$; Power-Law: coefficient = 0.22; SE = 0.046, Z = 4.75; $p < 0.001$; Composite: coefficient = 0.45, SE = 0.38, Z = 11.9, $p < 0.001$; see Fig. 3b for distributions; see Table S6 for model summary). For the Markov model trained on condensed action sequence data (model 2), datasets with shorter maximum sequential distances favoured the composite model; whereas intermediary and longer maximum sequential distances preferred the exponential model and power-law model equally (GLM output for data from model 2: Intercept: coefficient = 2.15, SE = 0.022, Z = 96.5, $p < 0.001$; Power-Law: coefficient = 0.012; SE = 0.19, Z = 0.061; $p = 0.952$; Composite: coefficient = -0.34, SE = 0.038, Z = -8.99, $p < 0.001$). For both of the homogenised Markov models (models 3 & 4), shorter maximum sequential distances led to a preference for fitting the exponential model; intermediary maximum sequential distances led to a preference for the composite model; and greater maximum sequential distances led to a preference for the power-law model (Model 3: Intercept: coefficient = 1.28, SE = 0.048, Z = 26.7, $p < 0.001$; Power-Law: coefficient = 0.87; SE = 0.08, Z = 10.81; $p < 0.001$; Composite: coefficient = 0.40, SE = 0.06, Z = 6.55, $p < 0.001$. Model 4: Intercept: coefficient =

1.19, SE = 0.045, Z = 26.3, p < 0.001; Power-Law: coefficient = 0.86; SE = 0.11, Z = 7.63; p <0.001; Composite: coefficient = 0.51, SE = 0.059, Z = 8.57, p < 0.001).

2.4 Discussion

The hierarchical structuring of behaviour, and the presence of nonadjacent dependencies within sequences, exist across numerous domains of behaviour in humans (Chomsky, 2002b; Dawkins, 1976; Fitch and Martins, 2014; Lashley, 1951; Mel'čuk, 1988; Rispens and Soto de Amesti, 2017; Rosenbaum et al., 2007; Wilson et al., 2020). However, these cognitively demanding systems of sequential organisation are sporadically distributed across animal taxa, raising a number of questions surrounding the emergence and evolution of complex sequential behaviours. In particular, understanding the presence of these structuring mechanisms across human behaviours would be aided through the use of non-human primates as comparative models, where the presence of shared hierarchical behaviours may reflect homologous evolutionary origins. The purpose of this study was: (1) to determine whether chimpanzees regularly produce nonadjacent dependencies within their sequential actions during tool use, and if so (2) to determine whether the reduction in frequency of nonadjacent dependencies with increasing sequential distances support previous descriptions that chimpanzees rely on hierarchical organisation of behaviour during tool action. To answer both of these questions, we analysed 251.85 minutes of video footage, and coded 8261 actions of eight wild chimpanzees at Bossou, Guinea, as they spontaneously produced sequential actions during a natural tool-use task (nut cracking). For our analysis, dependencies between sequence elements were estimated using mutual information scores that are adjusted to compensate for the occurrence of chance relationships (MI_{Adj}).

To determine whether nonadjacent dependencies occur in the sequential organisation of chimpanzee tool action - and whether they occurred at distances greater than what could be expected by sequences produced by Markovian structuring - we compared the maximum sequential distances at which MI_{Adj} was greater than zero to a distribution of maximum distances produced from simulated Markovian data. For six out of eight of individuals, including four out of six adults (we take adulthood to be a proxy for experience in tool-use), nonadjacent dependencies were identifiable at sequential distances which significantly exceeded those produced in simulated Markovian sequences. To determine the extent to which

nonadjacent dependencies were caused by repeats of actions, we ran an identical analysis on condensed sequence data, where repeating elements were replaced by a single action. Following sequence compression, three out of eight individuals (including three out of six of adults), produced dependencies at greater sequential distances than those found in Markov models. The greatest reduction in the maximum sequential distance over which dependencies were detected was for Flanle, an infant male (distance before compression: 100 elements; distance following compression: 9 elements). As the youngest individual in our analysis, Flanle was highly inexperienced in nut cracking and only observed to crack open a single nut during the period of observation (for contrast, the other seven individuals for our analysis cracked a total of 302 nuts; mean = 43 nuts each, SD = 26.9). Many of the action sequences produced by Flanle involved play behaviours with stone tools, which may have contributed to the production of repetitive actions, and dependencies between distant elements. It is also possible that the greater flexibility seen in Flanle's behaviours with nuts and stone tools may have influenced estimations of MI_{Adj} at greater sequential distances. Flanle demonstrated the highest number of action types (59), indicating a greater diversity of different action types compared to the action sequences of adult chimpanzees during nut cracking (for whom action sequences were highly stereotyped on a small number of actions). Exactly how estimations of MI are influenced by the number of sequence-element types, and the repetition of elements, within biological systems requires further investigation. This is particularly true for goal-directed action, where individuals may vary in both the goals of their behaviour (e.g. play vs. nut-cracking), and the flexibility with which they approach behaviours (i.e. stereotyped using few action types vs. flexible with many possible action types). Additionally, the relationship between how individuals learn tool-use behaviours, how this influences the sequences of actions employed during tool-use, and how individuals ultimately produce and account for distant dependencies is of interest, and is a recommended direction for future study.

Thus, our data suggest that for the sequential actions produced by multiple chimpanzees during stone-tool use, nonadjacent dependencies occur at distances which cannot be accounted for by equivalent Markov models. However, the extent to which these dependencies are driven by repeating actions is variable, with three of six adult chimpanzees maintaining dependencies at greater distances than Markov distributions following sequence compression. Tool use may therefore represent an ecologically-relevant behaviour where chimpanzees naturally produce and account for sequential dependencies between

nonadjacent actions, including through repetition of actions, as well as through more systematic organisation of behaviour. This finding is supported by previous studies on the ability of chimpanzees to detect nonadjacent sequential dependencies in visual and auditory grammar learning paradigms (Sonnweber et al., 2015; Watson et al., 2020), and expands on such studies to exemplify how such abilities may be adaptive within the ecology of wild chimpanzees.

The sequential manual actions of non-human apes – including those used in tool-use – have previously been described using qualitative frameworks which either explicitly, or implicitly, encompass hierarchical organization (Boesch et al., 2020; Byrne et al., 2013; Byrne and Russon, 1998; Carvalho et al., 2008; Estienne et al., 2017); however, it is empirically challenging to exclude the possibility that these action sequences are produced by simpler structuring mechanisms (Vereijken and Whiting, 1998). We investigated the dynamics of MI decay across increasing sequential distances to evaluate the likelihood of action sequences being produced by Markovian, hierarchical, and composite systems of organisation (which respectively predict exponential, power-law, and composite decay in MI with increasing sequential distances). For action sequences produced by five of the eight chimpanzees sampled, the decay of MI with increasing sequential distances was best approximated by a composite decay model, which involves exponential decay of MI between elements at close proximity, and power-law decay of MI for elements separated by extended sequential distances. MI decay dynamics for one individual (Foaf) was best explained by a purely exponential model, possibly reflecting a reliance on Markovian sequencing of action in tool use by Foaf. However, this result could also be a product of a highly reduced sample size for Foaf (299 actions), where the opportunity to detect dependencies at greater distances is limited. For two individuals, MI decay was best described as a power-law relationship, thus reflecting what would be expected if their action sequences were structured purely hierarchically. Thus, for seven out of eight individuals, MI decay was best described by models which predict part or wholly hierarchical organisation of sequences.

Similarly to our previous analysis, we deemed it important to run the MI decay analysis on condensed action sequence data. Repeating elements may inflate MI estimates at greater sequential distances, preventing MI from decaying at the accelerating rate of the exponential model (thus biassing data to fit a power-law or composite model). Following sequence compression, the MI decay profiles for

three individuals were best explained by the composite decay model. For the action sequences of two individuals, MI decay following sequence compression was best described by the power-law model. Thus, for five of eight individuals, MI decay was best explained by a model which either included or consisted solely of a power-law decay term. In the action sequences produced by Jeje and Jire, MI decay was best explained by two models (AICc values: Jeje: Composite AICc = -43.0, Exponential = -41.2; Jire: Power-Law = -42.7, Exponential = -42.2). Whilst in both cases the AICc values for models involving periods of power-law decay offer slightly better explanatory power with respect to their complexity, the proximity of these AICc scores to those offered by the exponential decay models prevents us from concluding that these models are superior (difference in AICc < 2). Thus, following sequence compression, exponential models offer equal explanatory power for MI decay to the composite model in the case of Jeje, and the power-law model in the case of Jire. For one individual, Foaf, the exponential model continued to offer the best explanation of MI decay following sequence compression.

Overall, for seven of eight individuals, MI decay across action sequences was best characterised by models that include a period of power-law decay, and following compression, this fraction was five of eight individuals. We compared this ratio to a number of Markov generated sequences, which allowed us to determine the rate that model selection preferred models which contained periods of power-law decay (akin to a false-positive rate, where decay associated with hierarchical structuring was identified from Markovian sequences). For Markov sequences which featured repeating actions, models containing sections of power-law decay were identified as the sole preferred model in 42.4% of instances (16.5% for power-law, and 25.9% for composite), and exponential models were the sole preference in 37.6% instances. Thus, if chimpanzees were producing action sequences through Markovian structuring, we would expect models containing power-law decay to be the optimal model for approximately three out of eight individuals (observed data showed this preference for seven of eight individuals). Markov models which were trained using condensed data had a lower rate of identifying power-law relationships in MI decay, with the exponential model being the solely preferred in 53.4% of instances, the composite model in 40% of instances, and the power-law decay model in 0.68% of instances. Thus if action sequences were produced using Markovian structuring, and we remove the influence of repeated actions on MI decay, approximately four of eight individuals should show a sole preference for the exponential model (from

observed action sequence data, one of eight MI decay profiles was best explained by the exponential model); approximately three individuals should show a preference for the composite model (a match to the observed action-sequence data), and no individuals should show a preference for the power-law model (in observed data, this was two of eight individuals). Our analysis therefore provides two key insights: (1) when characterising MI decay from Markovian action sequences, model selection may prefer models which have a period of power-law decay (a result more often associated with hierarchical processes of sequence production) at a non-negligible rate, and (2) for the action sequences we observed in chimpanzee tool use, the rate at which power-law and composite models were preferred over exponential models exceeds the rates of model preferences when analysing equivalent Markovian sequences. Therefore, for observed action sequences, the preferences for power-law and composite models are unlikely due to a 'false positive' of identifying characteristically hierarchical decay dynamics from Markovian data.

We also investigated whether the Markov models trained on highly stereotyped sequential actions (as seen in chimpanzee tool-use) may in fact be able to reproduce the entire sequences of actions used to crack open nuts during chimpanzee tool-use, due to the fact that actions may have extremely high transition probabilities throughout nut processing. Under such circumstances, it may be possible for Markov models to produce longer strings of predictable elements, leading to distant dependencies and power-law decay dynamics. After homogenising transition probabilities in the Markov models - thus disrupting highly predictable action transitions - we found that there was a change in the rates of preferences for all three models; however, it did not necessarily permit exponential decay to be more readily identified. On the contrary, the preference for power-law decay dynamics increased following homogenization of transition probabilities, leading to a more common simultaneous preference for both power-law and exponential decay (and in the case of both the condensed Markov model, and the Markov model with repeating actions, there was a decrease in the rate at which the exponential model was identified as the sole preference during model comparison). Thus, the power-law decay dynamics observed in Markovian sequences were unlikely caused due to highly predictable transitions between actions, as disruption of these transition probabilities increased the rate at which power-law dynamics were identified.

The use of MI decay models for identifying grammars of action in human and nonhuman behaviour is growing in popularity (Sainburg et al., 2022, 2019). Given the rate at which models featuring periods of

power-law decay were preferred for Markovian sequences, we recommend that future research use estimated Markov models to identify rates of model preference for the MI decay dynamics of Markovian sequences. These rates will offer baselines for identifying MI decay dynamics associated with non-Markovian phenomena from Markovian sequence data, which we anticipate will be a highly useful tool for ensuring accurate interpretation of MI decay analyses. We identified that the preference for each decay model covaries with the maximum sequential distance over which MI may be estimated: when the maximum sequential distance MI may be estimated is shorter, the exponential decay model was more likely to be selected (most probably given it is the model which predicts the fastest rate of decay). Additionally, our findings illustrate how transition probabilities may influence the likelihood that power-law dynamics are identified from Markovian sequences. Thus, we recommend that future research estimates the rates of MI decay model preferences on a case-by-case basis, where Markov models are trained on the biological data in question.

The composite model was a successful model for explaining MI decay across action sequences, being the best model for five individuals when action sequences featured repeating elements, and three individuals when action sequences were condensed (as well as a fourth individual, who showed equal preference for the composite and exponential model). A transition point analysis identified that for sequences with repeating actions, composite models transitioned from exponential to power-law decay at sequential distances of 2-8 actions (mean = 4.6 sequence elements, N = 5). Thus, the composite model behaved as would be expected if chimpanzees were combining short subroutines of 2-8 actions, which were predictable in structure from probabilistic neighbouring transitions, before organising these subroutines into longer bouts of behaviours. The organisation of sequential action of great apes has previously been described through the use of such subroutines, including during tool-use (Byrne et al., 2013; Byrne and Russon, 1998). Our findings demonstrate that the information contained in sequential actions of chimpanzees during tool use offers further support for the idea that chimpanzees rely on the hierarchical organisation of subroutines within sequential actions, including tool-use. Additionally, the results of our analysis provide support for this conclusion without prior judgement of where subroutines exist within the sequence of actions produced by chimpanzees, and without the need for observers to ascribe goals of subroutines within wider bouts of behaviours. Thus, we are able to use MI decay to detect

a frequent structuring system within the sequential behaviour of chimpanzees - the hierarchical organisation of subroutines - whilst circumventing many prevalent issues surrounding observer bias.

In the same vein as previous analyses of sequential behaviours through MI decay dynamics (Sainburg et al., 2022, 2019), we deem it outside of the scope of this study to determine what parsing rules chimpanzees may use to facilitate a structuring system which relies on hierarchical and Markovian dynamics at different temporal scales. Additionally, the present study is unable to provide insight into the exact representational mechanisms that chimpanzees use to produce successful sequences of tool action (Gruber et al., 2015). These limitations extend to both specific parsing procedures, and also the extent to which working memory is employed to account for distant dependencies, where strain on memory could be reduced in physical tasks through traces of previous actions being maintained within the environment (e.g. a nut positioned on top of an anvil would suggest it has already been placed there in a previous action) (Byrne and Russon, 1998). The MI decay analysis presented in this study is an observational investigation of how information changes across sequences, and compares the findings to key predictions of hypothesised structuring systems found in the behaviours of humans and other animals. Thus, we provide support to key hypotheses surrounding the sequential organisation of action in chimpanzees, without providing an exhaustive analysis of all theoretically possible systems which may produce sequences of action. We encourage further research into the morphology of possible grammars of action, such as through the use of computational models which may statistically approximate the generative rules of a corpora of sequences, drawing upon various hierarchical and non-hierarchical means (e.g. Hierarchical Hidden Markov Models (Fine et al., 1998), or dictionary-based compression (Gomez-Marin et al., 2016; Larsson and Moffat, 2000). Modelling of such grammars of action may provide further clarity on the mental rules that chimpanzees follow to produce sequences of actions within natural tool tasks.

The hierarchical organisation of sequential action, and the presence of nonadjacent dependencies between actions in a sequence, are two systems of behavioural organisation which are supported by MI estimation in chimpanzee tool-action sequences. MI estimation has previously been used to detect the presence of power-law decay dynamics, and underlying distant dependencies of the grooming behaviours of Drosophila flies (*Drosophila melanogaster*) over an hour , and the swimming behaviours of Zebrafish (*Danio rerio*) during phototaxis paradigms (Sainburg et al., 2020), and for both species, the composite

model was the best choice for explaining information decay over the action sequences of individuals. Our results suggest a possible homologous structuring system exists as a common method for chimpanzees to sequence actions in a highly complex natural tool-use behaviour: nut cracking. Additionally, the hierarchical complexity of early hominin tool-related action is believed to have increased throughout the course of hominin evolution, with the production of more ancient Oldowan tools requiring less complex hierarchical organisation than the production of more recent Acheulian stone tools (Stout et al., 2021). Thus, the hierarchical organisation of tool-use behaviours may have been an adaptation which was present in the evolutionary ancestor of humans and apes - stemming from more basal hierarchical systems of action - which was then elaborated across the course of human evolution into a state of higher complexity. Understanding the dynamics of this evolutionary transition would be greatly aided through further comparative research into the sequential organisation of actions used by chimpanzees and humans during lithic tool tasks.

Outside of tool use, the presence of hierarchical thinking in primates may also manifest within alternative behavioural contexts and social cognition. Within the play behaviours of chimpanzees, individuals appear to structure bouts of actions based on highly proximate elements of behavioural sequences, reflecting a very low occurrence rate of nonadjacent dependencies (Mielke and Carvalho, 2022); however, there has been suggestion that these Markovian grammars of action used by chimpanzees during play may be hierarchically organised as ‘games’, where chimpanzees swap between grammars of action based on the game being played, and games which are more similar are more likely to co-occur within bouts of play (Mielke and Carvalho, 2022). Additionally, baboons are known to have a precise understanding of social hierarchies within troops (Bergman et al., 2003), including an understanding of individual rank based on both the family unit, as well as the birth order of individuals within a family (Bergman et al., 2003). Understanding how these hierarchical concepts may compare with the structuring of actions during goal directed tool-use is of significant interest. In the context of play, it would be relevant to know how the fast-paced switching of goals may influence the hierarchical depth of behavioural organisation, as well as the formation of nonadjacent dependencies, compared to the sustained goals of tool-use, which endure over longer periods of time. In the context of social hierarchies, it is of interest to understand whether species which are able to solve inherently hierarchical tasks in one domain are also

able to solve hierarchical tasks in alternative domains of behaviour, particularly given that tool use is less common in the natural behavioural repertoire of baboons. This comparative work may provide insight into the different ways hierarchical cognition operates based on its modality, with possible interest for research into the exaptation of hierarchical cognition across domains of behaviour.

Within communication, a preference for the composite decay model has been found when evaluating MI decay in the songs of various species of birds (Sainburg et al., 2019) and in the phonetic associations of various human languages (Sainburg et al., 2022, 2019). Currently little resolution is available in how birds may employ these two structuring mechanisms when externalising songs; however, the preference for the composite model is compatible with our understanding of the duality of patterning in language. Within human language, phonological syntax (the relation of phonemes to form words) can be largely generalised through local statistical associations (Kaplan and Kay, 1994), whereas higher levels of syntax (relating words into phrases, clauses and sentences) relies on hierarchical associations (Chomsky, 2002b, 1956). As such, it is intuitive that MI estimates based on phonological associations would show exponential decay dynamics at shorter timescales, and power-law decay dynamics at greater sequential distances (Sainburg et al., 2019). Such parallels in the structure of human language and the sequential action of both humans and animals has led to the proposal of the statistical scaffolding hypothesis (Sainburg et al., 2020). This hypothesis posits that long-range statistical dependencies in non-linguistic behaviours, and a generalised sensitivity to such behaviours, has led to a scaffold onto which language could evolve, where hierarchical syntax and semantics can be understood as later additions that exploit such structures and sensitivities. Other, similar hypotheses have been suggested to explain the evolution of hierarchical structures in language via exaptation of pre-existing cognitive resources. The Cognitive Coupling hypothesis suggests that the pre-existing cognitive architecture responsible for hierarchical tool behaviours was coupled with cognitive machinery responsible for communication, where such coupling occurred in multiple steps across hominin evolutionary history, driven by the need to socially learn and transmit increasingly more complex tool behaviours (Kolodny and Edelman, 2018).

We believe that our findings are consistent with, but not confirmatory of, both the statistical scaffolding hypothesis, and the cognitive coupling hypothesis. We have presented data herein that supports the presence of nonadjacent dependencies in the sequential action of chimpanzee tool use, as well as

decay dynamics of MI that are best generalised by models associated with the hierarchical organisation of action. Support for these structuring systems in the sequential organisation of behaviours in chimpanzees may imply a homologous origin with the sequential organisation of action in humans, with these behaviours also shared in their last common ancestor. The emergence of the hierarchical organisation of communicative behaviours, as well as the use of nonadjacent dependencies in communication, may then have evolved as human-specific traits, following the evolutionary divergence of the human and *Pan* lineages. This evolutionary scenario is further supported by the current absence of evidence that chimpanzees – like other non-human primates – have vocal communication systems whose syntax employs hierarchical structuring (Fitch and Hauser, 2004; Hauser et al., 2002; ten Cate and Okanoya, 2012). Thus, hierarchical tool-use behaviours, and the ability to produce and account for distantly related elements in behavioural sequences, may have emerged prior to these features evolving within communicative syntax in hominin evolution.

In sum, we have shown that the estimation of MI across sequences is useful for studying the dynamics of action organisation in the tool-use behaviour of a nonhuman animal: chimpanzees. MI estimations reveal nonadjacent dependencies that exceed what can be expected if sequences are produced by Markov chains, and for many adult individuals, this cannot be solely attributed to the repetition of actions. Additionally, whilst MI decay dynamics for sequential tool-use sometimes did not follow the predicted decay dynamics for Markovian sequences, our results from chimpanzee action sequences repeatedly indicate a period of power-law decay in the MI decay profiles of sequential actions, a key prediction from the hierarchical organisation of behaviour. We argue that our results provide strong evidence against the idea that the sequential actions in chimpanzee tool use can be generated by Markovian sequencing dynamics, and reaffirm that hierarchical structuring is an important feature of the lithic tool action of chimpanzees. As such, we reinstate that sequential action in tool use – in contrast to communication – reflects a domain of behaviour where non-human primates may readily employ hierarchical sequencing, as well as the production of nonadjacent dependencies within behavioural sequences. We welcome further research into the action sequences employed by chimpanzees in other natural tool tasks, as this may further speak to how task complexity (e.g., object number, task length, etc.) may influence the hierarchical structures of actions used to accomplish such tasks. Moreover, studying the

sequential actions of other taxa known to naturally engage in tool behaviours may further contribute to our understanding of whether hierarchical sequential structures are widespread, or even universal to systems of complex action. Such investigations may then feed into a variety of evolutionary models, including those concerning tool use, animal songs, and syntax in human language.

Acknowledgments: E.H.S. thanks National Environmental Research Council (NERC) and United Kingdom Research and Innovation (UKRI) for financial support (grant ref. NE/L002612/1). T.G. thanks the Swiss National Science Foundation (SNSF) for financial support (grant ref. PCEFP1_186832). T.M. was supported by grants from Ministry of Education, Culture, Sports, Science and Technology, Japan (MEXT - #12002009, #16002001, #20002001, #24000001, #16H06283) and Japan Society for the Promotion of Science (JSPS) (Core-to-core CCSN and U04-PWS). M.H. was supported by grants MEXT/JSPS 15K00204, 19K21824, and JP17H06381 (Evolinguistics). D.S. was supported by grants from The Clarendon Fund, Boise Trust Fund, and Wolfson College, University of Oxford. We thank Susana Carvalho (University of Oxford, UK) for their help in curating the Bossou video archive, and Tim Sainburg (University of Harvard, USA) for statistical advice. The authors would like to acknowledge the use of the University of Oxford Advanced Research Computing (ARC) facility in carrying out this work: http://dx.doi.org/10.5281/zenodo.22558. We are also grateful to all the KUPRI researchers who have helped collect data at Bossou in the past. Special thanks are due to Direction General de la Recherche Scientifique et l'innovation Technologique (DGERSIT) and the Institut de Recherche Environnementale de Bossou (IREB), République de Guinée, for assistance and research permission to conduct field work at Bossou; as well as research assistants Boniface Zogbila, Gouanou Zogbila, Henry Gbelegbe, Marcel Doré, and Gilles Doré for their help in the field.

Competing Interest Statement: All authors declare no competing interests.

2.5 Figures

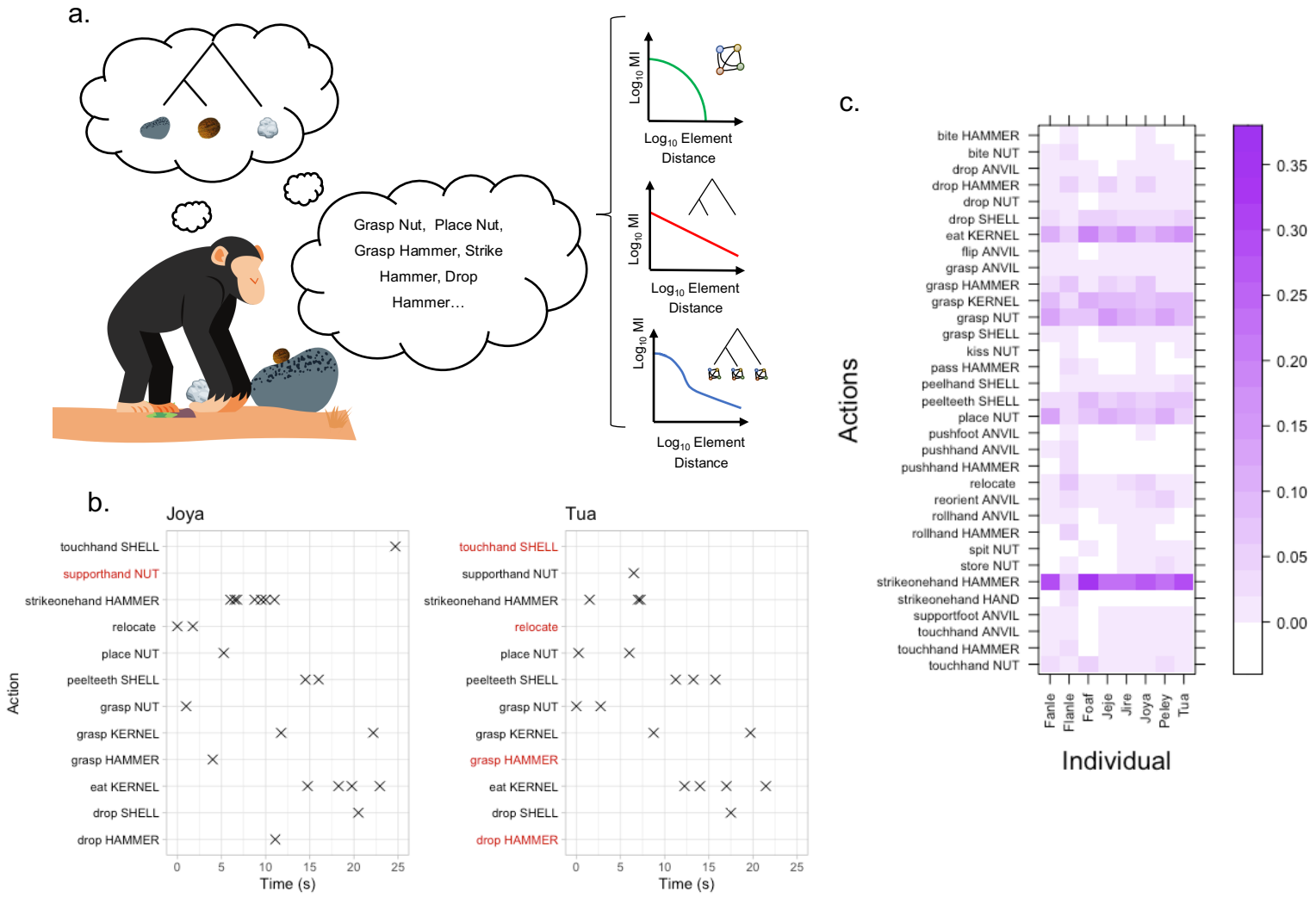


Figure 1. MI Decay models and the diversity of tool-use actions employed by chimpanzees during nut-cracking. (a) A chimpanzee using two stone tools to crack open a nut (tree structure diagram represents hierarchical association of objects - see Matsuzawa 1996), and a complementary sequence of actions to facilitate object associations. To the right of the action sequence, three candidate structuring mechanisms are outlined, alongside their characteristic MI decay profiles (from top to bottom: purely Markovian, purely hierarchical, a composite of a hierarchical structure with Markov models at the terminal nodes). **(b)** Two representative behaviour time-plots showing the sequence of actions used by Joya (left) and Tua (right) to crack and consume a nut. Crosses mark the where an action is coded as a discrete timepoint. Red action labels indicate where an action-type was not used by an individual when cracking and consuming each specific nut; however, they do not preclude these actions from being used by either individual when processing other nuts, and do not represent all possible actions. **(c)** A heatmap showing the proportion of different action types in the total corpus of action-sequence data for each individual (restricted to action types which constituted at least 1% of total observed actions for at least one individual). The darker purple shading means action types constitute a greater proportion of the corpus for each individual.

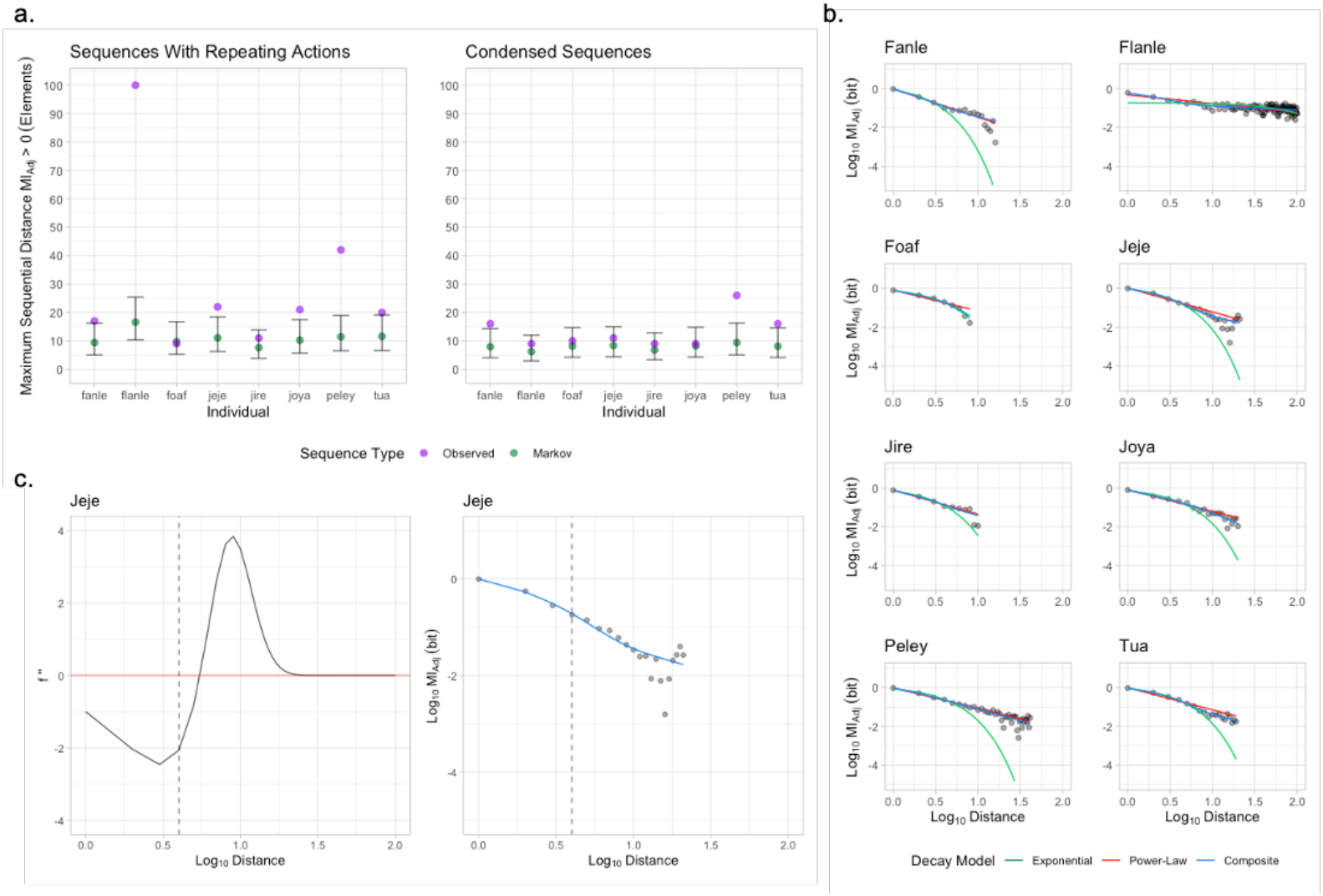


Figure 2. The Maximum Sequential Distance and Decay Dynamics of MI_{Adj}. (a) The maximum sequential distance over which MI_{Adj} was greater than zero, for action sequences observed from individual chimpanzees (purple) and their corresponding Markov models (green). The panel on the left is for data which includes repeating actions; the panel on the right corresponds to condensed action-sequence data. Bars represent a 95% confidence interval around estimated means for Markovian sequence data. **(b)** Individual MI_{Adj} decay profiles, with three candidate decay models fitted. **(c)** The panel on the right shows the composite model describing MI decay for Jeje. The panel on the left illustrates the second differential of this composite function, and the vertical dashed line highlights the transition point, where decay switches from primarily exponential to power-law.

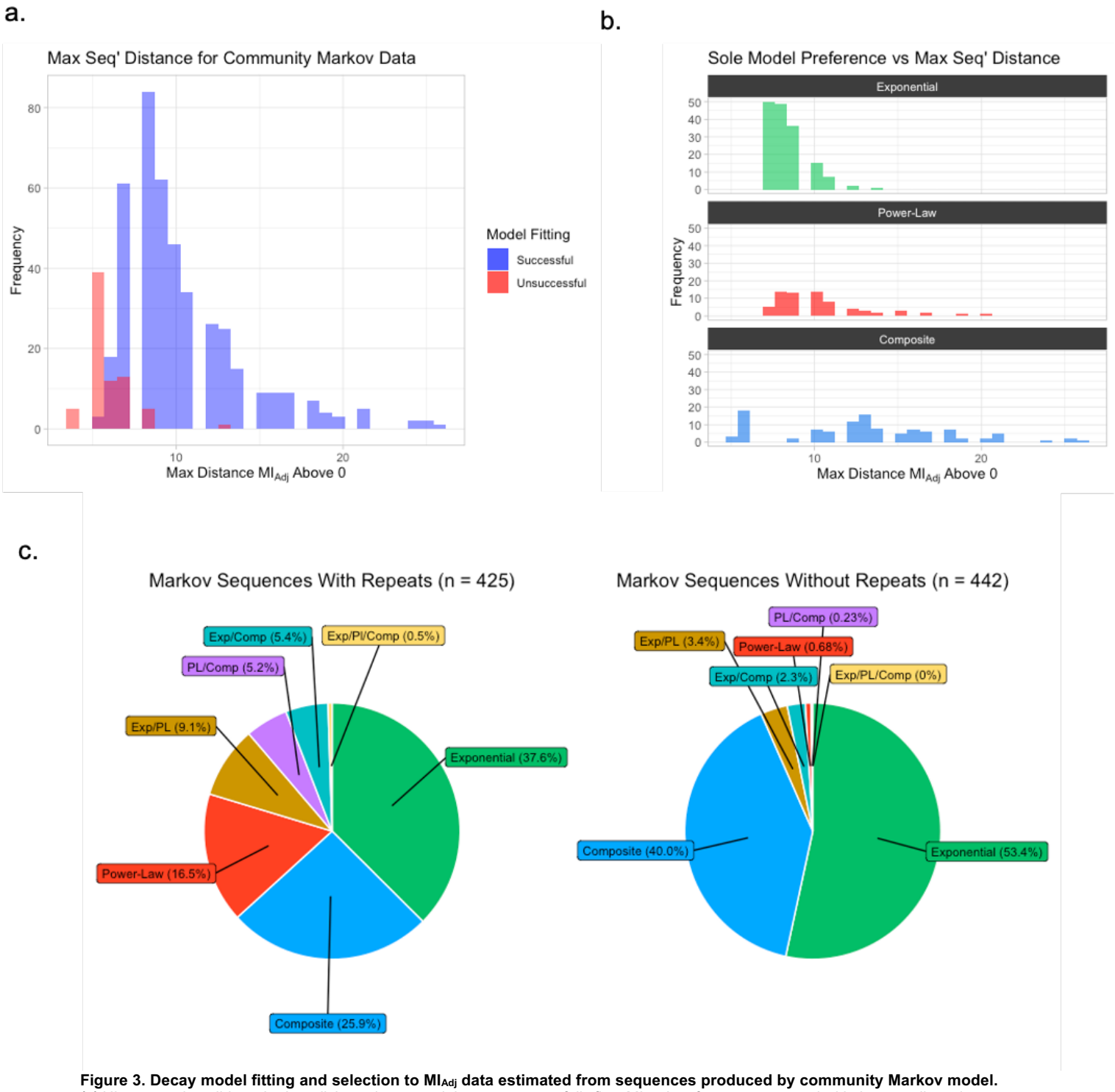


Figure 3. Decay model fitting and selection to MI$_{Adj}$ data estimated from sequences produced by community Markov model. **(a)** Histogram describing whether all three decay models were successfully fit to MI$_{Adj}$ data frames, compared with the overall maximum sequential distance at which MI$_{Adj}$ was positive in each data frame. The presented data was estimated from sequences produced by community Markov model 1 (which allowed for repeated actions). **(b)** Three histograms showing the maximum sequential distances of datasets which showed a sole preference for each decay model type (exponential, power-law, composite). The presented data is also for sequences generated by Markov model 1. **(c)** Pie diagrams showing the proportion of preferred models for describing MI$_{Adj}$ decay in sequences generated by community Markov model 1 (with repeating elements - on the left) and community Markov model 2 (without repeating actions - on the right)

2.6 Tables

Table 1. Summary of sequence data collected from the 2011/2012 field season at Bossou (including all complete and incomplete sequences). Eight individuals were included in MI decay modelling. 'Time Coded' relates to the total duration of time individuals were seen to be engaging with nuts, nut fragments and stone tools throughout all video footage. An 'Element' is defined as each action coded within a sequence, whereas 'Action Types' represent the different types of coded actions in a sequence (e.g., "Grasp Nut" "Place Nut" "Grasp Nut" – Number of elements: 3, Number of Action Types: 2). 'Nuts Cracked' marks the number of nuts observed to have been cracked by an individual across all available video footage. Mean Sequence Length Per Nut refers to the mean number of elements in a sequence that is directed at cracking open each individual nut. SE for all means were calculated via the normal approximation of the Poisson distribution. Ages marked with * are an estimate, as these individuals were present when long-term monitoring at Bossou began.

Individual	Sex	Age (years)	Sampled for MI Analysis	Time Coded (MM:SS)	Number of Sequences	Sequence Elements (Total)	Mean Sequence Length ± SE	Number of Action Types	Nuts Cracked	Mean Sequence Length Per Nut ± SE
Fanle	F	14	✓	44:55	21	1368	65.1 ± 1.8	34	85	13.9 ± 0.4
Flanle	M	7	✓	24:03	35	453	12.9 ± 0.6	59	1	48
Foaf	M	31	✓	07:22	8	299	37.4 ± 2.2	18	10	31.2 ± 1.8
Jeje	M	14	✓	40:33	18	1373	76.3 ± 2.1	36	39	29.4 ± 0.9
Jire	F	53*	✓	19:27	12	482	40.2 ± 1.8	33	22	16.0 ± 0.9
Joya	F	4	✓	36:52	39	1178	30.2 ± 0.9	55	22	36 ± 1.3
Peley	M	13	✓	34:05	15	1168	77.9 ± 2.3	44	45	21.7 ± 0.7
Tua	M	54*	✓	55:33	15	1940	129.3 ± 2.9	43	79	22.4 ± 0.5
Velu	F	52*	×	01:07	2	16	8 ± 2	12	0	0

Table 2. AICc scores for MIAdj decay models, derived from condensed sequences. For each individual, Max Element Distance highlights the greatest element distance included in the MIAdj datasets, and models are given in the order of preference (as determined by AICc – rows in bold indicate highest preferences). K represents the number of parameters estimated in each model. AICc describes the AIC score corrected for smaller sample size (see section 4.6). ΔAICc represents the difference between a given model's AICc score and the optimal model's AICc score for each individual. AICc.Wt describes the proportion of the total predictive power of all three models contained in each model, and Cum.Wt describes the accumulation of predictive power in order of model preference. LL represents the log-likelihood of each model given the data - AICc is estimated using both K and LL.

Individual	Max Element Distance	Model	K	AICc	ΔAICc	AICc.Wt	Cum.Wt	LL
Fanle	15	**Composite**	**5**	**-70.5**	**0.0**	**0.93**	**0.93**	**43.6**
		Power-Law	3	-65.2	5.3	0.07	1.00	36.7
		Exponential	3	-47.2	23.3	0.00	1.00	27.7
Flanle	8	**Power-Law**	**3**	**-18.5**	**0.0**	**0.98**	**0.98**	**15.3**
		Exponential	3	-10.3	8.2	0.02	1.00	11.2
		Power-Law	5	0.8	19.4	0.00	1.00	19.6
Foaf	9	**Exponential**	**5**	**-36.7**	**0.0**	**1.00**	**1.00**	**23.8**
		Power-Law	3	-22.7	14.1	0.00	1.00	16.8
		Composite	3	-14.1	22.6	0.00	1.00	22.1
Jeje	10	**Composite**	**5**	**-43.0**	**0.0**	**0.72**	**0.72**	**34.0**
		Exponential	**3**	**-41.2**	**1.8**	**0.28**	**1.00**	**25.6**
		Power-Law	3	-23.0	20.0	0.00	0.00	16.5
Jire	8	**Power-Law**	**3**	**-22.7**	**0.0**	**0.54**	**0.54**	**17.4**
		Exponential	**3**	**-22.4**	**0.3**	**0.46**	**1.00**	**17.2**
		Composite	4	10.7	12.0	0.00	1.00	25.4
Joya	8	**Power-Law**	**3**	**-26.5**	**0.0**	**1.00**	**1.00**	**19.2**
		Exponential	3	-15.0	11.5	0.00	1.00	13.5
		Composite	5	-2.3	24.2	0.00	1.00	21.2
Peley	26	**Composite**	**5**	**-121.8**	**0.0**	**0.80**	**0.80**	**67.5**
		Power-Law	3	-119.1	2.7	0.20	1.00	63.1
		Exponential	3	-80.0	41.8	0.00	1.00	43.6
Tua	16	**Composite**	**5**	**-92.2**	**0.0**	**1.00**	**1.00**	**54.5**
		Exponential	3	-70.7	21.5	0.00	1.00	39.4
		Power-Law	3	-49.0	43.3	0.00	1.00	28.6

Table 3. Summary of maximum comparative distances, model preferences, and transition points for action sequences with repeating actions. Transition point describes the element distance where the composite model switches from a primarily exponential decay dynamic to one which is better generalised by a power-law. For each individual, the transition point, and mean number of actions used to crack open individual nuts, is provided. Total sample size for nut sequence length (i.e., number of nuts cracked throughout the study period) is included in brackets.

Individual	Maximum Sequential Distance $MI_{Adj} > 0$	Preferred Model	Transition Point	Mean Sequence Length Per Nut ± SE (no. of nuts cracked)
Fanle	16	Power-Law	-	13.9 ± 0.4
Flanle	100	Composite	2	48 (1)
Foaf	8	Exponential	-	31.2 ± 1.8
Jeje	21	Composite	4	29.4 ± 0.9 (39)
Jire	10	Power-Law	-	16.0 ± 0.9
Joya	20	Composite	8	36 ± 1.3 (22)
Peley	41	Composite	2	21.7 ± 0.7 (45)
Tua	19	Composite	7	22.4 ± 0.5 (43)

2.7 Methods

2.7.1 Study site

Bossou-Nimba (07° 390' N; 008° 300' W) is one of a small number of long-term field sites focused on the study of wild West-African chimpanzees (Matsuzawa et al., 2011). Located in South-Eastern Guinea, Bossou is surrounded by primary and secondary forest, and is home to a small community of wild chimpanzees whose behaviour and ecology has been studied systematically since 1976. The community's home range covers an area of approx. 5-6 km (Sugiyama, 1981). Bossou chimpanzees are known to perform a wide variety of tool-use behaviours, including nut-cracking(Biro et al., 2006, 2003; Carvalho et al., 2008; Hayashi, 2015; Inoue-Nakamura and Matsuzawa, 1997; Matsuzawa, 1994); leaf-folding (Tonooka, 2001), ant-dipping (Humle and Matsuzawa, 2002), and pestle-pounding (Yamakoshi and Sugiyama, 1995).

2.7.2 Data collection

Data collection on nut-cracking behaviours is conducted at the "outdoor laboratory" at Bossou (Biro et al., 2006; Carvalho et al., 2008; Matsuzawa, 1994) (see Fig. S1). Located in close proximity to the peak of Mount Gban, the outdoor laboratory is a natural rectangular clearing measuring approx. 7 × 20 m^2 and operating as an in-situ experimental facility during the dry season of each year (November – February). Chimpanzees visit the clearing spontaneously as part of their daily ranging (at a rate that varies from once or twice a day on consecutive days, to returning after several days), and are provided with a selection of numbered stones of varying sizes, shapes and raw-material types, several piles of naturally available oil-palm nuts (*Elaeis guineensis),* and a branch of oil-palm fruits, which is replenished frequently. The outdoor laboratory also features a wide cavity inside of an available tree trunk, which acts as a water point. The outdoor laboratory is surrounded by thick vegetation on three sides, and on the fourth side an artificial wall made of palm fronds is used to allow human observers to observe chimpanzee behaviours out of sight, whilst simultaneously recording behaviours using tripod-mounted cameras. These conditions allow chimpanzee behaviours to be recorded in their natural habitat from close range but with minimal interference from human observers.

The several decades of video footage collected at Bossou have recently been compiled into a longitudinal video archive, spanning 1988 to the present (Schofield et al., 2019). As such, the Bossou video archive presents a unique opportunity to study wild chimpanzee behaviour in situ through both longitudinal and cross-sectional lenses. This study takes a cross-section of video footage data from the Bossou video archive, focusing on nut-cracking behaviours collected at the outdoor laboratory in the 2011/2012 field season.

2.7.3 Subjects

Since the start of systematic research at Bossou, the site is known to have supported a community of around 18-22 individuals; however, the population has been in decline since a disease outbreak in 2003 (Matsuzawa et al., 2004), and as of April 2022, they number only 6 individuals. In the 2011/2012 field season, the community consisted of 10 adult individuals (4 male and 6 female), 1 juvenile female and 2 infants males, with a community age range estimated to be from ~ 1 to ~ 54 years (see Table S1). All available videos from the 2011/2012 field season were used during behaviour coding (see below), and all individuals who visibly interacted with a stone-tool, nut, or nut-fragment (including shells and kernels from their own or another's previous nut-cracking event) whilst present in the outdoor laboratory were included in behaviour coding.

2.7.4 Behaviour coding

Behaviour coding was conducted using BORIS (Behavioural Observation Research Interactive Software) (Friard and Gamba, 2016). Digitised video recordings were passed to BORIS and visualised on a 59 cm monitor. An ethogram of codable behaviours was developed based on Inoue-Nakamura & Matsuzawa's (1997) nut cracking ethogram (Inoue-Nakamura and Matsuzawa, 1997), including 34 codable actions, e.g. "Grasp", "Place", "Strike", "Peel" etc. (see Table S2 for full ethogram). For each action coded, a corresponding object was also coded alongside. Available objects to code included: 1. Nut (uncracked), 2. Hammer, 3. Anvil, (Anvils were distinguished from Hammers on a case-by-case basis, based on how chimpanzees used each stone-tool), 4. Kernel – taken to be the edible inner part of the nut, 5. Shell – taken to be the inedible outer parts of the nut, 6. Bare Hand. Coded objects could then be combined with actions

to create a more informative description of how chimpanzees were manipulating the available materials through externalised sequences of behaviours, e.g. “Drop Hammer'', “Grasp Nut”, “Place Nut”. Some object-directed actions are continuous over time, and may occur simultaneously alongside other behaviours, e.g., a chimpanzee may support an anvil with its foot for an extended duration of time, whilst successively striking a nut with a hammer stone. To allow for analysis by mutual information decay, simultaneous actions were coded at the first point at which they were elicited; thus, all actions were coded as discrete-time points. This allows for actions to be described in one linear sequence (permitting MI decay analyses), whilst also retaining information surrounding the order in which chimpanzees began to externalize each object-directed action. Following action coding, the combined descriptions of both actions and objects were taken to constitute the individual sequence ‘elements’ in our analysis (i.e. “Grasp Nut” = 1 sequence element).

The ethogram also features two event codes to denote the ‘Start’ and ‘End’ of nut-cracking sequences; the start of the sequence was taken to be at any point when an individual ceased another behaviour (e.g. resting, travelling, grooming) and began interacting with a stone-tool, nut or nut-fragment. The end of the sequence was taken to be when any individual ceased interacting with nuts and stone-tools to engage in another behaviour. Individuals who ceased interacting with nuts, nut-fragments and stone-tools for longer than one minute, but were not clearly engaging in another behaviour, were deemed to have begun resting, and this was used to mark the end of a sequence. Sequences which followed a chimpanzee from the start to the end of their engagement with nuts and stone-tools were marked as ‘Complete’. A ‘Not Visible’ code was used to represent when an individual engaging in nut-cracking behaviours could no longer be clearly observed from the video footage, such as through manoeuvring their body to block their behaviours from being visible to cameras, moving out of shot of the cameras, or cameras panning away from focal individuals. In such instances of early termination of behavioural coding due to poor visibility, sequences were marked as ‘incomplete’ to denote their cessation prior to the completion of the chimpanzee’s behavioural sequence. Under instances where chimpanzees moved back into view following termination of a sequence due to poor visibility, and there was reason to believe they had not ceased engaging in nut-cracking behaviours, coding was resumed in the absence of a ‘Start’ element, and these sequences were also marked as incomplete.

Sequence data collected in BORIS were exported to Excel. Start, End and Not Visible codes were used to split the data into continuous sequences of observed actions. Start, End and Not Visible codons were then removed prior to MI Decay analysis. Sequences were reviewed to determine whether they included successful or unsuccessful instances of nut-cracking (i.e., nut kernels were visibly extracted and eaten by the subject vs instances where sequences do not feature extraction and consumption of kernels, respectively), and labelled accordingly. In sequences which featured successful instances of nut-cracking, sequences were copied, and separated to describe actions associated with individual nuts. Consequently, sequences of actions could be visualised at two levels: the actions associated with cracking open individual nuts, or the wider sequence of actions used to crack multiple nuts across a continuous observable period of nut-cracking.

2.7.5 Mutual information estimation

To estimate MI values at various element distances, sequences for each individual were concatenated in order of collection. Mutual information can be determined by the reduction in entropy of a point in a sequence, when the state of another sequence element is known. As such, information can be estimated through independent measures of entropy at different points in a sequence (the marginal entropy of points X and Y), and also the joint entropy of actions co-occurring together at a given sequential distance. To estimate information in our action sequences, marginal and joint entropies were estimated across concatenated sequences at distances ranging from 0 to 100 elements apart. MI was estimated at each distance as:

$$\widehat{MI}(X,Y) = \hat{S}(X) + \hat{S}(Y) - \hat{S}(X,Y),$$

where X is the distribution of the initial elements; Y is distribution of elements n-items further along the sequence; $\hat{S}(X)$ and $\hat{S}(Y)$ are the marginal entropies of X and Y respectively, $\hat{S}(X,Y)$ is the joint entropy of elements n distance apart, and $\widehat{MI}(X,Y)$ is the mutual information estimate for elements n distance apart. During entropy estimation, we followed the recommendations of Sainburg et al. (Sainburg et al., 2022, 2020, 2019) and Lin & Tegmark (Lin and Tegmark, 2017) by using the Grassberger method (Grassberger, 2003), which accounts for under-estimation of true entropy from finite samples:

$$\hat{S} = log_2(N) - \frac{1}{N}\sum_{i=1}^{k} N_i \psi(N_i),$$

where $\hat{S}$ is the marginal or joint entropy; N is the total number of elements in the distribution; K is the number of different groups of elements in the distribution, and ψ is the digamma function. To account for lower bounds of estimated MI, sequences underwent 1000 pseudorandom permutations to generate randomised joint-entropy distributions. MI was then estimated using the mean of the permuted joint-entropy distribution, and the marginal entropy values from the in-sequence data, using the same equation as before. This MI estimate is taken to approximate MI measures which arise from our data due to chance relationships (Sainburg et al., 2022, 2020). The chance MI measure - $\widehat{MI}_{sh}(X,Y)$ - was subtracted from our data, to give an adjusted MI score which more accurately reflects the intentional structure of observed action sequences - MI_{Adj}:

$$\widehat{MI}_{sh}(X,Y) = \hat{S}(X) + \hat{S}(Y) - \hat{S}_{sh}(X,Y),$$

$$\widehat{MI}_{Adj} = \widehat{MI} - \widehat{MI}_{sh}$$

During MI estimation, it is possible for MI to decay to zero before reaching the maximal comparative distance of 100 elements. Therefore, we used the 1000 sequence permutations to construct 95% confidence intervals surrounding $\widehat{MI}_{sh}(X,Y)$ at each sequential distance between 0-100 elements. At each sequential distance between 1-100 elements, we took the upper value of the 95% confidence limit, and subtracted this value from the $\widehat{MI}$ estimated from the original action-sequences at each corresponding distance:

$$\widehat{MI} - CI_{95\%}^{Upper}\{\widehat{MI}_{sh}(X,Y)\} < 0$$

where we took the first comparative distance this value fell below zero to indicate that estimated MI was no longer significantly different to what could be expected from chance relationships, and therefore could no longer be treated as different to zero. For MI decay profiles which decayed to zero before reaching the maximum comparative distance of 100 elements, MI decay data was restricted to include solely the comparative distances that preceded the complete decay of MI. For all subsequent analyses and modelling, the adjusted MI score was used (MI_{Adj}).

2.7.6 MI decay model fitting and selection

Three models were used to characterise decay of adjusted MI scores: (1) an exponential model to approximate MI_{Adj} decay dynamics where sequences are produced by Markovian adjacent-dependencies (Lin and Tegmark, 2017; Sainburg et al., 2022, 2020, 2019); (2) a power-law model to approximate MI_{Adj} decay predicted by fully-nested hierarchical sequences (Sainburg et al., 2022, 2020, 2019); and (3) a composite model to approximate MI_{Adj} decay from sequences which utilise nested hierarchical structuring at higher orders of abstraction, before ordering elements through Markovian dynamics at local scales (Sainburg et al., 2022, 2020, 2019):

$$Exponential\ Decay = a * e^{-x*b}$$

$$Power - Law\ Decay = a * x^{b}$$

$$Composite\ Decay = a * e^{-x*b} + c * x^{d}$$

where x represents inter-element distance. As reducible and periodic Markov chains may produce MI_{Adj} scores which decay to positive constants (Lin and Tegmark, 2017), best-estimate Markov chains were modelled from sequence data for each individual, and checked to determine whether they were irreducible and aperiodic. Markov models were estimated in R using the *markovchainFit()* function from the *markovchain* package (Spedicato, 2017). Irreducibility and periodicity of these Markov models were then determined using the functions *is.irreducible()* and *period()* respectively. As all best-estimate Markov chains were identified as irreducible and aperiodic, we fitted our exponential model in the absence of a constant, allowing models of MI_{Adj} to decay towards zero. Both the power-law and composite decay models were also fitted in the absence of constants to also allow these models of MI_{Adj} to fall towards zero with increasing sequential distances (see the Quantification and Statistical Analysis section for more information on model fitting).

The fit of the three models were compared using an adaptation of the Akaike Information Criterion (AIC). AIC provides a numerical means to compare goodness-of-fit between models constructed on identical data-sets, whilst also penalising extra parameters used to construct the model. Such penalization of additional model parameters thus helps to reduce the likelihood of overfitting more complex models to

their underlying data. Models with lower AIC scores are taken to give more accurate approximations of data, relative to the number of parameters used to fit them. To mirror similar analyses of MI decay on birdsong, language, and human action (Sainburg et al., 2022, 2020, 2019), we opted to compare model fits using AICc. AICc scores models similarly to AIC; however, AICc introduces an additional penalty for each model parameter, to correct for overfitting on smaller datasets (Cavanaugh and Neath, 2019; Sainburg et al., 2022, 2020, 2019)

As repeating elements in a sequence, e.g. successively striking a hammer, can produce nonadjacent sequential dependencies, we repeated the analyses outlined above – specifically in the sections *Mutual Information Estimation* and *MI Decay Model Fitting and Selection* – on a corpora of condensed sequences for each individual. Condensed sequences were produced by passing the concatenated sequence corpus for each individual through an algorithm which removed repeated actions are replaced them with a single codon (e.g. 'Strike Hammer', 'Strike Hammer', 'Strike Hammer', is replaced by a single codon: 'Strike Hammer). By analysing this condensed corpus of sequences in parallel with observed sequences of chimpanzee tool action, we are able to separate out dependencies produced by repeated actions, and those produced by alternative means, including the hypothesised use of nested subroutines.

2.7.7 Estimating transition points in composite models

For those individuals whose MI_{Adj} decay profiles were best fit by a composite model, we identified the point at which the model transitioned from exponential decay to power-law decay using the change in gradient of the curve in log-space ($\log_{10}$ MI_{Adj} and $\log_{10}$ element distance). Through finding the second differential of the curve in log-space, we took the minimand of this function to be the point immediately prior to where the function begins to switch to a power-law decay. The point at which the composite model switches to primarily a power-law decay can be considered to be the furthest inter-element-distance over which Markovian dynamics are likely to influence the structure of observed action sequences.

2.7.8 Markov models and simulated sequences

Sequences produced from some Markovian grammars may produce dependencies which span over multiple elements (including short-range nonadjacent elements), especially when Markov models have highly predictable element transitions, leading to multiple elements being produced in highly stereotyped strings. It is therefore necessary to determine whether the distances over which sequential dependencies occur in chimpanzee tool-action are significantly greater to those that can be readily generated by equivalent Markov models. Using the Markov models generated from observed action sequence data from individual chimpanzees (see section above: *MI Decay Model Fitting and Selection*), we generated 100 Markov sequences matching the total corpus length for each individual. For all Markov sequences, we estimated MI_{Adj} Decay using the same method as outlined in the sections *Mutual Information Estimation* and *MI Decay Model Fitting and Selection*. From the 100 Markov Sequences for each individual, we constructed a probability distribution for the maximum sequential distances where dependencies could be detected, using the maximum sequential distance $MI_{Adj} > 0$ for each sequence. From these probability distributions, 95% confidence intervals were constructed using the exact method for Poisson distributions. To determine whether dependencies occurred at greater distances in observed action sequences compared to those expected from Markovian structuring, we compared the maximum sequential distances where $MI_{Adj} > 0$ in observed action sequences versus to their corresponding 95% confidence interval for Markov sequences. This process was repeated for each individual using condensed sequence data, to determine whether the maximum distances over which dependencies were detected was influenced by repeating actions in both observed and Markov sequences.

To determine the extent to which Markovian approximations of chimpanzee tool-action produce MI_{Adj} decay profiles which are best approximated by exponential decay dynamics, we used several generalized Markov models to produce control sequences. We concatenated sequence data from all eight individuals, and used this extended corpus to train an initial 'community' Markov model which reflected possible sequential-action combinations seen by all individuals within our analysis (similar to E-Languages in linguistics, which reflect the corpus of externalized utterances within a population (Chomsky, 1986)). From this community Markov model, we simulated 500 sequences, each 1000 elements long, which were used for MI_{Adj} Decay analyses and Model fitting as outlined in sections *Mutual Information Estimation* and *MI Decay Model Fitting and Selection*. The proportion of MI decay profiles which were best characterized

by exponential decay dynamics were calculated using AICc scores. This process was repeated with condensed sequence data, to produce a second community Markov model which approximated sequential relationships in the absence of repeating actions. We also produced two further community Markov models which are structurally identical to the previous two models, however we homogenised transition probabilities between nodes (e.g. if one node offered two possible transitions to two separate nodes, the transition probabilities would be set as 0.5 for each). This allowed us to evaluate how model selection may be influenced by highly directed Markov models (e.g. one action is very likely to be followed by just one other) compared to Markov models which are less directed, but still approximate biologically relevant combinations of actions.

For MI Decay analyses from Markovian sequences, the University of Oxford's Advanced Research Computing Facility was used to meet the high computational demands of processing numerous MI Decay analyses in parallel (Richards, 2015).

2.7.9 Quantification and statistical analysis

All statistical analyses were run in R Studio v.1.2.5001, using R v.4.2.1 (2022-06-23) – "Funny-Looking Kid" (R Core Team, 2022). For both mean sequence length (including sequences aimed at individual nuts, as well as sequences of continuous coding during data collection), and for the mean maximum sequential distances where $MI_{Adj} > 0$, 95% confidence intervals were estimated using the exact method for data following a Poisson distribution. Where standard errors are presented for these means, they were produced using the normal approximation of the Poisson Distribution. During MI_{Adj} estimation, permuted sequences were generated to estimate positive MI values produced by chance relationships, which could then be subtracted from MI values estimated from observed action sequences. MI at each sequential distance (0-100 elements) was averaged across all 1000 permuted sequences by finding the arithmetic mean. 95% confidence intervals about this mean were calculated using the standard error of MI at each sequential distance, and the following formula:

$$\underline{X} \pm 1.96 * \sigma_{\underline{X}}$$

where $\underline{X}$ corresponds to the arithmetic mean value at each sequential distance, and $\sigma_{\underline{X}}$ is the corresponding standard error.

All information surrounding estimation of transition matrices for Markov models can be found in the Method Details. The candidate MI decay models (exponential, power-law and composite) were fit to MI_{Adj} data using the nlsLM() function of the minpack.lm package (Elzhov et al., 2016), which uses the Levenberg-Marquardt algorithm to fit non-linear curves by least-squares. Following model fitting, MI estimates, predicted MI values, and inter-element distances were logged to base 10 to allow for decay dynamics to be visualised in log-space. AICc scores for each model were calculated in R using the Multi-Model Inference package (MuMIn) (Bartoń, 2009).

2.8 References

Arnold, K., Zuberbühler, K., 2012. Call combinations in monkeys: Compositional or idiomatic expressions? Brain Lang. 120, 303–309. https://doi.org/10.1016/j.bandl.2011.10.001

Asano, R., Boeckx, C., 2015. Syntax in language and music: what is the right level of comparison? Front. Psychol. 6, 1–16. https://doi.org/10.3389/fpsyg.2015.00942

Bartoń, K., 2009. Mu-Min: Multi-model inference. R Package Version: 1.46.0.

Bergman, T.J., Beehner, J.C., Cheney, D.L., Seyfarth, R.M., 2003. Hierarchical Classification by Rank and Kinship in Baboons. Science 302, 1234–1236. https://doi.org/10.1126/science.1087513

Berwick, R.C., Okanoya, K., Beckers, G.J.L., Bolhuis, J.J., 2011. Songs to syntax: The linguistics of birdsong. Trends Cogn. Sci. 15, 113–121. https://doi.org/10.1016/j.tics.2011.01.002

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. Anim. Cogn. 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. Cogn. Dev. Chimpanzees 476–508. https://doi.org/10.1007/4-431-30248-4_28

Boesch, C., Kalan, A.K., Mundry, R., Arandjelovic, M., Pika, S., Dieguez, P., Ayimisin, E.A., Barciela, A., Coupland, C., Egbe, V.E., Eno-Nku, M., Michael Fay, J., Fine, D., Adriana Hernandez-Aguilar, R., Hermans, V., Kadam, P., Kambi, M., Llana, M., Maretti, G., Morgan, D., Murai, M., Neil, E., Nicholl, S., Ormsby, L.J., Orume, R., Pacheco, L., Piel, A., Sanz, C., Sciaky, L., Stewart, F.A., Tagg, N., Wessling, E.G., Willie, J., Kühl, H.S., 2020. Chimpanzee ethnography reveals unexpected cultural diversity. Nat. Hum. Behav. 4, 910–916. https://doi.org/10.1038/s41562-020-0890-1

Byrne, R.W., Russon, A.E., 1998. Learning by imitation : A hierarchical approach. Behav. Brain Sci. 21, 667–721.

Byrne, R.W., Sanz, C.M., Morgan, D.B., 2013. Chimpanzees plan their tool use, in: Sanz, C.M., Call, J., Boesch, C. (Eds.), Tool Use in Animals. Cambridge University Press, pp. 48–64. https://doi.org/10.1017/CBO9780511894800.004

Carvalho, S., Cunha, E., Sousa, C., Matsuzawa, T., 2008. Chaînes opératoires and resource-exploitation strategies in chimpanzee (Pan troglodytes) nut cracking. J. Hum. Evol. 55, 148–163. https://doi.org/10.1016/j.jhevol.2008.02.005

Cavanaugh, J.E., Neath, A.A., 2019. The Akaike information criterion: Background, derivation, properties, application, interpretation, and refinements. Wiley Interdiscip. Rev. Comput. Stat. 11, 1–11. https://doi.org/10.1002/wics.1460

Cheung, V.K.M., Meyer, L., Friederici, A.D., Koelsch, S., 2018. The right inferior frontal gyrus processes nested non-local dependencies in music. Sci. Rep. 8, 1–12. https://doi.org/10.1038/s41598-018-22144-9

Chomsky, N., 2002a. An Elementary Linguistic Theory, in: Syntactic Structures; Second Edition. Berlin ; New York : Mouton de Gruyter, pp. 18–25. https://doi.org/10.1515/9783110218329

Chomsky, N., 2002b. Phrase Structure, in: Syntactic Structures; Second Edition. Berlin ; New York : Mouton de Gruyter, pp. 26–33. https://doi.org/10.1515/9783110218329
Chomsky, N., 1986. Knowledge of language: its nature, origin, and use, Convergence. Praeger, New York.
Chomsky, N., 1956. Three models for the description of language. IRE Trans. Inf. Theory 2, 113–124.
Clay, Z., Zuberbühler, K., 2009. Food-associated calling sequences in bonobos. Anim. Behav. 77, 1387–1396. https://doi.org/10.1016/j.anbehav.2009.02.016
Dawkins, R., 1976. Hierarchical organization: a candidate principle for ethology., in: Growing Points in Ethology. Cambridge University Press.
Elzhov, T.V., Mullen, K.M., Spiess, A.-N., Maintainer, B.B., 2016. minpack.lm: R Interface to the Levenberg-Marquardt Nonlinear Least-Squares Algorithm Found in MINPACK, Plus Support for Bounds.
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. Am. J. Primatol. 79, e22672. https://doi.org/10.1002/ajp.22672
Fine, S., Singer, Y., Tishby, N., 1998. The hierarchical hidden Markov model: Analysis and applications. Mach. Learn. 32, 41–62. https://doi.org/10.1023/A:1007469218079
Fitch, W.T., Hauser, M.D., 2004. Computational Constraints on Syntactic Processing in a Nonhuman Primate. Science 303, 377–380. https://doi.org/10.1126/science.1089401
Fitch, W.T., Hauser, M.D., Chomsky, N., 2005. The evolution of the language faculty: Clarifications and implications. Cognition 97, 179–210. https://doi.org/10.1016/j.cognition.2005.02.005
Fitch, W.T., Martins, M.D., 2014. Hierarchical processing in music, language, and action: Lashley revisited. Ann. N. Y. Acad. Sci. 1316, 87–104. https://doi.org/10.1111/nyas.12406
Friard, O., Gamba, M., 2016. BORIS: a free, versatile open-source event-logging software for video/audio coding and live observations. Methods Ecol. Evol. 7, 1325–1330. https://doi.org/10.1111/2041-210X.12584
Gagniuc, P., 2017. Markov Chains: From Theory to Implementation and Experimentation. https://doi.org/10.1002/9781119387596
Genty, E., Byrne, R.W., 2010. Why do gorillas make sequences of gestures? Anim. Cogn. 13, 287–301. https://doi.org/10.1007/s10071-009-0266-4
Girard-Buttoz, C., Zaccarella, E., Bortolato, T., Friederici, A.D., Wittig, R.M., Crockford, C., 2022. Chimpanzees produce diverse vocal sequences with ordered and recombinatorial properties. Commun. Biol. 5, 410. https://doi.org/10.1038/s42003-022-03350-8
Gomez-Marin, A., Stephens, G.J., Brown, A.E.X., 2016. Hierarchical compression of *Caenorhabditis elegans* locomotion reveals phenotypic differences in the organization of behaviour. J. R. Soc. Interface 13, 20160466. https://doi.org/10.1098/rsif.2016.0466
Grassberger, P., 2003. Entropy Estimates from Insufficient Samplings 1–5.
Greenfield, P.M., 1991. Language, tools and brain: The ontogeny and phylogeny of hierarchically organized sequential behavior. Behav. Brain Sci. 531–595.
Greenfield, P.M., Schneider, L., 1977. Building a tree structure: The development of hierarchical complexity and interrupted strategies in children's construction activity. Dev. Psychol. 13, 299–313. https://doi.org/10.1037/0012-1649.13.4.299
Gruber, T., Clay, Z., 2016. A Comparison Between Bonobos and Chimpanzees: A Review and Update. Evol. Anthropol. 25, 239–252. https://doi.org/10.1002/evan.21501
Gruber, T., Zuberbühler, K., Clément, F., van Schaik, C., 2015. Apes have culture but may not know that they do. Front. Psychol. 6, 1–14. https://doi.org/10.3389/fpsyg.2015.00091
Hauser, M.D., Chomsky, N., Fitch, W.T., 2002. The faculty of language: What is it, who has it, and how did it evolve? Evol. Hum. Lang. Biolinguistic Perspect. 298, 14–42. https://doi.org/10.1017/CBO9780511817755.002
Hayashi, M., 2015. Perspectives on object manipulation and action grammar for percussive actions in primates. Philos. Trans. R. Soc. B Biol. Sci. 370. https://doi.org/10.1098/rstb.2014.0350
Hayashi, M., 2007. A new notation system of object manipulation in the nesting-cup task for chimpanzees and humans. Cortex 43, 308–318. https://doi.org/10.1016/S0010-9452(08)70457-X
Hayashi, M., Takeshita, H., 2022. Hierarchical object combination and tool use in the great apes and human children. Primates. https://doi.org/10.1007/s10329-022-01003-2

Hedwig, D., Mundry, R., Robbins, M.M., Boesch, C., 2015. Contextual correlates of syntactic variation in mountain and western gorilla close-distance vocalizations: Indications for lexical or phonological syntax? Anim. Cogn. 18, 423–435. https://doi.org/10.1007/s10071-014-0812-6

Hedwig, D., Robbins, M.M., Mundry, R., Hammerschmidt, K., Boesch, C., 2014. Acoustic structure and variation in mountain and western gorilla close calls: A syntactic approach. Behaviour 151, 1091–1120. https://doi.org/10.1163/1568539X-00003175

Hobaiter, C., Byrne, R.W., 2011. Serial gesturing by wild chimpanzees: Its nature and function for communication. Anim. Cogn. 14, 827–838. https://doi.org/10.1007/s10071-011-0416-3

Hobaiter, C., Byrne, R.W., Zuberbühler, K., 2017. Wild chimpanzees' use of single and combined vocal and gestural signals. Behav. Ecol. Sociobiol. 71. https://doi.org/10.1007/s00265-017-2325-1

Humle, T., Matsuzawa, T., 2002. Ant-dipping among the chimpanzees of Bossou, Guinea, and some comparisons with other sites. Am. J. Primatol. 58, 133–148. https://doi.org/10.1002/ajp.10055

Inoue-Nakamura, N., Matsuzawa, T., 1997. Development of Stone Tool Use by Wild Chimpanzees (Pan troglodytes). J. Comp. Psychol. 111, 159–173. https://doi.org/10.1037/0735-7036.111.2.159

Isac, D., Reiss, C., 2013. Finite State Languages, in: I-Language: An Introduction to Linguistics as Cognitive Science. Oxford University Press, pp. 99–107.

Jäger, G., Rogers, J., 2012. Formal language theory: Refining the Chomsky hierarchy. Philos. Trans. R. Soc. B Biol. Sci. 367, 1956–1970. https://doi.org/10.1098/rstb.2012.0077

Kaplan, R.M., Kay, M., 1994. Regular Models of Phonological Rule Systems. Comput. Linguist. 20, 331–378.

Koelsch, S., Rohrmeier, M., Torrecuso, R., Jentschke, S., 2013. Processing of hierarchical syntactic structure in music. Proc. Natl. Acad. Sci. U. S. A. 110, 15443–15448. https://doi.org/10.1073/pnas.1300272110

Kolodny, O., Edelman, S., 2018. The evolution of the capacity for language: The ecological context and adaptive value of a process of cognitive hijacking. Philos. Trans. R. Soc. B Biol. Sci. 373. https://doi.org/10.1098/rstb.2017.0052

Larsson, N.J., Moffat, A., 2000. Off-Line Dictionary-Based Compression. Proc. IEEE 88.

Lashley, K., 1951. The problem of serial order in behavior. Cereb. Mech. Behav. 112–147.

Leroux, M., Bosshard, A.B., Chandia, B., Manser, A., Zuberbühler, K., Townsend, S.W., 2021. Chimpanzees combine pant hoots with food calls into larger structures. Anim. Behav. 179, 41–50. https://doi.org/10.1016/j.anbehav.2021.06.026

Leroux, M., Schel, Anne M, Wilke, Claudia, Bosco, Chandia, Zuberbühler, Klaus, Slocombe, Katie, Townsend, Simon, 2023. Call combinations and compositional processing in wild chimpanzees. Nat. Commun. 14, 1–8. https://doi.org/10.1038/s41467-023-37816-y

Leroux, M., Townsend, S.W., 2020. Call combinations in great apes and the evolution of syntax. Anim. Behav. Cogn. 7, 131–139. https://doi.org/10.26451/abc.07.02.07.2020

Lin, H.W., Tegmark, M., 2017. Critical behavior in physics and probabilistic formal languages. Entropy 19, 1–25. https://doi.org/10.3390/e19070299

Matsuzawa, T., 1996. Chimpanzee intelligence in nature and in captivity: Isomorphism of symbol use and tool use, in: Great Ape Societies. pp. 196–212.

Matsuzawa, T., 1994. Field Experiments on use of Stone Tools in the wild, in: Chimpanzee Cultures. pp. 351–370.

Matsuzawa, T., 1991. Nesting cups and metatools in chimpanzees. Behav. Brain Sci. 14, 570–571. https://doi.org/10.1017/S0140525X00071417

Matsuzawa, T., Hulme, T., Sugiyama, Y., 2011. The Chimpanzees of Bossou and Nimba.

Matsuzawa, T., Humle, T., Koops, K., Biro, D., Hayashi, M., Sousa, C., Mizuno, Y., Kato, A., Yamakoshi, G., Ohashi, G., Sugiyama, Y., Kourouma, M., 2004. Wild chimpanzees at Bossou-Nimba: Deaths through a flu-like epidemic in 2003 and the green corridor project. Primate Res 20, 45–55.

Mel'čuk, I., 1988. Dependency Syntax: Theory and Practice, SUNY Series in Linguistics. Albany: State U of New York.

Mielke, A., Carvalho, S., 2022. Chimpanzee play sequences are structured hierarchically as games. PeerJ 10, e14294. https://doi.org/10.7717/peerj.14294

Miksis-Olds, J.L., Buck, J.R., Noad, M.J., Cato, D.H., Stokes, M.D., 2008. Information theory analysis of Australian humpback whale song. J Acoust Soc Am 124, 2385–93. https://doi.org/10.1121/1.2967863

Milne, A.E., Mueller, J.L., Männel, C., Attaheri, A., Friederici, A.D., Petkov, C.I., 2016. Evolutionary origins of non-adjacent sequence processing in primate brain potentials. Sci. Rep. 6, 1–10. https://doi.org/10.1038/srep36259

R Core Team, 2022. R: A language and environment for statistical computing.

Richards, A., 2015. University of Oxford Advanced Research Computing. https://doi.org/10.5281/zenodo.22558

Rispens, J., Soto de Amesti, V., 2017. What makes syntactic processing of subject–verb agreement complex? The effects of distance and additional agreement features. Lang. Sci. 60, 160–172. https://doi.org/10.1016/j.langsci.2016.09.004

Rohrmeier, M., Zuidema, W., Wiggins, G.A., Scharff, C., 2015. Principles of structure building in music, language and animal song. Philos. Trans. R. Soc. B Biol. Sci. 370, 20140097. https://doi.org/10.1098/rstb.2014.0097

Rosenbaum, D.A., Cohen, R.G., Jax, S.A., Weiss, D.J., van der Wel, R., 2007. The problem of serial order in behavior: Lashley's legacy. Hum. Mov. Sci. 26, 525–554. https://doi.org/10.1016/j.humov.2007.04.001

Sainburg, T., Mai, A., Gentner, T.Q., 2022. Long-range sequential dependencies precede complex syntactic production in language acquisition. Proc R Soc B 289:, 2020.08.19.256792. https://doi.org/10.1098

Sainburg, T., Mai, A., Gentner, T.Q., 2020. Long-range sequential dependencies precede complex syntactic production in language acquisition. bioRxiv 2020.08.19.256792.

Sainburg, T., Theilman, B., Thielk, M., Gentner, T.Q., 2019. Parallels in the sequential organization of birdsong and human speech. Nat. Commun. 10, 1–11. https://doi.org/10.1038/s41467-019-11605-y

Sanz, C.M., Morgan, D.B., 2010. The Complexity of Chimpanzee Tool-Use Behaviors, in: The Mind of the Chimpanzee: Ecological and Experimental Perspectives. The University of Chicago Press, pp. 127–140.

Schlenker, P., Chemla, E., Schel, A.M., Fuller, J., Gautier, J.P., Kuhn, J., Veselinović, D., Arnold, K., Cäsar, C., Keenan, S., Lemasson, A., Ouattara, K., Ryder, R., Zuberbühler, K., 2016a. Formal monkey linguistics. Theor. Linguist. 42, 1–90. https://doi.org/10.1515/tl-2016-0001

Schlenker, P., Chemla, E., Schel, A.M., Fuller, J., Gautier, J.P., Kuhn, J., Veselinović, D., Arnold, K., Cäsar, C., Keenan, S., Lemasson, A., Ouattara, K., Ryder, R., Zuberbühler, K., 2016b. Formal monkey linguistics: The debate. Theor. Linguist. 42, 173–201. https://doi.org/10.1515/tl-2016-0010

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. Sci. Adv. 5, 1–10. https://doi.org/10.1126/sciadv.aaw0736

Sonnweber, R., Ravignani, A., Fitch, W.T., 2015. Non-adjacent visual dependency learning in chimpanzees. Anim. Cogn. 18, 733–745. https://doi.org/10.1007/s10071-015-0840-x

Spedicato, G.A., 2017. Discrete Time Markov Chains with R. R J.

Stout, D., Chaminade, T., Apel, J., Shafti, A., Faisal, A.A., 2021. The measurement, evolution, and neural representation of action grammars of human behavior. Sci. Rep. 11, 13720. https://doi.org/10.1038/s41598-021-92992-5

Sugiyama, Y., 1981. Observations on the population dynamics and behavior of wild chimpanzees at Bossou, Guinea, in 1979-1980. Primates 22, 435–444. https://doi.org/10.1007/BF02381236

Suzuki, R., Buck, J.R., Tyack, P.L., 2006. Information entropy of humpback whale songs. J. Acoust. Soc. Am. 119, 1849–1866. https://doi.org/10.1121/1.2161827

Tanner, J.E., Perlman, M., 2017. Moving beyond 'meaning': Gorillas combine gestures into sequences for creative display. Lang. Commun. 54, 56–72. https://doi.org/10.1016/j.langcom.2016.10.006

ten Cate, C., Okanoya, K., 2012. Revisiting the syntactic abilities of nonhuman animals: Natural vocalizations and artificial grammar learning. Philos. Trans. R. Soc. B Biol. Sci. 367, 1984–1994. https://doi.org/10.1098/rstb.2012.0055

Tonooka, R., 2001. Leaf-folding behavior for drinking water by wild chimpanzees (Pan troglodytes verus) at Bossou, Guinea. Anim. Cogn. 4, 325–334. https://doi.org/10.1007/s100710100110

Traxler, M.J., Boudewyn, M., Loudermilk, J., 2012. What's Special About Human Language? The Contents of the "Narrow Language Faculty" Revisited. Linguist. Lang. Compass 6, 611–621. https://doi.org/10.1002/lnc3.355

Vereijken, B., Whiting, H., 1998. Hoist by their own petard: The constraints of hierarchical models. Behav. Brain Sci. 21, 705–705. https://doi.org/10.1017/S0140525X98451744

Watson, S.K., Burkart, J.M., Schapiro, S.J., Lambeth, S.P., Mueller, J.L., Townsend, S.W., 2021. Reply to comment on “Nonadjacent dependency processing in monkeys, apes, and humans.” Sci. Adv. 7, 5–6. https://doi.org/10.1126/sciadv.abj1517

Watson, S.K., Burkart, J.M., Schapiro, S.J., Lambeth, S.P., Mueller, J.L., Townsend, S.W., 2020. Nonadjacent dependency processing in monkeys, apes, and humans. Sci. Adv. 6. https://doi.org/10.1126/sciadv.abb0725

Wilson, B., Slater, H., Kikuchi, Y., Milne, A.E., Marslen-Wilson, W.D., Smith, K., Petkov, C.I., 2013. Auditory artificial grammar learning in Macaque and Marmoset monkeys. J. Neurosci. 33, 18825–18835. https://doi.org/10.1523/JNEUROSCI.2414-13.2013

Wilson, B., Spierings, M., Ravignani, A., Mueller, J.L., Mintz, T.H., Wijnen, F., van der Kant, A., Smith, K., Rey, A., 2020. Non-adjacent Dependency Learning in Humans and Other Animals. Top. Cogn. Sci. 12, 843–858. https://doi.org/10.1111/tops.12381

Yamakoshi, G., Sugiyama, Y., 1995. Pestle-pounding behavior of wild chimpanzees at Bossou, Guinea: a newly observed tool-using behavior. Primates 36, 489–500.

2.9 Supplementary materials

2.9.1 The outdoor laboratory and behaviour coding



Figure S1. The outdoor laboratory, Bossou. Key features of the outdoor laboratory are: 1. Provided piles of oil-palm nuts (two piles are indicated; typically, a total of 6-12 piles of 40-50 nuts each were provided), 2. Central matrix of available stone tools, 3. Water point, 4. Bunch of oil-palm fruits.

Table S1. Chimpanzees present at Bossou in the 2011/2012 field season. Ages are listed as of Jan 2012.

Individual	Sex	Age Category	Birth	Age	Relation	Hand use***
Tua	M	Adult	1957*	54*	None	L
Foaf	M	Adult	1980 late	31	Son of Fana	R
Jeje	M	Adult	1997 Dec	14	Son of Jire	L
Peley	M	Adult	1998 Apr	13	Son of Pama	L
Fana	F	Adult	1956*	55*	Mother of Fanle**	R
Jire	F	Adult	1958*	53*	Mother of Jeje	L
Velu	F	Adult	1959*	52*	None	R
Yo	F	Adult	1961*	50*	None	L
Pama	F	Adult	1967*	44*	Mother of Peley	—
Fanle	F	Adult	1997 Oct	14	Daughter of Fana	R
Joya	F	Juvenile	2004 Sep 2	7	Daughter of Jire	L
Flanle	M	Infant	2007 Sept 14	4y 4m	Son of Fanle	(L) in Dec
Fanwa	M	Infant	2011 Nov 4	0y2m	Son of Fanle	—

* Estimated age; these individuals were already present at Bossou when long-term study started in 1976.

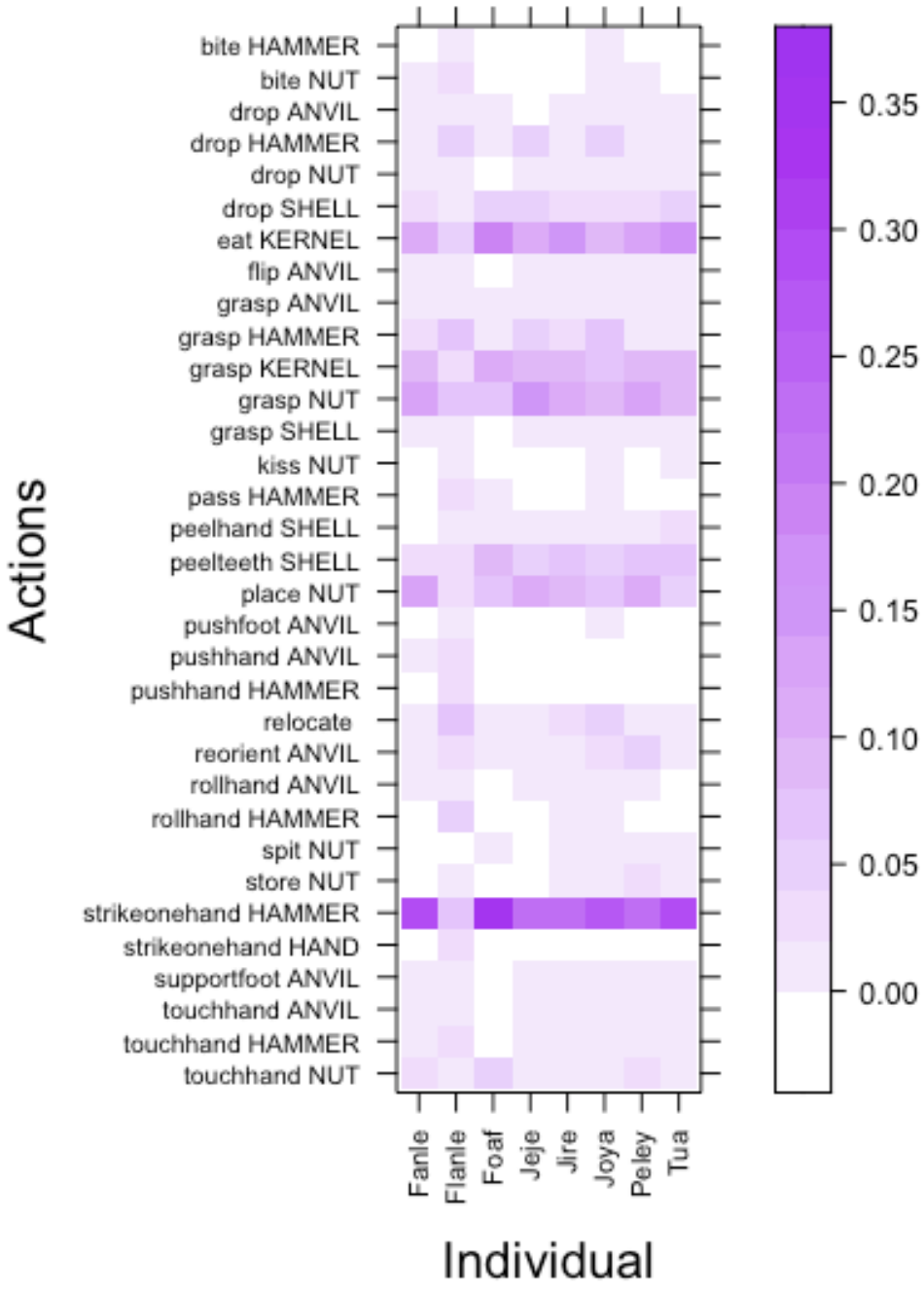
** Fana is also the grandmother of Flanle and Fanwa; she took care of Flanle from the age of 4, following the birth of Fanwa.

*** Hand use refers to the hand (L, left or R, right) the individual uses to hold the hammer stone during nut-cracking. "—" refers to individuals that have never or not yet been seen to crack nuts using tools.

Table S2. Ethogram of codable actions for observations of nut-cracking behaviours. Actions in bold are coded alongside a corresponding object. There are 6 possible corresponding objects: 1. Nut, 2. Hammer, 3. Anvil, 4. Kernel, 5. Shell, 6. Bare Hand. Event codes in italics are used to denote the start and end of observable sequences. Coding commenced when individuals began interacting with stones, nuts, or nut-fragments. Coding ceased when individuals began engaging in a new behaviour e.g. play, grooming, eating oil-palm fruits. On the occasions where an individual moved out of clear sight of the video recording, or actions became obscured by an individual's body position, sequences were terminated with a 'Not Visible' codon, and marked as incomplete.

Action	Description
Bite	Place object in mouth and bite with teeth. Differs from 'Eat' as there is no consumption. Differs from 'Store' as object moves in and out of mouth whilst chimp is stationary. Differs from 'Peel Teeth' as bite applies general force, whereas peel with mouth is to remove shell fragments from kernel dexterously. Differs from 'Kiss' as object enters inside the mouth.
Brush	Brush objects off the anvil.
Drop	Place object(s) on ground.
Eat	Consume object. Differs from bite and store as it requires successful ingestion.
Flip	Flip object over.
Grasp	Grasp an object and move off the ground.
Kick	Apply rapid, hard force on object with the foot, so that the object is displaced.
Kiss	Place object to lips or nose, but not inside of the mouth.
Pass	Pass object between hands.
Peel Hand	Peel shell off of kernel with hands.
Peel Teeth	Peel shell off of kernel with teeth.
Place	Place an object on an anvil.
Provide	Directly hand an object to another individual.
Pull Foot	Pull an object across the ground with foot.
Pull Hand	Pull an object across the ground with hand.
Push Foot	Push an object across the ground with foot.
Push Hand	Push an object across the ground with hand.
Rake Foot	Pull many objects towards oneself using foot/leg.
Rake Hand	Pull many objects towards oneself using hand/arm.
Reorient	Rotate object horizontally.
Roll Foot	Roll object along the floor with foot.
Roll Hand	Roll object along the floor with hand.
Spit	Let object fall from mouth or lips.
Stomp	Whilst standing, apply strong force to object with foot.
Store	Place object(s) in mouth for transportation. Separated from bite, eat, peel teeth as it is followed by transportation across the outdoor laboratory, before then being removed from the mouth intact.
Strike One Hand	Strike with one hand, (and associated object).
Strike Two Hand	Strike with two hands, (and associated object).
Support Foot	Support object with foot.
Support Hand	Support object with hand.
Take	Receive an object directly from another individual.
Throw	Throw object away from self, horizontally or vertically.
Touch Foot	Touch or grasp object without moving it using foot.
Touch Hand	Touch or grasp object without moving it using hand.
Relocate	Stand up and move to a new area; is immediately followed by another coding action.
Start	Start of a sequence.
End Bout	End of a sequence.
Not Visible	Individual moves out of view, and coding cannot continue. Differs from 'End Bout', as there is no evidence the individual has stopped engaging with stones, nuts or nut-fragments.

Figure S2. Enlarged heatmap of action types used by chimpanzees during nut cracking. The shading relates to the proportion of actions of a given action type that occurred in the data for each individual. This is a larger replication of figure 1.c. in the main manuscript.



2.9.2 Evaluating the maximum sequential distance at which nonadjacent dependencies occur

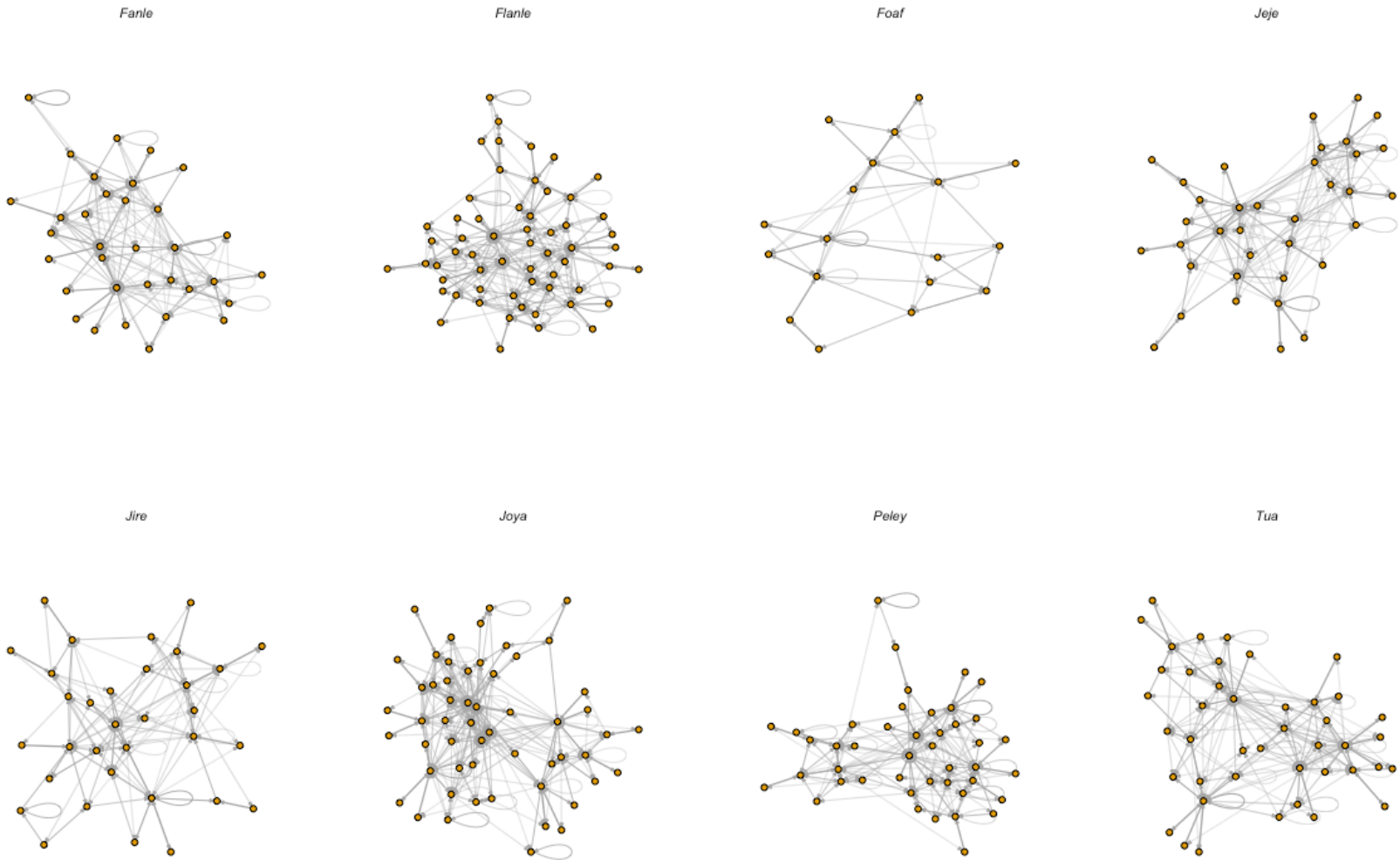


Figure S3. Estimated Markov models for each individual. Nodes in each network represent an action, e.g. *Drop Hammer, Spit Shell, Eat Kernel,* etc. Edges represent probabilistic transitions between the different action types. Probabilistic transitions are estimated from sequences using neighbouring elements – therefore, these models represent first order Markov chains, which contain no memory of states previously activated during sequence construction.

Figure S4. Histograms of maximum sequential distances over which markovian data produced positive MI_{Adj}. Histograms are faceted by individual. Distributions were created using 100 sequences generated from the Markov Models approximating action transitions for each individual.

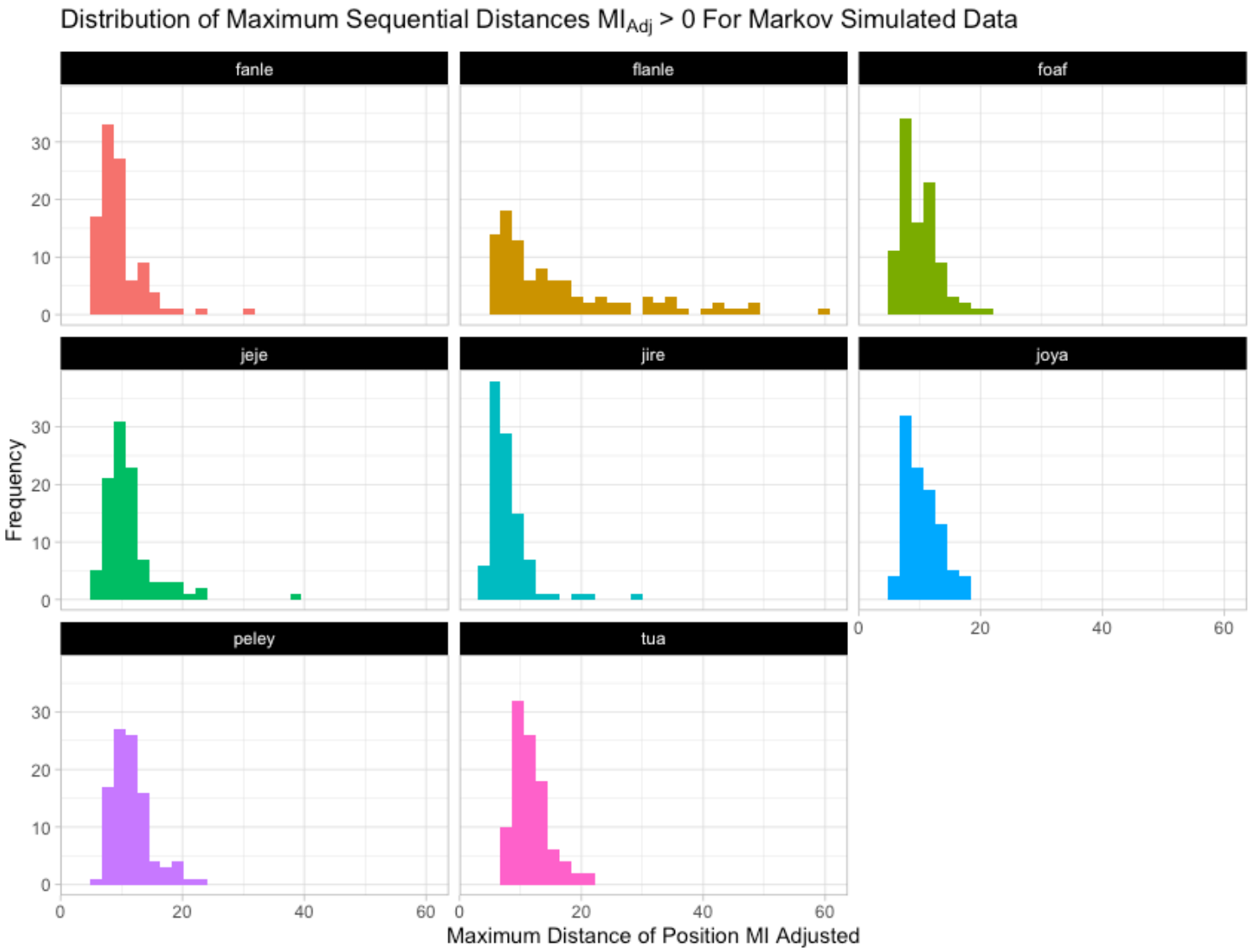


Figure S5. Histograms of maximum sequential distances over which Markovian data produced positive MIAdj, when based on condensed sequence data. Histograms are faceted by individual. Distributions were created using 100 sequences generated from the Markov Models approximating action transitions for each individual.

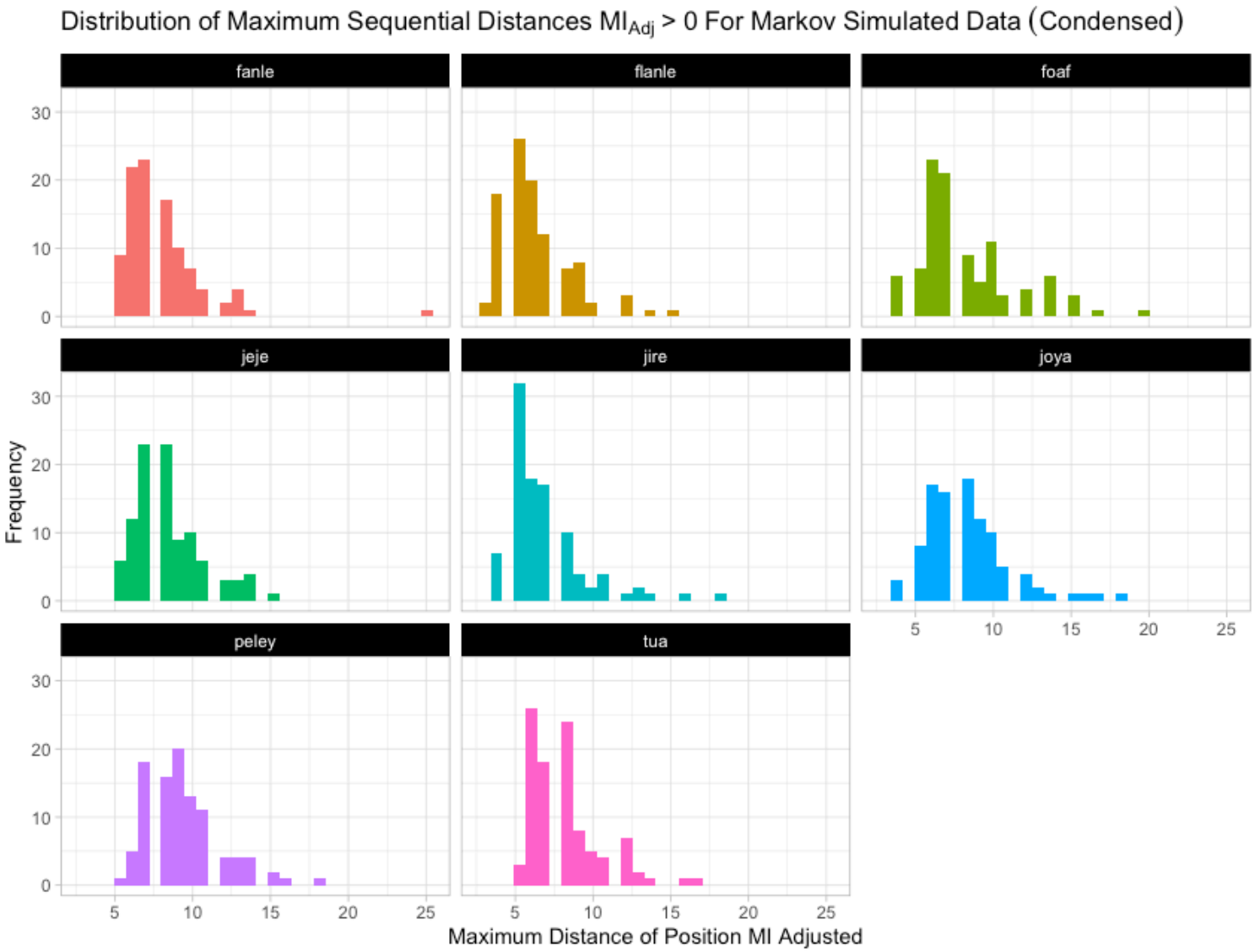


Table S3. Maximum distances $MI_{Adj} > 0$ for sequences produced by chimpanzees and Markov models. Confidence intervals were estimated using the exact method for the Poisson distribution. An asterisk (*) indicates that the maximum distance MIAdj > 0 in sequences recorded from chimpanzees (including sequences which feature repeating actions, and those that have been condensed) were greater than the 95% confidence interval for the mean maximum distance in Markovian Sequences. In these instances, we take this to mean that the distance was significantly greater for alpha = 0.05.

Individual	Sequence Type	Max Distance MIAdj > 0	Mean Max Distance MIAdj > 0 from Markov Data (Elements)	Variance in Max Distance MIAdj > 0 from Markov Data (Elements)	Lower 95% CI for Mean Max Distance MIAdj > 0 from Markov Data (Elements)	Upper 95% CI for Mean Max Distance MIAdj > 0 from Markov Data (Elements)	Individual Distance Outside of 95% CI for Markov?
Fanle	Observed	17	9.39	15.1	5.06	16.3	*
	Condensed	16	7.93	7.30	4.07	14.3	*
Flanle	Observed	100	16.56	147	10.3	25.4	*
	Condensed	9	6.25	5.12	2.97	12.0	
Foaf	Observed	9	9.74	9.75	5.31	16.7	
	Condensed	10	8.18	10.07	4.24	14.7	
Jeje	Observed	22	11.06	20.1	6.24	18.5	*
	Condensed	11	8.4	5.33	4.39	15.0	
Jire	Observed	11	7.61	13.1	3.85	13.9	
	Condensed	9	6.81	6.68	3.33	12.8	
Joya	Observed	21	10.27	8.58	5.68	17.4	*
	Condensed	9	8.27	7.45	4.30	14.8	
Peley	Observed	42	11.44	11.6	6.51	19.0	*
	Condensed	26	9.4	5.98	5.07	16.3	*
Tua	Observed	20	11.57	9.02	6.61	19.1	*
	Condensed	16	8.12	5.60	4.20	14.6	*

2.9.3 The dynamics of MI_{Adj} decay

Table S4. AICc scores for MI_{Adj} decay models (where data includes repeats of actions). For each individual, Max Element Distance highlights the greatest element distance included in the MI_{Adj} datasets, and models are given in the order of preference (as determined by AICc). K represents the number of parameters estimated in each model. AICc describes the AIC score corrected for smaller sample size (see section 4.6). ΔAICc represents the difference between a given model's AICc score and the optimal model's AICc score for each individual. AICc.Wt describes the proportion of the total predictive power of all three models contained in each model, and Cum.Wt describes the accumulation of predictive power in order of model preference. LL represents the log-likelihood of each model given the data - AICc is estimated using both K and LL.

Individual	Max Element Distance	Model	K	AICc	ΔAICc	AICc.Wt	Cum.Wt	LL
Fanle	16	Power-Law	3	-80.8	0.0	0.92	0.92	44.4
		Composite	5	-75.9	5.0	0.08	1.00	45.9
		Exponential	3	-50.6	30.2	0.00	1.00	29.3
Flanle	100	Composite	3	-387.4	0.0	1.00	1.00	199.0
		Power-Law	3	-348.2	39.3	0.00	1.00	177.2
		Exponential	3	-268.2	119.3	0.00	1.00	137.2
Foaf	8	Exponential	3	-27.6	0.0	1.00	1.00	19.8
		Power-Law	3	-15.2	12.4	0.00	1.00	13.6
		Composite	5	8.8	18.7	0.00	1.00	24.1
Jeje	21	Composite	5	-105.6	0.0	1.00	1.00	59.8
		Exponential	3	-85.4	20.2	0.00	1.00	46.4
		Power-Law	3	-76.0	29.6	0.00	1.00	41.7
Jire	10	Power-Law	3	-38.0	0.0	0.99	0.99	24.0
		Exponential	3	-26.6	11.4	0.00	1.00	18.3
		Composite	5	-26.1	12.0	0.00	1.00	25.5
Joya	20	Composite	5	-101.0	0.0	0.99	0.99	57.6
		Power-Law	3	-92.6	8.4	0.01	1.00	50.0
		Exponential	3	-67.4	33.6	0.00	1.00	37.5
Peley	41	Composite	5	-245.5	0.0	1.00	1.00	128.6
		Power-Law	3	-226.3	19.2	0.00	1.00	116.5
		Exponential	3	-142.9	102.6	0.00	1.00	74.8
Tua	19	Composite	5	-109.2	0.0	1.00	1.00	61.9
		Exponential	3	-78.7	30.4	0.00	1.00	43.2
		Power-Law	3	-64.9	44.3	0.00	1.00	36.2

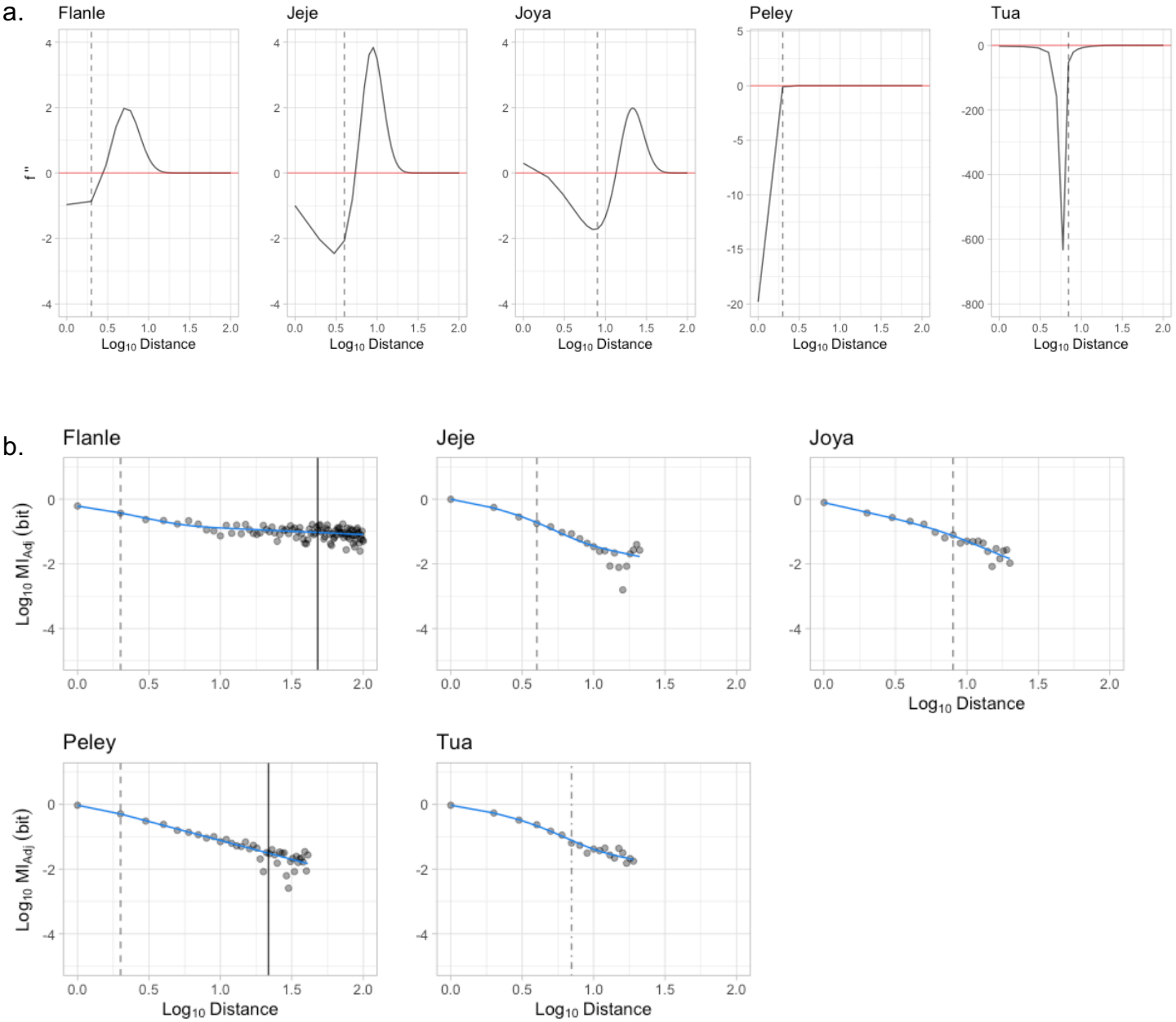


Figure S6. Transition point profiles and composite decay models. (a) Transition point profiles for each individual who showed a high preference for the composite model when data contained repeating elements. The point at which the profile is at its most negative identified where the change in gradient is also the most negative; the point immediately after this minimand indicates where the gradient is becoming less negative, and the composite model begins to 'pull upward' into a power-law decay. We mark this transition point on each profile with a dashed line. **(b)** The composite model for each individual for whom it offered the lowest AICc of all candidate decay models. On each composite model, the corresponding transition point is marked with a dashed line. For individuals whose average sequence length per nut is less than the maximum sequential distance $MI_{Adj} > 0$, the average sequence length per nut is marked with a solid black line.

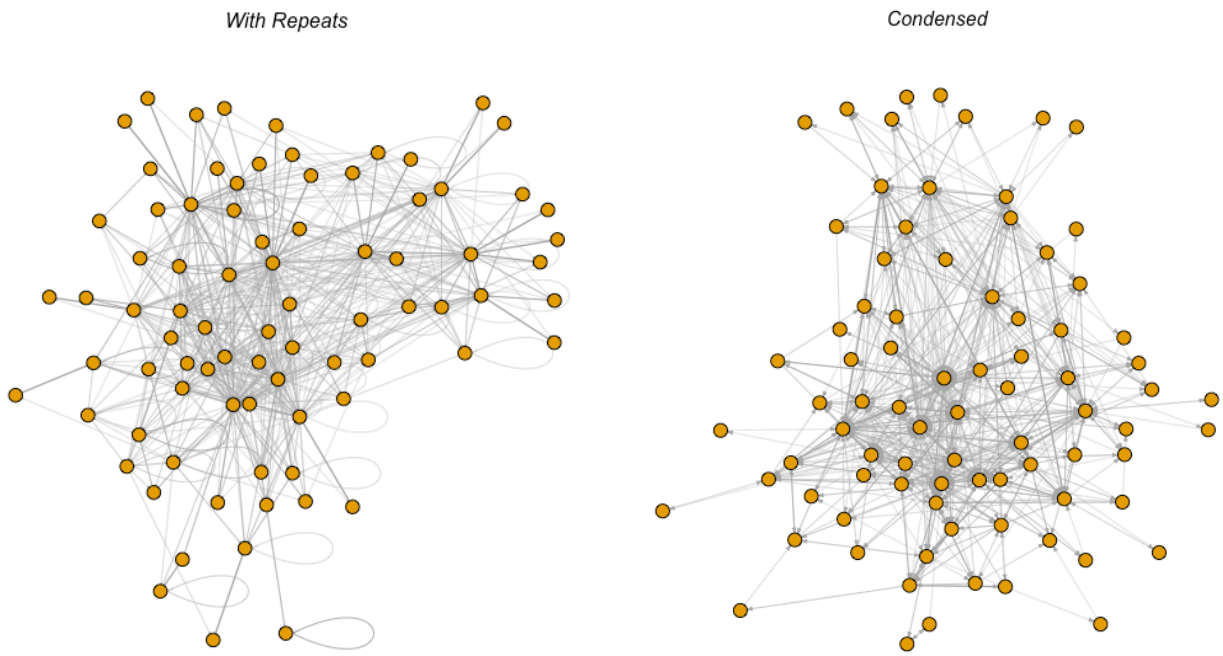


Figure S7. Community Markov models. The Markov models built using action-sequence data for all individuals; nodes represent action types, and edges represent the transition probabilities between action types in a sequence (darker = more likely). The Markov model on the left was built using action sequences with repeating actions. The model on the right was built using condensed data, where repeats were removed and replaced with a single action (e.g. the repeat 'Peel Shell', 'Peel Shell', would be replaced with a single codon: Peel Shell). Homogenized Markov models had identical connections to the graphs below, however outward transition probabilities from an action type were all equal; e.g. If there are two possible actions following 'Grasp Nut': 'Place Nut' (80% probability) or 'Drop Nut' (20% probability), these probabilities were replaced with an equal probability (50%)

Table S5. Output of GLM investigating success of fitting all three decay models, as a function of the maximum distance over which MIAdj > 0. Binomial distribution for the rate of successfully fitting all three models. GLMs are fit with binomial distributions, and Logit link functions. Distance relates to the maximum sequential distance over which MI_{Adj} was greater than zero. *** means significant to p < 0.001; ** means significant to p < 0.01; * means significant to p < 0.05; . means significant to p < 0.1.

Markov Model	Coefficients	Estimate	Std. Error	Z value	P value	Significance
With Repeats	Intercept	-9.2522	1.1292	-8.193	2.54e-16	***
	Distance	1.5266	0.1703	8.963	< 2e-16	***
Condensed	Intercept	-1.5068	0.6556	-2.298	0.0216	*
	Distance	0.5410	0.1071	5.053	4.36e-07	***
Homogenized With Repeats	Intercept	0.6272	0.5671	1.106	0.26870	
	Distance	0.4042	0.1386	2.917	0.00353	**
Condensed And Homogenized	Intercept	1.2119	0.6524	1.858	0.0632	.
	Distance	0.3642	0.1659	2.196	0.0281	*

Table S6. Output of GLM investigating whether Markovian datasets which showed sole preferences for each model type differed in their average maximum sequential length $MI_{Adj} > 0$. Intercept relates to the average for the exponential model, and other models are presented relative to this value. GLM models are fit with a Poisson distribution. *** means significant to $p < 0.001$.

Markov Model	Coefficients	Estimate	Std. Error	Z value	P value	Significance
With Repeats	Intercept	2.11851	0.02741	77.289	< 2e-16	***
	Power-Law	0.21916	0.04616	4.748	2.05e-06	***
	Composite	0.45271	0.03803	11.904	< 2e-16	***
Condensed	Intercept	2.14752	0.02224	96.543	<2e-16	***
	Power-Law	0.01197	0.19737	0.061	0.952	
	Composite	-0.33895	0.03769	-8.992	<2e-16	***
Homogenized With Repeats	Intercept	1.27956	0.04795	26.687	< 2e-16	***
	Power-Law	0.86888	0.08041	10.806	< 2e-16	***
	Composite	0.39532	0.06039	6.546	5.89e-11	***
Condensed And Homogenized	Intercept	1.18526	0.04499	26.344	< 2e-16	***
	Power-Law	0.86244	0.11304	7.630	2.35e-14	***
	Composite	0.50901	0.05942	8.567	< 2e-16	***

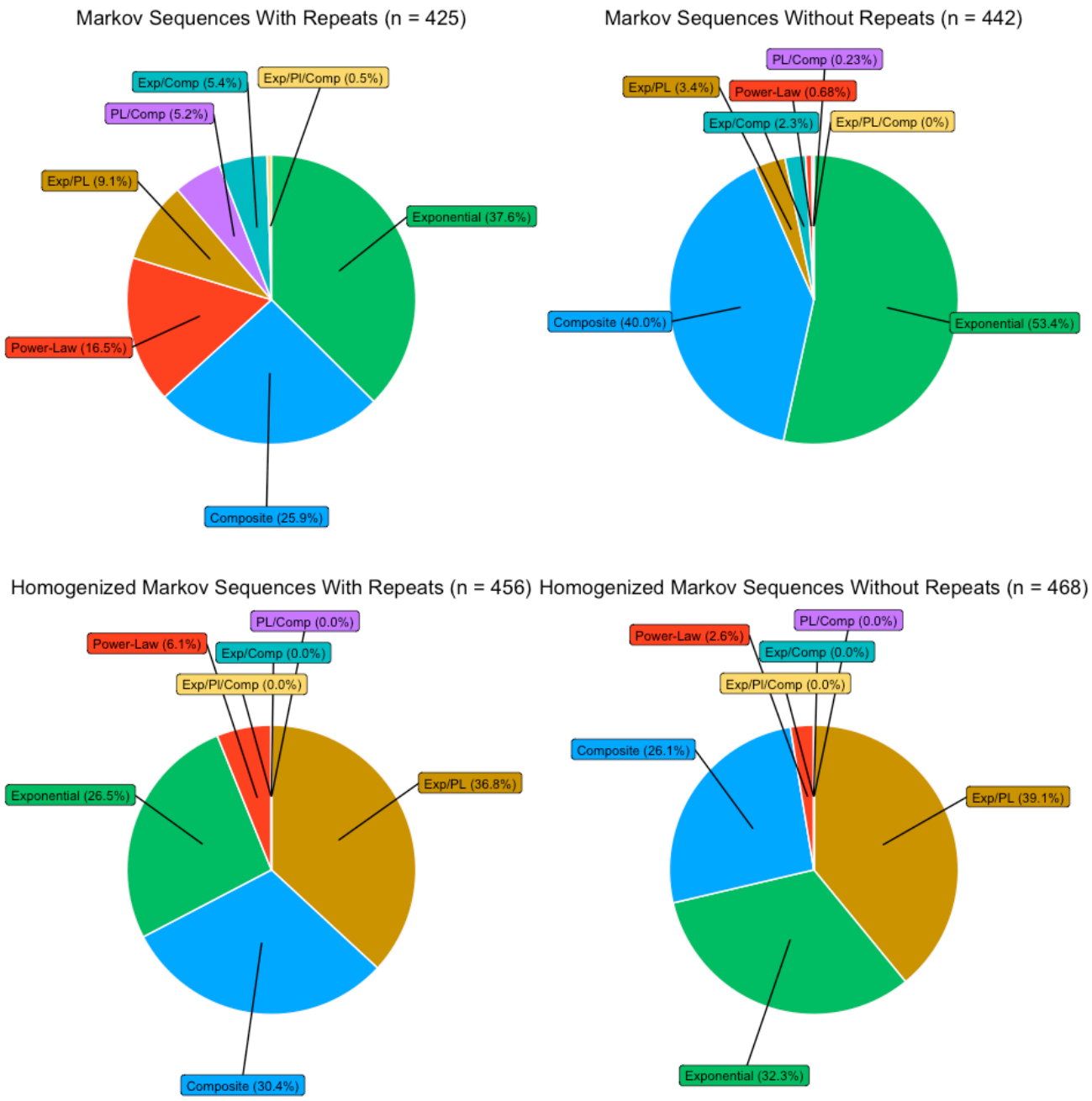


Figure S8. Proportion of Markovian datasets where each decay model was preferred. Pie charts of model preferences, where MI_{Adj} decay profiles were estimated from sequences produced by community Markov models. Each pie chart relates to sequences produced by different community Markov models. **Top-Left:** Data from a Markov model was trained on observed actions sequences, including repeating elements. **Top-Right:** Data from a Markov model was trained on observed actions sequences, but condensed to remove repeats. **Bottom-Left:** Data from a Markov model was trained on observed actions sequences, including repeating elements, and then transition probabilities were homogenized. **Bottom-Right:** Data from a Markov model was trained on observed actions sequences, but condensed to remove repeats, and transition probabilities homogenized.

Chapter 3

Hierarchical Subroutines in Chimpanzee Nut Cracking are Identifiable Through Dictionary-Based Compression

3.1 Abstract

The organization of manual actions into goal-directed behaviours is theorized to occur hierarchically. Actions are combined into subroutines, which address specific subgoals of behaviours, and subroutines are combined to form wider behavioural sequences. The morphology of a sequential hierarchy is a key metric of behavioural complexity, and may offer insight into how animals understand and generate their behaviours. However, parsing sequences of behaviours into hierarchies is inherently challenging, as behaviours are externalized by animals serially over time. We employ a dictionary-based compression algorithm to identify reoccurring patterns of actions used by eight wild chimpanzees during one of their most complex forms of tool-use: nut cracking. Through comparing compression to sequences generated by Markov models, we identify that observed action sequences and Markov sequences compress to a similar extent; however, many of the rules produced during the compression of action sequences are not readily generated through compression of Markov sequences, indicating different pathways to compression. We also discuss the utility of dictionary-based compression in identifying flexible behavioural strategies both within and between the repertoires of individuals. We discuss the utility of dictionary-based compression for characterizing the hierarchical organization of animal tool behaviours, and make recommendations for future work that includes the use of dictionary-based compression to characterize sequential organizations of behaviour.

3.2 Introduction

It has long been theorised that to produce efficient, goal-directed behaviours, the constituent actions must be organised hierarchically (Byrne et al., 2013; Byrne and Russon, 1998; Dawkins, 1976; Fitch and Martins, 2014; Greenfield, 1991; Lashley, 1951; Rosenbaum et al., 2007). The hierarchical organisation of sequential actions involves decomposition of a wider behavioural goal (e.g. *eat a banana*) into smaller subgoals (e.g. *peel banana*, *consume banana*), which are addressed by complementary sequences of actions (e.g. for *peel banana*: *grasp, break skin, pull skin*, *pull skin, pull skin;* for *consume banana*: *raise to mouth*, *bite*, *chew*, *swallow*). Organising sequential actions in this way is theorised to allow for the production of complex, flexible, and highly targeted behavioural responses using reduced neural resources (Dawkins, 1976). Hierarchical systems of sequential action organisation are also argued to confer stability for complex behaviours across evolutionary time, where smaller modules of behaviour (stereotyped subroutines of actions addressing a specific subgoal) are more likely to evolve, and are more easily adaptable to changing environments compared to complex behaviours which are not able to be parsed into smaller elements (see *the evolutionary rate advantage* in Dawkins 1976).

Under hierarchical systems of sequential action organisation, actors must therefore recursively organise behaviours from the level of their most overarching goal, down to the minutiae of muscle contractions and nervous impulses (Fitch and Martins, 2014; Greenfield, 1991; Lashley, 1951; Pastra and Aloimonos, 2012). Given the complexity of organising behaviours at multiple levels, hierarchical sequencing is theorised to present a number of cognitive challenges, including for planning and executive functioning (especially working memory) (Byrne et al., 2013; Fitch and Hauser, 2004; Read, 2008; Wilson et al., 2020), as well as challenges for organising behaviours at the level of motoric control (Seeds et al., 2014). Given the challenges presented by the hierarchical organisation of behaviour, the hierarchical complexity of sequential action has previously been highlighted as an important metric for characterising the complexity of the spontaneous behaviours of humans and non-human animals (Byrne, 2007; Byrne et al., 2001; Byrne and Byrne, 1993; Dawkins and Dawkins, 1976; Sainburg et al., 2022, 2019; Stout et al., 2021). Yet, characterising the hierarchical complexity of observed behaviours – including identifying latent subgoals from observed sequences of action - is methodologically challenging (Dawkins and Dawkins, 1976; Uddén et al., 2020; Vereijken and Whiting, 1998).

Much of the research into the organization of sequential behaviours of animals, including their hierarchical complexity, has focussed heavily on the actions of nonhuman primates (Boesch et al., 2020; Byrne, 2007; Byrne et al., 2013, 2001; Carvalho et al., 2008; Estienne et al., 2017; Hayashi, 2015; Hayashi and Takeshita, 2022; Matsuzawa, 1996, 1991; Mielke and Carvalho, 2022). This focus is in part due to the phylogenetic proximity of nonhuman primates to humans, for whom many behaviours employ elaborate and highly complex hierarchical systems of organisation, which involve the arrangement of atomic elements of a behaviour into many concurrent layers of organisation. These behaviours include the organisation of phonemes and words into language (Chomsky, 2002, 1956; Fitch and Martins, 2014; Lashley, 1951; Sainburg et al., 2022), notes into music (Asano and Boeckx, 2015; Fadiga et al., 2009; Koelsch et al., 2013; Martins et al., 2019), and the organisation of actions during the production and use of technologically complex tools (Greenfield, 1991; Steele et al., 2012; Stout et al., 2021). Nonhuman primates share many homologues to these behaviours (Babiszewska et al., 2015; Byrne et al., 2013; Coye et al., 2018; Gruber and Clay, 2016; Hattori and Tomonaga, 2020; Leroux et al., 2023; Leroux and Townsend, 2020; Steele et al., 2012); therefore, nonhuman primates offer an excellent opportunity to investigate the evolutionary trajectory of highly hierarchical human behaviours through comparative study, including through research into the organization of their communicative (Clay and Zuberbühler, 2009; Leroux et al., 2023; Leroux and Townsend, 2020), rhythmic (Babiszewska et al., 2015; Hattori and Tomonaga, 2020), and technological behaviours (Boesch et al., 2020; Bril et al., 2015; Byrne, 2007; Carvalho and McGrew, 2012; Matsuzawa, 2001; Sanz and Morgan, 2010).

Within the behavioural repertoire of nonhuman primates, manual action is a domain which has been argued to involve the most complex hierarchical organisation, particularly in the case of tool use (Byrne, 2007; Byrne et al., 2001; Byrne and Russon, 1998; Estienne et al., 2017; Hayashi, 2015; Hayashi and Takeshita, 2022; Matsuzawa, 1996, 1991; Mielke and Carvalho, 2022; Sanz and Morgan, 2010). During specific forms of tool use, hierarchical relationships may emerge between tool objects (Hayashi, 2015; Hayashi and Takeshita, 2022; Matsuzawa, 1996; Sanz and Morgan, 2010). Additionally, the movement of tool objects during a behavioural sequence has been argued to offer readily observable behavioural process which may be drawn upon to infer subgoals of behaviour (e.g. tool-acquisition, tool-production, tool-modification, tool disposal – the *chaîne operatoire* approach) (Byrne et al., 2013; Carvalho et al., 2008;

Sanz and Morgan, 2010; Sellet, 1993; Tonooka, 2001). Thus, it is likely that tool-use represents a domain of behaviour where primates readily employ hierarchical organisation of actions. Furthermore, understanding how nonhuman primates organise actions into 'techniques' during behaviour is of significant interest for the field of animal culture, where individual and population-level differences in how functionally identical tool-use behaviours are performed may be indicative of underlying social learning mechanisms, and possible cultural evolutionary processes (Boesch et al., 2020; Estienne et al., 2017; Sanz and Morgan, 2009).

Despite tool use offering a likely candidate behaviour which involves the hierarchical organisation of sequential actions by nonhuman primates, characterising the morphology and complexity of hierarchical action during tool use is difficult. Methodologies that involve the inference of subgoals from qualitative descriptions of observed behaviour risk the introduction of subjective bias, where observers may prescribe their own interpretation of a desired subgoal onto an observed sequence of actions (Vereijken and Whiting, 1998). Moreover, where researchers aim to classify meaningful subroutines of action, they are faced with the challenge of separating infrequent, yet meaningful combinations of actions (i.e. behaviourally relevant subroutines) from combinations of actions which repeat through chance association. This is particularly true if rare subroutines are important for the success of tool-use behaviours under specific environmental conditions, and therefore are only identifiable if researchers are able to assess for patterns in large corpora of sequential actions (Gomez-Marin et al., 2016). Likewise, whilst observers are often able to describe overarching goals of behaviours (e.g. to acquire and consume a specific food object), and the atomic units used to achieve such goals (i.e. the individual actions employed to achieve a task), it can be difficult to characterise the morphology of the middle of an action hierarchy (i.e. which goals are decomposable into meaningful subgoals, and which decomposable into further subgoals, and so on). The number of subgoals within a hierarchy is an important aspect of its complexity (Stout et al., 2021), thus there is a need for a methodology that can not only detect patterns of actions, but patterns of patterns within behavioural sequences (Dawkins, 1976; Gomez-Marin et al., 2016).

Consequently, there is the need for unbiased, statistical approaches for identifying hierarchical units of organisation in the behaviours of animals, including nonhuman primates, and particularly in the case of nonhuman primate tool use. The use of such models will allow for unbiased hierarchical

representations of action to be estimated from observed sequences of behaviour. In the case of nonhuman primate tool use, the successful implementation of such models would be highly useful for a number of avenues of research, including understanding the evolution of complex hierarchical behaviours in humans; mapping how fundamental elements of behavioural organisation (e.g. muscle contractions, limb movements, primitive actions) combine to produce complex behaviours (e.g. tool use); as well as for characterising individual and population differences in the sequential organisation of behaviour through providing hierarchical models of behavioural techniques – a key point of interest for studies of social learning and animal culture.

Dictionary-based compression offers a recursive algorithmic approach for identifying regularities within the structure of sequences of discrete elements (Gomez-Marin et al., 2016; Larsson and Moffat, 2000; Nevill-Manning and Witten, 1997, 2000). During dictionary-based compression - specifically in the use of 'off-line' compression algorithms - sequences are iteratively scanned and compressed based on regularities within sequences, allowing for a hierarchical model to be produced for a given sequence, akin to a phrase structure grammar (Gomez-Marin et al., 2016; Nevill-Manning and Witten, 2000). At each pass of the algorithm, a sequence is scanned for repeating constructions of elements, allowing for a list of repeating subsequences to be identified. A repeating subsequence is then selected to be used for compression of the global sequence, based on a pre-programmed criterion (e.g. compress the sequence based on the construction that is the longest, or the most frequent, or that offers the greatest possible global compression [an intermediate metric of length and frequency]; Nevill-Manning and Witten, 2000). During compression, the focal construction is removed at each occurrence within the sequence, and is replaced with a non-terminal symbol (e.g. if the sequence [*abcabbd*] is compressed at the subsequence [*ab*] using the non-terminal symbol [*1*], the sequence would become [*1c1bd*]). The compression rule is then stored in a dictionary of rules, which documents the information stored during dictionary-based compression (for the previous example, this rule would be $1 \rightarrow ab$). The algorithm repeats this process recursively, and is able to identify sequential patterns which include non-terminal compression rules, thus producing hierarchical models of sequential structures which include 'patterns of patterns' – a key prediction of the hierarchical structuring of behaviour (Dawkins, 1976; Gomez-Marin et al., 2016). Overall, the percentage of compression of a sequence is directly related to the extent to which it may be decomposed into smaller

repeating patterns, thus percentage compression of a sequence is a readily measurable estimate of stereotypy within sequential structure.

Dictionary-based compression therefore allows for hierarchical models of sequential relationships to be estimated from linear sequences of elements. Hierarchical relationships are estimated based on frequently co-occurring elements, without the need for observers to provide prior hypotheses surrounding the morphology of a sequential hierarchy (Gomez-Marin et al., 2016). Thus, dictionary-based compression may represent a useful tool for detecting goal-directed subroutines of action within the sequences of behaviours used by animals without the introduction of observer bias. The ability of dictionary-based compression to identify patterns of patterns also allows for subroutines to be detected at multiple hierarchical levels within a string of behaviour. Therefore, dictionary-based compression may be useful for indicating both the semantic nature of higher and lower subgoals within a wider bout of behaviour, as well as providing some estimation of the overall hierarchical depth of a behavioural sequence. Furthermore, dictionary-based compression allows for the identification of rare, but meaningful regularities within the behavioural repertoire of animals (see Gomez-Marin *et al.* 2016 for example of the locomotion behaviour of *C. elegans*). Through the use of a minimal description length principle - where at each pass of the algorithm, compression only takes place if there is a global reduction in required memory - dictionary-based compression embodies a form of Occam's razor: sequences are only compressed by rules which offer a meaningful explanation of its structure (see Methods for more information on how algorithms evaluate the need to compress; Gomez-Marin et al., 2016). Consequently, dictionary-based compression provides a method for separating rare but meaningful subroutines from combinations of elements which reoccur by chance association.

Dictionary-based compression is therefore a likely fruitful tool for modelling '*grammars of action'* within the behavioural repertoire of animals, with the unique ability to produce hierarchical models of grammars of action, whilst avoiding biases introduced by observers. In the present study, we employ a dictionary-based compression algorithm that uses a 'compressive heuristic' (where the algorithm selects for subroutines that offer maximal global compression of sequences at each pass) to produce hierarchical models of organisation for the sequential actions used by chimpanzees during one of their most challenging natural tool-use behaviours: the cracking of hard-shelled nuts with hammer and anvil stones (henceforth

nut cracking). The use of a compressive heuristic offers a composite measure between the frequency with which rules occur, and their length, and thus offers a useful model for understanding likely subroutines based on both the regularity with which they are produced, and the number of predictable actions from which they are constituted. We draw upon a database of action sequences we have previously coded from video footage of eight West-African chimpanzees (*Pan troglodytes verus*) engaging in nut cracking at Bossou, Guinea (Howard-Spink *et al.*, in review). Within our analysis, we compare the compression of observed action sequences to various comparable simulated sequences (including randomised sequences, and those produced by different Markov models) to evaluate the hierarchical compressibility of observed action sequences as a metric of stereotypy (defined here as the extent to which sequences are composed of recurring subsequences of actions). We also compare the dictionaries generated during the compression of action sequences produced by five chimpanzees during tool use, including four adult chimpanzees and one sub-adult. We report that observed action sequences compress to a similar extent to simulated Markov sequences; however, many of the rules used to compress observed action sequences do not readily occur in the dictionary of compressed Markov sequences, indicating different pathways of compression. Moreover, the dictionaries produced during the compression of chimpanzee stone-tool action sequences share a small number of highly frequent subroutines required for successful nut cracking. We also report that numerous rare rules emerge during compression, including those confined to individuals. However, we argue that for dictionary-based compression to be a useful methodology for comparing sequential behaviours across individuals, attention must be given to the precise rules produced during dictionary compression, given the tendency for dictionary-based compression to overestimate the number of truly unique or hierarchically complex rules.

3.3 Methods

3.3.1 Action sequence data

All data collected on chimpanzee sequential actions during tool use were collected from video footage filmed at Bossou, Guinea. Established in 1976, Bossou-Nimba (07° 390' N; 008° 300' W) is a long-term research site for the study of wild West-African chimpanzees (Matsuzawa, 2011). Bossou chimpanzees regularly engage in a number of tool-use behaviours, including nut cracking (Biro et al., 2006, 2003;

Carvalho et al., 2008; Hayashi, 2015; Inoue-Nakamura and Matsuzawa, 1997; Matsuzawa, 1994); leaf-folding (Tonooka, 2001), ant-dipping (Humle and Matsuzawa, 2002), and pestle-pounding (Yamakoshi and Sugiyama, 1995).

Nut cracking by Bossou chimpanzees has been studied in detail since 1988 through the use of an "outdoor laboratory" (Biro et al., 2006; Carvalho et al., 2008; Hayashi, 2015; Inoue-Nakamura and Matsuzawa, 1997; Matsuzawa, 1994). The outdoor laboratory is a natural, maintained clearing in Bossou forest, where piles of oil-palm nuts (*Elaeis guineensis*) and stone tools, and occasionally Coula nuts (*Coula edulis*), are provided for chimpanzees for a period during the dry season (approx. November – February). Stone tools are distributed in a central matrix in the middle of the outdoor laboratory, and nuts are provided in a number of piles across the clearing. Chimpanzees are free to enter and leave the outdoor laboratory as part of their daily ranging behaviours. When chimpanzees enter the outdoor laboratory, researchers record their behaviours from behind a wall of palm fronds using video cameras. Data collected at the outdoor laboratory has recently been assembled into a longitudinal video archive of chimpanzees engaging in stone-tool use at Bossou, spanning over three decades (Schofield et al., 2019, 2023).

For the present study, we analysed data on chimpanzee action sequences during nut cracking which we had previously collected from video footage recorded in the 2011-2012 field season between 20th January 2012 and 10th February 2012. (Howard-Spink et al., in review). Action sequences were recorded using an ethogram of 33 action types. Actions were coded to include both the functional action exerted by the chimpanzee (e.g. 'grasp', 'drop', 'flip') and one of six relevant objects: anvil stone, hammer stone, nut (uncracked), kernel (edible interior of the nut), shell (inedible exterior of the nut), and bare hand (indicating absence of an object; e.g. for instances where juveniles strike nuts and anvils in the absence of a hammer stone). The resulting actions were bigrams of both action and focal object, with actions in lower case, and objects in upper case; e.g. 'grasp HAMMER', 'drop SHELL'. The coding of a given action sequence commenced when a chimpanzee began interacting with stones, nuts, or nut-fragments (including scavenging of pre-cracked kernels of other individuals), and stopped when the individual ceased engaging with stone tools, nuts, or nut fragments to engage in an alternative behaviour (e.g. grooming, play, drinking, consuming oil-palm fruits, etc.). If individuals oriented their bodies so that their actions were no longer clearly visible, or moved out of frame of the recording, action coding ceased. Following the coding of all

available action sequences from the 2011-2012 field season at Bossou, this repository contained over 8261 actions, combined into 163 sequences across eight individuals (counting individuals who had at least 200 actions coded; we excluded individuals with smaller corpora of action sequences from our analysis). The mean corpus size for each individual was 1033 actions (N = 8; range = 299 to 1940 actions). For each individual, the available corpus of action sequences was concatenated into a single extended sequence, and the junctures between observed sequences were indicated using a 'SPLIT' codon. 'SPLIT' codons were used to prevent the dictionary-based compression algorithm from condensing sequences using combinations of elements which spanned between observed sequences of actions (see below).

3.3.2 Dictionary-Based Compression Algorithm

We used dictionary-based compression to identify and extract repeating patterns of actions from the coded action sequences used by chimpanzees during nut cracking. A number of dictionary-based compression algorithms offer means to compress sequences of discrete elements. Many popular dictionary-based compression algorithms are termed 'on-line', as they are able to condense sequences from left to right in a single pass of the algorithm (e.g. Sequitur; Nevill-Manning and Witten, 1997, 2000; Sainburg et al., 2022). Whilst these algorithms are able to condense sequences rapidly, they are biased towards detection of subroutines at the left-hand side of sequences, as these subroutines are detected first. Conversely, off-line dictionary-based compression algorithms run iteratively across sequences, monitoring for the presence of subroutines across entire sequence lengths, and condensing the global sequence based on a preprogramed heuristic (Gomez-Marin et al., 2016; Nevill-Manning and Witten, 2000). Thus, whilst off-line dictionary-based compression algorithms reach final compression more slowly, and require greater computational resources than on-line algorithms, they avoid the bias of higher likelihood of detecting subroutines at either end of a sequence.

We employ a dictionary-based compression algorithm that draws upon a globally compressive heuristic for condensing sequences at each pass. Dictionary-based compression algorithms which select for the most globally compressive subroutine at each pass of the algorithm trade-off the length of subroutines, and the frequency with which they occur in a sequence (Nevill-Manning and Witten, 2000). Compressive algorithms offer some of the greatest compression compared to other heuristics including

sequence compression by the longest subroutines (regardless of frequency), and the most frequent (regardless of length; Nevill-Manning and Witten, 2000). At each pass of the algorithm, the sequence is scanned using a sliding frame to identify how elements are combined into combinations of 2-5 actions long. We chose to use a maximum length of 5 sequence elements, as previous analyses on the sequential organisation of nut-cracking behaviours suggest that chimpanzees structure actions into subroutines of approx. 5 elements long (Howard-Spink et al., in review). We follow the convention of referring to element combinations through the generalised term n-grams, where the smallest identifiable element combination in a single hierarchical unit is a 2-gram, and the longest possible is a 5-gram (Gomez-Marin et al., 2016). Following the scanning of the entire sequence, all available n-grams are tallied to determine the frequency with which they occur in the sequence. If an n-gram contains a 'SPLIT' codon, they are removed from the list of possible n-grams for substitution (thus preventing condensing of sequences based on actions which were only in close proximity due to sequence concatenation, which is biologically meaningless). The possible compression offered by each n-gram is calculated through the following formula proposed by Nevill-Manning and Witten (2000):

$$S = WN - (W + N + 1)$$

where *S* is available compression, *W* represents the length of an n-gram, and *N* is the number of times the n-gram may be substituted into a sequence. The left-hand side of the equation describes the total number of elements which are removed from a sequence during compression. On the right-hand side, (*W* + *N* + *1*) represents the number of additional elements added to the system through storing a rule in the dictionary (where the rule is length *W*), the addition of a new non-terminal symbol to the dictionary to define a rule (*1*), and the addition of this non-terminal element into a sequence at each point where compression occurred (*N*). Thus, compression (*S*) considers not only the available reduction in sequence size, but the overall memory required to store global information in the sequence and dictionary (Gomez-Marin et al., 2016; Nevill-Manning and Witten, 2000).

When estimating the number of possible times an n-gram may be substituted into a sequence, it was important to account for repeating elements, particularly when the n-gram was a subsection of this repetition; e.g. in the sequence [*aaaaa*], a sliding frame would identify the presence of the 2-gram [*aa*] on four occasions, beginning at terms 1,2,3 and 4; however, this 2-gram would only be substitutable into this

sequence twice. Therefore, we traced where n-grams overlap with themselves within sequences by identifying where the locations of substitution (sequence terms) formed an uninterrupted progression that exceeded the length of the n-gram; for example, if a 2-gram may be substituted across terms 33, 34, and 35, in a sequence of 100 elements, this indicates that there are three repeating elements in a row, e.g. [*aaa*], which contains a singularly overlapping 2-gram [*aa*]. To estimate how many times an n-gram may be substituted into a sequence, we therefore adopted the following formula:

$$N = \sum \frac{Q - rem(Q, W)}{W}$$

For each section of a sequence where there were overlapping substitutions, we took the number of repeating elements in a sequence *Q* (for the example [*aaaaa*], *Q* = 5), and found the remainder of *Q* if divided by the n-gram (if [*aa*], rem(5,2) = 1). We subtracted this remainder from the original repeats to determine how many elements could be removed from the sequence during compression (5 - 1 = 4), and divided by n-gram length to find the number of possible substitutions (4/2 = 2; therefore there are two available substitutions of [*aa*] into [*aaaaa*]). To estimate total possible substitutions across the entire sequence (*N*), this process was repeated at each point where an n-gram may be substituted, and the total number of possible substitutions summed, ensuring accurate estimation of possible substitutions for n-grams.

Once the total possible compression had been estimated for each unique n-gram (*S*), the most compressive n-gram was selected and replaced across the sequence from left-to-right. If multiple n-grams were tied for the most compressive available n-gram, we followed the convention of choosing the n-gram which occurs left-most within the sequence (Gomez-Marin et al., 2016; Nevill-Manning and Witten, 2000). During substitution, n-grams were substituted with non-terminal symbols across the sequence from left-to-right, ensuring repeatability in the compression process. The n-grams used for substitution were stored in a dictionary alongside their non-terminal rule number (e.g. 1 → n-gram). The rule symbols in a sequence were treated equally to actions, and thus n-grams containing rules may also be selected for compression and stored in the dictionary (e.g. 2 → [*a1a*]). This entire process runs recursively until the algorithm detects no available n-grams which offer meaningful compression of the sequence (*S* is equal to or less than zero for all detected n-grams).

The dictionary-based compression algorithm we employ is 'greedy': the algorithm would not choose to compress using an n-gram which was less than maximally compressive at one pass, to favour a greater amount of compression at a later pass. Thus, we do not necessarily reach the maximum global compression available for a behavioural sequence (Gomez-Marin et al., 2016). However, maximal global compression is not in itself a prediction of hierarchical behavioural organisation, and therefore we do not consider this to be a valid critique of our method. Rather, our algorithm is able to identify highly stereotyped patterns within action sequences, and thus is a suitable model for the detection of hierarchically organised units of behaviour. Moreover, our algorithm, like other dictionary-based compression algorithms, is lossless (Gomez-Marin et al., 2016; Nevill-Manning and Witten, 1997, 2000). Following compression, the sequence may be expanded back into its original form using the rules of the dictionary. Thus, during compression, information in a sequence is conserved. As part of this lossless quality, our algorithm does not produce rules which call on themselves (e.g. 1 → [*a1*]), as this would lead to unpredictable recursion during sequence expansion, and would disrupt the mapping of condensed sequences back into their expanded forms. Due to rules being unable to call on themselves, our model is not able to explicitly model recursive processes, including centre-embedding of sequences (Nevill-Manning and Witten, 2000). However, the algorithm is able to identify subsequences which differ only by the addition of central, terminal actions (e.g. [*aa*] vs [*aba*]); therefore, whilst dictionary-based compression is not able to account for infinite recursion, it is able to account for finite embedding of short strings of terminal symbols, including individual actions.

3.3.3 Compressibility as a measure of stereotypy

Sequences which show higher levels of stereotypy compress faster, and to a greater extent than sequences which feature more randomly arranged elements (Gomez-Marin et al., 2016; Sainburg et al., 2022). Thus, compression is a useful metric of stereotypy. Sequences which are longer often undergo a greater percentage compression than shorter sequences, as their extended lengths provide greater opportunity for rare subroutines to be identified and used for compression (Gomez-Marin et al., 2016; Sainburg et al., 2022). We therefore investigated how readily action sequences produced by individuals compressed as a measure of stereotypy, and compared the percentage and rate of compression to overall sequence length.

For each individual, concatenated sequences were copied and spliced into shorter sequences of varying lengths. We sampled subsequences from the action sequences of each individual, at lengths which increased from 100 elements (smallest subsequence), to the maximum sequence length, increasing the length of sampled subsequences by 100 elements at a time (e.g. for a sequence of 420 actions, subsampled sequences of 100, 200, 300, 400, and 420 actions would be produced). To prevent our analysis from being biassed to compression at the left-most side of the sequence, sampling of subsequences occurred across the action sequence at 50 element intervals (e.g. for a sequence of 420 actions, when sampling subsequences of 100 actions in length, we sampled a 100-element subsequence starting at the 0th, 50th, 100th, 150th, 200th, 250th and 300th sequence elements). For each subsequence, we applied the dictionary-based compression algorithm. To calculate compression, we used the percentage change in the total number of elements across the compressed sequence and dictionary, compared with the original uncompressed sequence (Gomez-Marin et al., 2016; Nevill-Manning and Witten, 2000). Percentage compression was blocked across subsequences of the same length for each individual, providing a point-estimate and confidence interval for percentage compression at each sequence length.

To investigate how the compression of observed action sequences (with hypothetically hierarchical organisation) compared to sequences produced by alternative, non-hierarchical structuring systems, we ran an identical analysis on simulated Markovian and random sequence data. Markov models are commonly used null models for identifying hierarchical systems of sequential organisation (Gomez-Marin et al., 2016; Sainburg et al., 2022, 2019). Markov models produce non-random sequences using a finite-state grammar, where each element in a sequence is highly predictable by the element that precedes it. Under Markovian systems of sequence generation, a transition matrix describes the probability of all possible transitions from one element type to another, and sequences are produced through serial chaining between neighbouring elements (Gagniuc, 2017). To produce Markovian sequences comparable to our action-sequence data, we estimated a transition matrix for each individual chimpanzee, based on neighbouring actions in their corpus of action sequences. Transition matrices were estimated using the *createSequenceMatrix* function of the *markovchain* package (Spedicato, 2017), where each unique sequence recorded for an individual was passed to the function separately. Following estimation of the transition matrix, Markovian sequences were produced at equal lengths to the sequences used to train the

matrix, with sequence generation starting at the same initial action for each sequence (e.g. if the first action in a sequence is 'grasp NUT', this was used as the starting action for sequence generation from the transition matrix). Once all Markovian sequences were generated for an individual, they were concatenated in the same way as observed action sequences, using 'SPLIT' codons to indicate boundaries between individually generated sequences.

In instances where Markov models are trained on highly stereotyped sequence data, it is possible to produce a transition matrix which contains a small number of highly probable transitions between sequence elements (thus, transition probabilities between action types are highly heterogeneous). Consequently, these models may be able to produce predictable chains of numerous sequence elements, generating sequences which contain highly stereotyped subsequences. We therefore decided to generate an additional corpus of sequences for each individual, using Markov models where transition probabilities between neighbouring actions were homogenised (henceforth 'homogenized Markov models'). In both types of Markov model, the transition matrix describes which actions are able to follow other actions during neighbouring element transitions across sequences (e.g. in both models, 'grasp KERNEL' was only followed by 'eat KERNEL', 'place KERNEL' or 'drop KERNEL'). However, in the case of the homogenized Markov model, the likelihood of transitioning to each action type was rendered equal (thus, the probability of each action type following 'grasp KERNEL' would be 1/3). Homogenized Markov models allow for characterization of sequences using the Markov property, whilst also avoiding instances where Markov models mimic the highly stereotyped behaviour of observed action sequences. Sequence generation from homogenised Markov models, and subsequent dictionary-based compression, was performed identically to Markov models with heterogeneous transition probabilities.

As well as Markov models, we ran an identical analysis on randomised sequence data. We included two types of random sequence data: (1) internalised-random sequences, where the order of actions within each sequence were randomised prior to concatenation. Sequences were concatenated in the order in which they were observed. (2) pooled-random sequences, where action sequences were concatenated, and the position of sequence elements randomised across the global sequence. In the pooled random conditions, 'SPLIT' codons stayed in the same position, and therefore sequences were maintained at equal lengths to those in internal-random, Markov, and homogenised Markov treatments. Across all random and

Markov sequence types, we used 50 generated sequences in our analysis for each individual, allowing us to estimate error for each form of simulated sequence.

3.3.4 Extracting dictionary rules: comparing individuals

Dictionary rules represent the means through which sequences are compressed. As rules are selected based on repeating element combinations within a sequence, dictionaries offer the opportunity to detect candidate subroutines in a sequential behaviour, and compare subroutines between individuals. We decided to perform this analysis on condensed action sequences, where successive repetitions of actions across neighbouring sequence elements were replaced with a single action. This removed the possibility of dictionary rules being generated through successive repeating actions, e.g. successively striking the hammer stone.

Sequences that are longer offer the opportunity to detect a greater number of subroutines. Thus, for the five individuals who had a condensed action sequence of over 900 actions, we capped the length of their concatenated action sequences at this length (thus producing a sequence of the first 900 observed actions). We then compressed the action-sequences for these five individuals, producing five unique dictionaries, and compared the rules present in the dictionaries for each of the five individuals.

3.3.5 Extracting dictionary rules: comparing with markovian and random data

For each individual, we wanted to identify the rules that were not readily produced by simulated sequence data (including all Markov and random sequences). These subroutines are of particular interest, as they are not readily characterizable by systems of action organisation which are either non-hierarchical, or randomly structured. We generated 500 sequences each 900 actions long using the same Markov transition matrices and randomization procedures outlined above (see *Compressibility*). The dictionary-based compression algorithm was applied to all random and Markov sequences independently, and the dictionaries combined.

We took each unique rule generated by the compression of observed action-sequences for each of the five focal chimpanzees, and identified the proportion of dictionaries which contained this sequence type for each simulated and random sequence for that individual. If a rule was found in under 5% of

dictionaries for a particular sequence type (e.g. Markov, internal random, etc.), we deemed it unlikely to be produced during the compression of that particular sequence type. We collated all rules from observed action sequence data which were unlikely to be produced during the compression of all Markov and random sequence types, and present these rules as unique to the observed action sequences of chimpanzees.

3.4 Results

3.4.1 Compression

We compared the global compression of observed action sequences between individuals, as well as with simulated sequences from Markov models and randomised sequences for each individual. We defined global compression as the percentage change in symbols across the sequence and dictionary (see Fig. 1 and Table 1).

All individuals demonstrated a greater percentage compression with increasing sequence length (see Fig. 1a). The maximum sequence length over which compression was performed varied based on the corpus size for each individual, with the shortest sequence length for Foaf (300 actions), and the longest for Tua (1900 actions). Therefore, to compare the global compression between individuals, we compared mean compression for sequence lengths of 300 actions. Overall, the sequences of actions produced by adult chimpanzees during nut cracking were more compressible than for individuals who were younger than 8 years old. The greatest compression was observed for two adult males: Foaf (Mean Compression = -40.3%, SE = 0), and Tua (-39.4%, 0.454), whereas Flanle (an infant male) experienced the lowest global compression at 300 actions (-7.42%, 0.809), followed by Joya, a sub adult female (-25.5%, 0.872). For both of these younger individuals, overall compression fell outside of the 95% confidence interval surrounding mean compression for all other adults (mean across all adults = -35.7%; CI_{upper} = -31.7%; CI_{lower} = -39.8%; N = 6).

Across individuals, observed action sequences and sequences generated by Markov models compressed to a similar extent (see Fig. 1b). Additionally, for all individuals, both of these sequence types compressed to a greater extent than randomised sequences, as well as sequences generated by homogenised Markov models. At the maximum sequential length over which we performed dictionary-based compression for each individual, four individuals showed the greatest compression in observed

action sequences (Flanle, Jeje, Joya and Tua), but only one individual (Tua) exhibited compression in their observed action sequence which fell outside of the 95% confidence interval for compression within Markov sequences (Length = 1900 actions; Observed [Mean Compression, $\pm CI_{95\%}$] = -54.2%, ±0.774; Markov = -52.6%, ±0.278; see Table 1). Four individuals exhibited less compression in their observed action sequences compared with Markov simulated sequences (Flanle, Foaf, Jire and Peley), and for three of these individuals (Flanle, Foaf and Jire) there was no overlap between the 95% confidence intervals for either sequence type at the maximum sequence lengths used (Flanle: Observed = -9.13%, ±0.735; Markov = -11.5%, ±0.457; Foaf: Observed = -40.3%, ±0; Markov = -41.4%, ±0.721; Jire: Observed = -30.4%, ±2.21; Markov = -33.9%, ±0.642).

Sequences generated from homogenized Markov models compressed less readily than Markov models with transition matrices which reflect observed action sequences. For five individuals, compression of homogenized Markov sequences occurred to a greater extent than random (Flanle, Foaf, Jeje, Jire, Peley) at the maximum sequence length for used for each individual (identified through no overlap between the confidence intervals produced from homogenized Markov models, or random sequences; see Fig. 1b). For one individual (Tua), sequences generated from homogenised Markov models compressed to a lesser extent than randomised sequences - a trend which persisted for all sequence lengths used for Tua. For two individuals, Joya and Fanle, compression of sequences from homogenised Markov models, and randomization procedures, occurred to a similar extent (identified by overlaps of 95% confidence interval between homogenised Markov and at least one randomised sequence type).

3.4.2 Dictionary rules: comparing individuals

Compression of the first 900 actions (not including repeating actions) for five individuals revealed 66 unique rules. Of these 66 rules, 32 rules involved the organisation of actions into a single compressed unit (hereafter referred to as ‘level-one’ rules, where all actions were organised over one hierarchical level). 25 rules contained at least two hierarchical levels. For 17 of these level-two rules, a previously compressed rule was compressed with a new action, whereas for eight other rules, multiple ‘level-one’ rules were compressed together. Nine rules were ‘level-three’, and were produced during the compression of at least one level-two rule with either another existing rule (in the case of two rules) or additional actions (in the

case of six rules). The number of actions contained within rules varied between two and ten (mean = 3.51 actions; SD = 1.61).

Across the total 66 rules identified, three rules were universal to the dictionaries of all individuals, 18 rules were shared among the dictionaries of multiple, but not all individuals; and 45 rules were unique to the dictionaries of just one individual. The three identified universal rules were short 2-grams which reflected fundamental actions for the cracking of nuts and consumption of kernel, including placing nuts on the anvil: [‘grasp NUT’, ‘place NUT’] (total substitutions across individuals = 208; mean across individuals = 41.6, SD = 35.5); grasping and consuming kernel: [‘grasp KERNEL’, ‘eat KERNEL’] (total = 286; mean = 57.2; SD = 16.6); and the peeling of inedible shell from the kernel by an individual using their teeth, before consuming the kernel: [‘peelteeth SHELL’, ‘eat KERNEL’] (total = 161; mean = 32.2; SD = 23.9).

To organise the 66 identified rules, we divided rules into three broad categories, including those which involved the acquisition of resources (defined as any period where an individual acquired a nut or stone tool, and either transported the object across the outdoor lab, or stored the object for transportation, e.g. storing uncracked nuts in the mouth); combining objects (any instance where two or more objects came into contact, such as placing the nut on the anvil, or striking with the hammer stone); and kernel processing (including grasping kernels, the peeling and disposal of inedible shell, and kernel consumption). Six rules were categorised as associated with acquiring resources, 30 with combining objects, and 24 with kernel processing. Six rules were categorised to span across these categories, all of which spanned between two and three hierarchical levels, and included nested rules associated with the combining of objects and the processing of kernels. All 66 rules are presented in supplementary tables S3-S6, alongside a short discussion of all identified rules.

Of all the rules that were unique to a specific individual, four rules contained actions which were unique to the dictionaries of a particular individual (see Fig. 2a). For rules associated with acquiring resources, [‘grasp NUT’, ‘store NUT’] was a rule that was unique to the dictionary generated for Peley. This rule contained the unique action ‘store NUT’, where an uncracked nut is placed in the mouth for transportation. Additionally the action ‘supporthand NUT’ was unique to an object combination rule identified for Tua: [‘grasp NUT’, ’place NUT’, ’supporthand NUT’, ’strikeonehand HAMMER’]; during this action, Tua would rest a finger against the side of a nut to hold it in place on the anvil, before striking down with the

hammer stone. Additionally for Tua, two rules contained the unique action 'peelhand SHELL': ['peelhand SHELL', 'eat KERNEL'] and ['drop HAMMER', 'peelhand SHELL']. This action described Tua grasping sections of shell and peeling them away from the Kernel using the hands, rather than the teeth, which was the more common strategy across individuals (across all observed actions, total occurrences of 'peelhand SHELL' = 77 ; 'peelteeth SHELL' = 385).

To understand the extent to which these actions were truly unique to individuals, we counted the number of times each of these actions occurred in the total number of actions for each individual (including those actions which occurred after the first 900). The action 'store NUT' (unique to the dictionary of Peley), was present in the action sequences of Tua and Joya. For Tua, these five instances were outside of the first 900 actions, and for Joya, one instance was within the first 900 actions, and one was outside of this boundary. However for Peley, who demonstrated this action 19 times in the first 900 actions, this was a far more common behaviour. Similarly, this pattern was reflected for both the actions 'supporthand NUT' and 'peelhand SHELL'. The action of supporting the nut by the hand during striking was only seen in one other individual (Fanle, action performed twice); however, Tua performed this action far more frequently (13 times). Peeling shell from kernels using the hands was observed in a total of four individuals (Tua, Peley, Jeje, Joya); however, the frequency with which the behaviour occurred for Tua was disproportionately higher (Tua = 25 times in the first 900 actions, and 24 times after; Jeje = 11 times in first 900 actions, 4 times after; Peley = 3 times (all in first 900 actions); Joya = 10 times (all in first 900 actions). Therefore, whilst the actions present in these rules were not confined to the repertoires of specific individuals, the presence of these actions in the dictionaries of particular individuals is a valuable indicator that these individuals performed these actions disproportionately more frequently.

We identified five key level-one rules which reflected less frequent modifications of more common rules. For each rule, an additional action was inserted into the centre of a behavioural sequence (see Fig. 2b). For the shared rule ['graspNUT', 'placeNUT', 'strikeonehandHAMMER'] (present in the dictionaries of Flanle, Joya, Peley and Tua), Tua showed a unique modification with the addition of the 'supporthand NUT' action (see above). Additionally, for the rule ['grasp HAMMER', 'strikeonehand HAMMER'] (present in the dictionaries for Jeje, Joya and Peley), Joya exhibited a unique modification which included a central action of placing the nut on the Anvil: ['grasp HAMMER' ,'place NUT', 'strikeonehand HAMMER']. In the former

rule, we assume the nut was already placed on the anvil prior to striking, thus representing a difference in the order of nut placement and the grasping of the hammer stone. Thirdly, the universal rule [‘grasp NUT’, ‘place NUT’] was combined with the central ‘reorient ANVIL’ action to produce a unique rule for Jeje: ['grasp NUT', 'reorient ANVIL', 'place NUT']. The final two modifications were associated with kernel processing. The shared rule [‘grasp KERNEL’, ‘peelteeth SHELL’, ‘eat KERNEL’] reflected a slightly longer version of both universal rules ['graspKERNEL', 'eatKERNEL'] and ['peelteethSHELL', 'eatKERNEL']. Finally, the rule ['peelteethSHELL’, 'eatKERNEL’] was modified in the dictionaries of Peley and Tua to include a central action for disposing of inedible shell: ['peelteethSHELL', 'dropSHELL', 'eatKERNEL'].

Of the 34 rules which contained two or three hierarchical levels, four were produced through the compression of repeating, short subroutines. For example, the repetition of the universal rule, [‘grasp KERNEL’, ‘eat KERNEL’], was compressed to produce a level-two shared rule [[‘grasp KERNEL’, ‘eat KERNEL’], [‘grasp KERNEL’, ‘eat KERNEL’]] (see Table 2 for all examples).

Twelve rules included identical sequences of actions to those of other rules; however, these actions were compressed into different hierarchical arrangements. This produced six pairs of rules where each pair contained identical action sequences (see Table 3). For example, the level-two rule [[‘grasp NUT’, ’place NUT’], strikeonehand HAMMER] involved the compression of an existing rule [‘grasp NUT’, ’place NUT’], with the additional action of striking with the hammer stone; however, this sequence of actions existed as a level-one rule for four individuals: [‘grasp NUT’,’place NUT’, ‘strikeonehand HAMMER’]. This also occurred in more hierarchically complex rules, including a level-three rule [‘grasp KERNEL’, [[‘peelteethSHELL’,’eatKERNEL’],’dropSHELL’]]. In this rule, a level-two rule is compressed with the antecedent action ‘grasp KERNEL’. However, in the level-two rule [‘grasp KERNEL’, [‘peelteethSHELL’,’eatKERNEL’,’dropSHELL’]], an identical sequence of actions is produced, but with fewer nested rules.

3.4.3 Dictionary rules: comparing with simulated and random sequences

For the compression of the first 900 actions for each of the five focal individuals, the dictionaries produced during compression possessed between 19 and 24 rules (mean = 21; SD = 1.67; N = 5). Across the five individuals, the number of rules in each dictionary that occurred in under 5% of dictionaries of all types of

Markov and random sequences varied from three to ten (see Table 2 for the rules which occurred in under 5% of dictionaries for all Markovian and random sequences, organised by individual). For four individuals, the percentage of rules which were considered to be infrequently generated during the compression of Markovian and random sequences varied between 47.6% and 65%, and for one individual (Jeje), this proportion was much lower (12.5%), indicating that most of the rules in the dictionary for Jeje were readily reproducible during the compression of simulated sequences. For each individual, we calculated the proportion of rules of each hierarchical category (level-one to level-three) that were not readily reproducible during the compression of sequences produced during randomization or from Markov models. We then averaged these proportions across individuals to find the mean proportion of rules of each hierarchical class that were readily produced in the dictionaries of either Markovian or random sequences. The mean proportion of level-one rules which were not readily generalizable by all types of simulated sequences was 38.9% (N = 5; SD = 12.4); whereas for level-two, this proportion was higher at 58.1% (N = 5; SD = 33.2); and for level three, this was 67.5% (N = 4; SD = 34.2).

Two of the four rules which contained actions that were unique to individuals (‘store NUT’ and ‘supporthand NUT’) were not reproduced during the compression of simulated sequences; however, both rules containing the action ‘peelhand SHELL’ occurred in over 5% of dictionaries for Markovian sequences. [‘peelhand SHELL’, ‘eat KERNEL’] was reproduced in 22.2% of dictionaries for Markov sequences, and [‘drop HAMMER’, ‘peelhand SHELL] occurred in 1% of dictionaries for Markov sequences. Of the five rules identified to show flexible additions of a central action (see Fig. 2b for list), all of these rules occurred in fewer than 5% of dictionaries for both Markov and random sequences. The longest rule, which contained a total of ten actions ([[[['peelteeth SHELL', 'eat KERNEL'], ['peelteeth SHELL', 'eat KERNEL', 'drop SHELL']], 'grasp HAMMER', 'place HAMMER', ['grasp NUT', 'place NUT', 'strikeonehand HAMMER']]), was never produced during the compression of either Markovian or randomised sequences.

3.5 Discussion

Many behaviours can be understood as sequences of discrete actions. Within sequential behaviours, repeating patterns of actions reflect subroutines: short, highly stereotyped subsequences, which reflect the execution of recurring programs of action which address specific subgoals (Byrne et al., 2001; Dawkins,

1976). Understanding how sequential behaviours can be parsed into repeatable subroutines of action may provide key insights into the way in which sequential programs are generated and stored within the minds of humans and animals, as well as the cognitive complexity of the behavioural tasks for which they are generated (Byrne et al., 2001; Dawkins, 1976). Moreover, the characterization of subroutines of action offers a window to evaluate whether different individuals vary in their organisation of behavioural responses to commonly-encountered, naturally occurring tasks. The characterization of subroutines may also provide indications of flexibility within the behavioural responses of specific individuals, through generation of highly similar subroutines, but with minor modifications, that address similar behavioural goals.

To understand the organisation of sequential actions of wild West-African chimpanzees during one of their most complex tool-use tasks (nut cracking), we applied a dictionary-based compression algorithm which detects repeating patterns within sequences, and selects 'rules' for sequence compression based on the maximal opportunity for compression at each pass. This algorithm ran across the action sequences used by eight individuals during nut cracking behaviours at the outdoor laboratory at Bossou, allowing us to analyse the overall compression of sequences (a metric of stereotypy) for all eight individuals, and the rules of compression (indications of repeatable subroutines) for five individuals. We compared these results from simulated data from Markov models for each individual, including sequences from Markov models where transition probabilities were homogenised, and two different types of randomised sequences.

For all individuals, total percentage compression was greater when longer sequences were provided to the compression algorithm. When comparing between individuals using a fixed sequence length (300 actions), action sequences produced by younger individuals (one juvenile and one subadult) compressed to a lesser extent than the action sequences produced by adults. This result suggests that adult chimpanzees, who are more experienced in nut cracking, produce more stereotyped sequences of actions than those produced by younger, less experienced individuals. This result is supported by the use of a greater diversity of action types by younger individuals, with Flanle (an infant male) exhibiting the greatest number of action types (59), and Joya (a subadult female) demonstrating the second greatest number (55 - mean for all other individuals 34.6; N = 6). Thus, the action sequences produced by Flanle and Joya contain a greater diversity of action types, constructed into less stereotyped sequences of actions. During the total period of observation for this study, Flanle successfully cracked only a single nut, and most

other behavioural sequences were recorded during a mixture of exploratory behaviours performed by Flanle when interacting with nuts and stone tools, as well as failed attempts to successfully crack open nuts. However, Joya successfully cracked 22 nuts, and thus this greater number of action types, and lower stereotypy, was still present when a large proportion of Joya's behaviour was directed towards nut cracking (for comparison, the number of nuts cracked over this study period by adult chimpanzees ranged from 10, using 299 actions, to 85 nuts, using 1368 actions).

Our results suggest that, following the acquisition of successful nut cracking, chimpanzees experience an extended period during which they refine the action sequences employed to successfully crack nuts, with increasing predictability in action sequence structure with increasing age. During the initial acquisition of nut cracking behaviours by chimpanzees at Bossou, chimpanzees perform increasingly complex object combinations at predictable ages as they progress through their development, leading to the successful cracking of nuts at between three and seven years old (Inoue-Nakamura and Matsuzawa, 1997; Matsuzawa, 2011). However, following the point at which successful cracking of nuts is acquired, the process through which individuals refine their solutions to nut cracking tasks over successive years is an ongoing question for research (Biro et al., 2006, 2003; Matsuzawa, 2001). Whilst physical changes during development are likely to influence aspects of sequential action organisation (e.g. the number of repetitive strikes of hammer stones needed to crack open nuts), cognitive development and individual learning are also likely to have profound influences on the action sequences used by individuals during nut cracking throughout the early stages of life. This is particularly true in the case of learning, where during nut cracking, inexperienced tool-users receive feedback on action sequence organisation through trial and error. Numerous studies have shown that understanding specific aspects of how to crack nuts, including selection of appropriate tools (Carvalho et al., 2008; Sirianni et al., 2015), and the force with which to strike nuts (Bril et al., 2009; Mangalam and Fragaszy, 2015), increase the efficiency with which chimpanzees successfully crack nuts. Moreover, for similar nut cracking behaviours in capuchin monkeys (*Sapajus spp.*), knowledge of how to strike nuts with hammer stones has been shown to offer increased success, and is independent of the physical attributes of individuals (Fragaszy et al., 2023). Additionally, individual capuchin monkeys of different life stages, and of differing social status, may alter their sequential organisation of tasks during nut cracking, either to avoid the usurpation of nuts, or to minimise energetic costs of material transport

(Corat et al., 2016), suggesting that action sequences may be revised during lifetimes to fit specific socioecological contexts.

Further investigation of how chimpanzees acquire stereotyped subroutines of actions, between the point of successfully learning to crack nuts during infancy, and the formation of highly stereotyped action sequences during adolescence and subadulthood, would improve our understanding of how chimpanzees learn and refine their execution of tool-use behaviours. This period is critical for understanding the intersection between social and individual learning in the acquisition of tool-use behaviours, including nut cracking. Nut cracking is confined to a small number of chimpanzee populations (Carvalho and McGrew, 2012), and to acquire this tool-use behaviour, infant chimpanzees are theorised to observe proficient adults performing nut cracking, and through such observations acquire information surrounding both the goals of the behaviour and the objects involved (Byrne and Russon, 1998; Matsuzawa, 2001; Myowa-Yamakoshi and Matsuzawa, 1999; Tomasello, 1990). However, the exact process through which chimpanzees acquire the correct sequences of actions to crack open nuts with stone tools is not yet well understood. Dictionary-based compression likely represents a valuable tool for characterising the pathways through which chimpanzees innovate and refine sequences of actions for tool-use, where compressibility offers a metric to readily quantify the extent to which chimpanzees are able to streamline their action sequences into stereotyped patterns of behaviours. We therefore recommend the use of dictionary-based compression for understanding this pathway, and where possible, recommend the use of longitudinal data which records the action sequences used by chimpanzees both prior to and after the acquisition of nut cracking behaviours, to the point of adulthood.

Observed action sequences and Markovian sequences compressed to a similar extent. Markovian sequences compress well under dictionary-based compression, as they are produced by following probabilistic transitions between neighbouring elements. Thus, Markov models are readily able to produce repeatable sequences of actions for short sequences (e.g. between two to three elements). For hierarchical behaviours, such as in the structure of human speech (Sainburg et al., 2022) and the postures of *Caenorhabditis elegans* during locomotion (Gomez-Marin et al., 2016), observed sequences of actions compress to a greater extent than those produced by comparable Markov models. Thus, the high similarity between the compression of observed action sequence data, and Markovian sequences, is unexpected if

the sequences of actions used by chimpanzees during nut cracking are also hierarchical. For previous analyses on human speech, and worm locomotion, a much larger corpus of sequential behaviours was used in the respective analyses (between 3000 and 15000 thousand sequence elements); thus, it may be possible that for many individuals, the provided sequence corpus was not long enough to find sufficient hierarchical patterns-of-patterns to permit greater compression of observed action sequence data. Alternatively, the total number of different sequence elements used in these analyses far exceeded ours (for example, our analysis included an average of 40 action types per individual, whereas the analysis of locomotion in *C. elegans* included 90 postures, Gomez-Marin et al., 2016). For sequential behaviours which have many possible different behavioural units (e.g. the phonemes of words, and the postures of worms) Markov models may detect and permit a greater number of possible transitions between element types. Thus, this greater flexibility may produce Markov sequences which are less compressible than observed hierarchical behaviours. In the case of nut cracking, adult individuals perform this behaviour frequently using around 5-6 different action types (Howard-Spink et al., in review), thus Markov models with high transition probabilities between a small number of specific actions may produce sequences which are readily compressible to observed action sequence data.

These non-mutually exclusive explanations for high compressibility are supported by our data; however, further analyses of how the number of actions, and the corpus size of highly directed behaviours, influences the compressibility of Markov sequences is required. Within our analysis, the majority of more hierarchical complex rules found in the dictionaries of observed action sequences were not readily reproducible during the compression of Markovian and random sequences, including both level-two and level-three rules. Additionally, a substantial proportion of level-one rules were also generated by under 5% of Markovian and random sequences, thus suggesting that whilst Markovian sequences compress to a similar extent to observed action sequences, their method of compression is likely different to the compression of observed action sequences. Furthermore, the longest corpus of actions, collected for Tua (1940 actions), demonstrated compression which was greater than the sequences produced by the comparable Markov model for Tua, including no overlap of 95% confidence intervals between the compression of the two sequence types for even the shortest sequences used in our analysis (100 actions). The effect of high transition probabilities between elements on the compression of Markov sequences was

also illustrated by our use of sequences produced by homogenised Markov models. Across individuals, sequences produced by homogenised Markov models compressed similarly to random sequences, thus illustrating their inability to produce stereotyped subsequences of behaviours.

We advise that future research looks to understand how both the number of different elements in a behavioural sequence, as well as the frequency with which individuals pass through similar patterns of behaviour during sequential action, influence the training, performance, and compressibility of Markovian sequences. This will be particularly important as compressibility continues to become a more common methodology for detecting the signatures of hierarchical behaviours from observed sequences of spontaneous action of both humans and non-human animals (Gomez-Marin et al., 2016; Sainburg et al., 2022; Stout et al., 2021). Within the present study, we are only able to demonstrate a greater compressibility of observed action sequences than Markovian for a single individual, and thus, we currently report that the sequential actions used by apes during tool-use compress similarly to Markovian sequences. Future analyses should employ the use of computer vision (including deep learning neural networks) and postural analyses to acquire much larger datasets of actions used by chimpanzees during tool-use (significant advances towards the possibility of such automated behavioural data collection are already being made; see e.g. Bain et al., 2021; Bala et al., 2020). Characterising sequential behaviours based on postures (reflecting body positions and limb movements) would offer a greater number of possible sequence elements than those contained within the present study (which has employed functional descriptions of behaviours as sequence units; Gomez-Marin et al., 2016). Moreover, the use of computer vision to collect data would allow for the collection of extended sequential corpuses through automated posture detection, as opposed to the time-consuming, manual behaviour coding used for the present (Gomez-Marin et al., 2016). Such analyses will offer further opportunities to interrogate the compressibility of sequential actions used by chimpanzees during tool-use, compared with simulated sequences from Markov models. Further research into the compressibility of these two sequence types will feed into discussion surrounding the extent to which tool-use behaviours reflect highly hierarchical forms of sequential behaviours in nonhuman apes.

Dictionaries offer a means to collate and compare the detected subroutines of actions for each individual. Rules were readily divisible into broad stages of the operation chain for nut cracking, including

the acquisition of resources; the combination of nuts and stone tools (e.g. placing the nut on the anvil, and striking with the hammer stone); and the processing of kernels following successful nut cracking. The majority of rules identified by dictionary compression were unique to individuals; a smaller number of rules were shared across several individuals, but not all individuals; and three rules were universal across all five dictionaries. The three universal rules represented fundamental subroutines which are imperative to successful nut cracking: placing a nut on an anvil, grasping and consuming pieces of kernel, and also the separation of edible kernel from inedible shell prior to its consumption - a behaviour which was most commonly performed with the teeth.

The majority of rules produced by dictionary compression were unique to the dictionaries of a single individual. Of these unique rules, we identified four rules which were unique to individuals due to their containment of three unique actions. The actions which made each of these rules unique were not confined to the repertoire of particular individuals (e.g. the 'peelhand SHELL' action only occurred in rules for Tua, despite being performed a small number of times by Fanle); however, the presence of these actions within the dictionary rules of an individual reflected its recurrent nature within the first 900 actions of a given individual (and in many instances, also across all observed actions after this point). Thus, dictionary-based compression is able to detect where specific individuals may more frequently employ actions which are rarely employed by other individuals - a key aspect of inter-individual differences in behaviours during nut cracking.

Of the remaining unique rules, a number of rules reflected flexible modifications of more common rules. This included five instances where a pair of rules differed by the addition of a single action into the centre of a behavioural rule. Whilst dictionary-based compression is not capable of modelling infinite recursion, the formation of pairs of rules which only differ by a central action may be indicative of centre-embedding of terminal actions within subroutines during behavioural organisation. During such a process, chimpanzees may alter more common rules by embedding a single action somewhere within the centre of a sequence, allowing a subroutine to be modified to achieve a specific goal. Centre-embedding is a feature of the organisation of many sequential behaviours in humans, including language (Friederici et al., 2011; Hauser et al., 2002) and action (Martins et al., 2019; Pulvermüller, 2014); however, centre-embedding is associated with a number of cognitive challenges, particularly for working memory (Read, 2008). The extent

to which nonhuman apes are able to readily perform centre-embedding is unclear, both in the case of embedding individual actions, and wider sequences of actions within subroutines of behaviour. Several studies claim that centre-embedding is outside of the abilities of nonhuman primates, particularly within the domain of communication (Fitch and Hauser, 2004; Traxler et al., 2012). However, experimental paradigms have demonstrated that rhesus macaques are able to successfully learn solutions to recursive matching paradigms of visual symbols, though not as readily as human participants, including toddlers (Ferrigno et al., 2020). Thus, it is possible that recursive processes, such as centre-embedding, may be a facet of behavioural organisation used by nonhuman apes when sequencing manual actions during complex feeding tasks, albeit a likely less frequent occurrence.

Through the application of dictionary-based compression, we have identified a number of subroutines which may reflect flexible processes of sequence generation within the organisation of actions during nut cracking, including possible centre-embedding. These constructions include the optional presence of central actions, with these actions being associated with the reorienting tool objects; supporting nuts on the anvil during striking, and for removing and discarding inedible shell from kernels prior to their consumption. Whilst our results may be explained by a process of centre-embedding, this is not the only possible mechanism which may permit such behavioural flexibility. Instead, the results of our analysis highlight that tool use is a promising candidate behaviour for the use of centre-embedding within the organisation of sequential behaviour in nonhuman apes. Further investigation into centre-embedding should proceed through experimental paradigms that reflect the natural foraging tasks encountered by apes, especially those which require the organisation of sequential manual actions and involve the use of tools. Further research in this area will likely be fruitful for understanding the evolution of a cognitive ability which is central to the highly generative behaviours of humans, including language, music, and complex tool production and use.

Within our results, we identified a number of dictionary rules whose uniqueness and hierarchical compressibility may have been an artefact of the compression process. A number of rules shared identical sequences of actions, but differed in the hierarchical arrangements of rules, e.g. in the pair of rules [‘grasp KERNEL’, ‘peelteeth SHELL’, ‘eat KERNEL’] and [‘grasp KERNEL’, [‘peelteeth SHELL’, ‘eat KERNEL’]], where in the latter instance, the actions of peeling the shell with the teeth and eating a fragment of kernel

are paired at a deeper hierarchical level. These pairs of rules were likely the product of the contingent nature of dictionary-based compression. A rule can only be condensed into another rule if it is already present in the dictionary. Therefore, these rules only differ in that for one rule, a smaller, more frequent rule was compressed prior to the wider sequence of actions (such as in the case of [‘grasp KERNEL’, [‘peelteeth SHELL’, ‘eat KERNEL’]]), whereas for other individuals, this smaller rule was not frequent enough to warrant compression at an earlier stage, leading to the compression of an entire sequence across a single hierarchical level. Whilst dictionary-based compression is able to predict the hierarchical arrangement of actions within sequences, it is unclear to what extent such differences between the arrangement of actions in these rules reflects a truly different hierarchical organisation of subsequences in the minds of chimpanzees. Thus, dictionary-based compression may overestimate the number of unique rules employed when parsing sequences of behaviours.

The hierarchical complexity of some rules may also be overestimated, particularly in the case of rules which are produced through compression of repeating subsequences. For example in the rule [[['grasp KERNEL', 'eat KERNEL'], ['grasp KERNEL', 'eat KERNEL']], ['grasp KERNEL', 'eat KERNEL']], the universal rule ‘grasp KERNEL’, ‘eat KERNEL’ is repeated three times. However during compression, this repetition is organised across three hierarchical levels, with the first two repetitions existing as a more closely paired hierarchical unit. We believe that this is an unlikely representation of the underlying mental process. It is more likely that such repetitions are produced through chimpanzees encountering smaller tasks of a behaviour which must be considered independently and in-turn, e.g. where chimpanzees identify, acquire, and consume a fragment of kernel, and repeat this process until all kernel is consumed. We do not believe that such a process would require nesting of repeats of this process closely to other repeats, so as to produce repetitions which cross numerous hierarchical arrangements. This argument carries for all repetitions identified within Table 3, including those which span two hierarchical levels, and includes repeating behaviours such as replacing nuts on the anvil (often after they roll off), and peeling shell away from kernel before biting and consuming an individual fragment.

Dictionary-based compression may therefore overestimate both the hierarchical complexity of rules, and also the extent to which rules constitute truly unique behaviours for individuals, based on contingencies within the compression process. Dictionary-based compression is an increasingly popular

method for characterising stereotypy within animal behaviour (Gomez-Marin et al., 2016; Sainburg et al., 2022; Stout et al., 2021); however, much of the literature focuses on the extent to which sequences compress, and the sizes of dictionaries, rather than their means of compression (the specific dictionary rules). We illustrate how the close examination of rules produced during dictionary-based compression is essential for understanding the power and limitations of the mechanism through which compression takes place. Without careful consideration of the rules of compression, both the sizes of dictionaries, and the hierarchical complexity of the rules they contain, may be overestimated. Future research using dictionary-based compression to study animal behaviour should include specific consideration of the nature of dictionary rules, particularly when drawing inter-individuals comparisons in dictionary sizes, the hierarchical complexity of rules, and their resultant influences on stereotypy.

The aim of our study was to determine whether dictionary-based compression represented an informative tool for the unbiased detection of subroutines of action in the sequential behaviours of chimpanzees during tool-use, and the extent to which individual differences may be characterised. We report that dictionary-based compression detected numerous rules for nut cracking which could be split into broad functional categories, including the acquisition of resources, combination of objects, the processing of kernels prior to consumption (including disposal of inedible shells), reflecting the wider operation chain used by chimpanzees when engaging in nut cracking (Carvalho et al., 2008). Many of the rules identified by dictionary compression were not readily reproducible by Markovian and random sequences, suggesting that whilst compression was similar between Markovian and observed action sequences, their pathways to compression were different. Dictionary-based compression identified a number of subroutines that were uniquely frequent within the corpus of actions produced by specific individuals, identified through the presence of rules containing unique actions. The presence of flexible combinations of actions were also detected for specific individuals, indicating that chimpanzees can be flexible in their approach to nut cracking tasks. Rules varied between one and three hierarchical levels, suggesting that the characteristic ‘patterns-of-patterns’ of hierarchical behavioural organisation spanned a total of three nested levels. However, for many rules, the extent to which rules were truly unique, and of high hierarchical complexity, is questionable, considering that some rules share identical sequences of actions, and rules containing repeating subroutines are unlikely to reflect truly nested sequences of behaviour. Therefore whilst

dictionary-based compression may be useful for identifying subroutines of actions during sequential behaviours, including where comparatively rare actions are more common for specific individuals, and flexibility in individual approach to tasks, careful examination of dictionaries rules is required to ensure that the uniqueness and hierarchical complexity of dictionary rules are not overestimated.

Knowledge of how to organise behaviours using sequences of smaller elements is fundamental to nearly all animals, and includes behaviours for foraging, tool use, communication, and even social behaviour, such as play. Understanding how individuals acquire and organize such behaviours may benefit from the use of dictionary-based compression; especially in the case of highly flexible sequential behaviours. For example, chimpanzee action sequences during play behaviours have been identified as non-random, and to constitute predictable 'games' based on the actions used by individuals (Mielke and Carvalho, 2022). Dictionary-based compression may be useful for detecting which sequences of actions individuals repeatedly use during such flexible behaviours, and how this may vary between individuals and groups, as long as the rules of compression are considered carefully. The careful examination of dictionary rules may be useful for comparing behavioural strategies between populations during tool-use, where dictionaries may illustrate population-level differences in the frequency with which specific subroutines of actions occur (in a similar vein to our analysis between individuals). Ultimately, we conclude that dictionary-based compression offers a valuable tool for characterising the behaviours of humans and non-human animals, but the use of dictionary-based compression in future research should also include specific consideration of the rules which underlie compressed outputs. Appropriate attention to the formation of dictionary rules could shed important insight into the morphology of observed sequential behaviours, with consequential benefit for understanding how sequential behaviours are acquired, flexibly manipulated, and compare across individuals, groups and species.

3.6 Figures

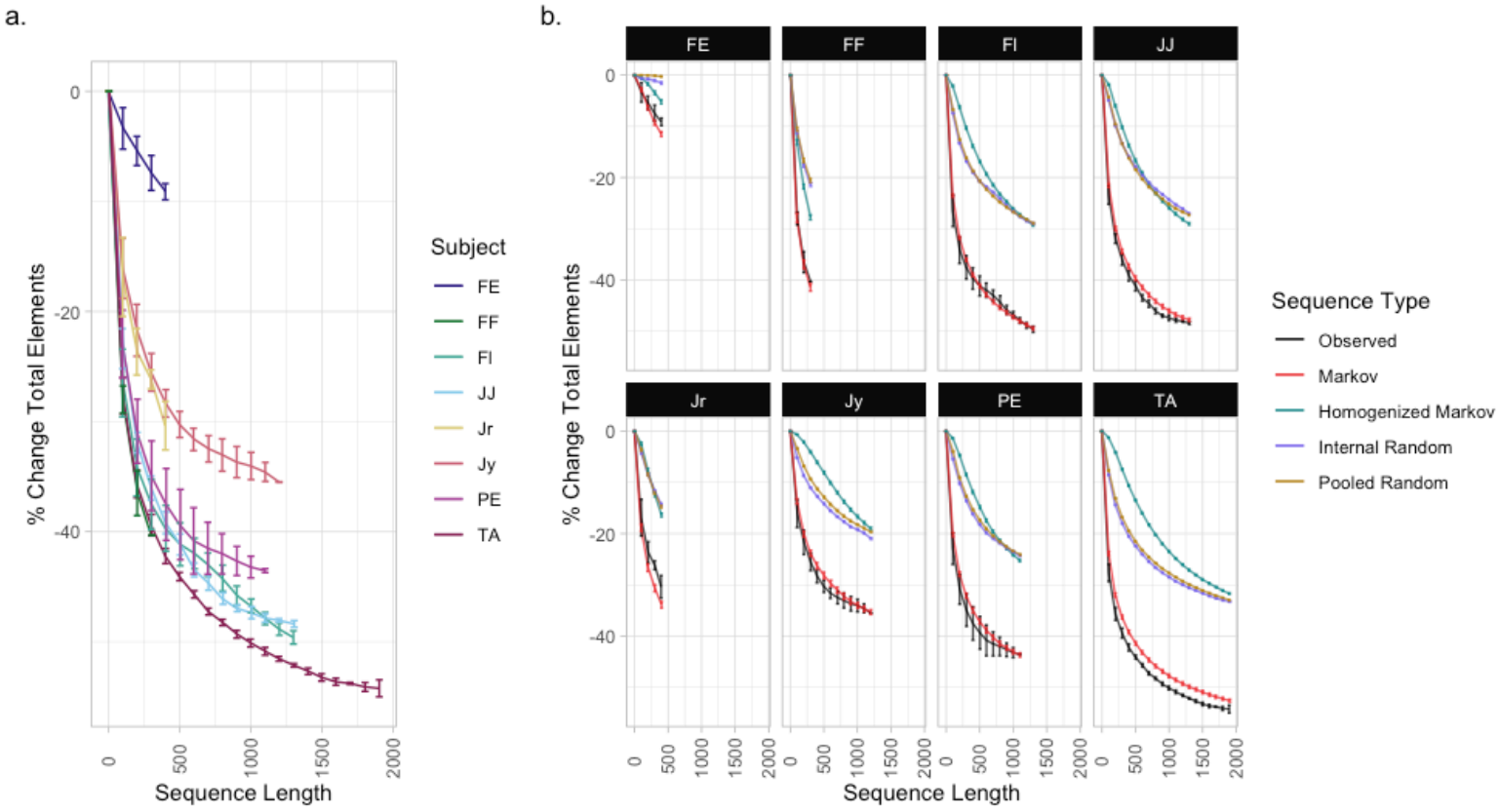
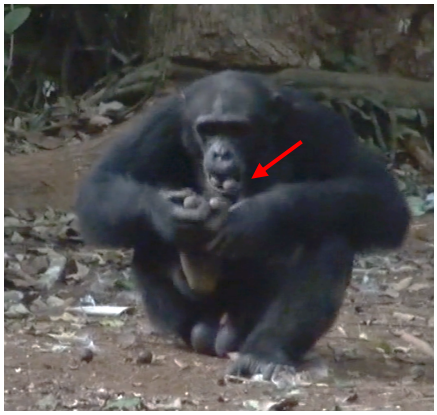
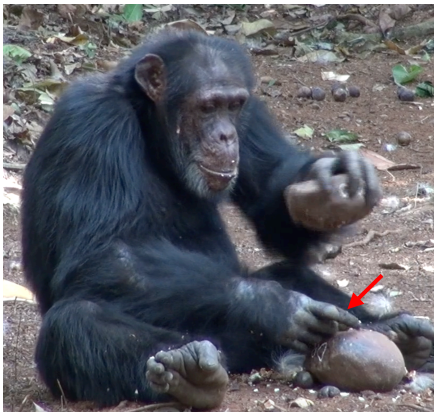


Figure 1. Compression as a function of sequence length. (a) Total percentage change of elements for each individual, using sequence inputs of increasing length. Elements include all actions in the sequence, and all elements stored in the dictionary. **(b)** Total percentage change of elements for observed action sequences compared with simulated and random sequences. Colours indicate sequence types, and each plot indicates a different individual, marked in the plot header.

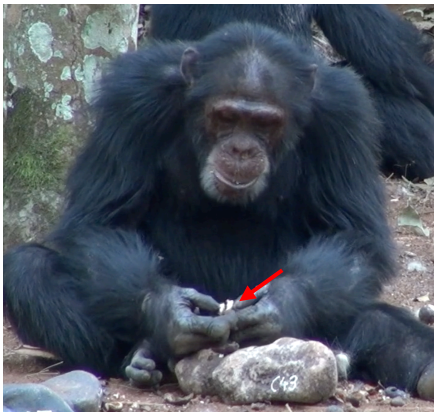
a.



['grasp NUT', 'store NUT']



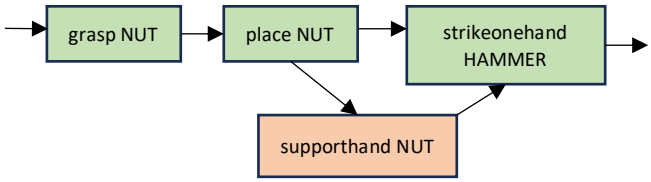
['grasp NUT', 'place NUT', 'supporthand NUT', 'strikeonehand HAMMER']



['peelhand SHELL', 'eat KERNEL']
['drop HAMMER', 'peelhand SHELL']

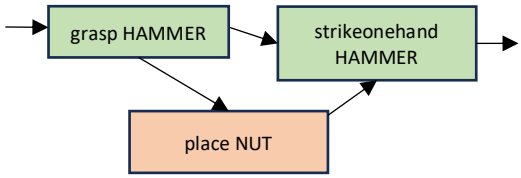
b.

i.



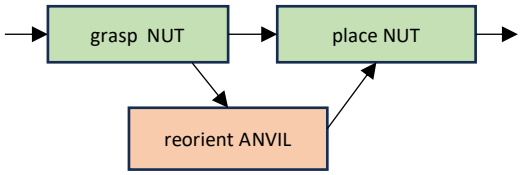
['grasp NUT', 'place NUT', 'strikeonehand HAMMER']
['grasp NUT', 'place NUT', 'supporthand NUT', 'strikeonehand HAMMER']

ii.



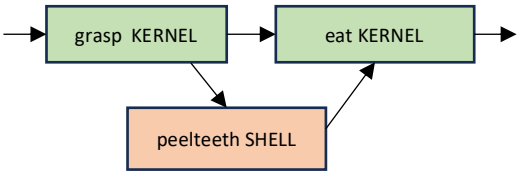
['grasp HAMMER', 'strikeonehand HAMMER']
['grasp HAMMER', 'place NUT', 'strikeonehand HAMMER']

iii.



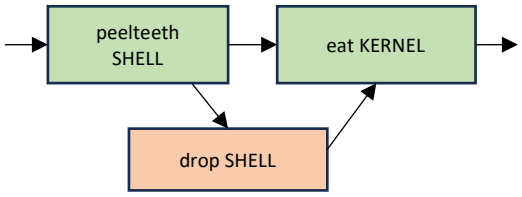
['grasp NUT', 'place NUT']
['grasp NUT', 'reorient ANVIL', 'place NUT']

iv.



['grasp KERNEL', 'eat KERNEL]
['grasp KERNEL', 'peelteeth SHELL', 'eat KERNEL]

v.



['peelteeth SHELL', 'eat KERNEL']
['peelteeth SHELL', 'drop SHELL', 'eat KERNEL']

Figure 2. Dictionary rules with actions unique to individuals, or flexible additions of central actions. (a) actions which were unique to the dictionaries of specific individuals (from left to right: 'store NUT', 'supporthand NUT', ' peelhand SHELL'). The rules which each action features in are presented below the image and indicated in red. On each image, a red arrow indicates where the action is taking place. **(b)** Pairs of rules which differ only by the addition of a central action. Flow diagrams indicate how action sequences may be modified - green boxes contain actions that are general to both rules, and orange boxes contain optional additional actions.

3.7 Tables

Table 1. Compression of observed, simulated and random sequences for each individual. Rows correspond to sequence data for a specific individual. Max sequence length is the longest sequence provided to the algorithm for compression by each individual. Mean compression at 300 elements is the longest common length used for compression across individuals. Observed sequences are those coded from video recordings of chimpanzees at Bossou, and all other sequence types related to compression of sequences produced by Markov models (Markov & homogenized Markov) as well as randomization procedures (Internal Random and Pooled Random).

Subject	Age	Mean % Compression at 300 Elements (SE)	Max Sequence Length	Mean % compression (SE)				
				Observed	Markov	Homogenised Markov	Internal Random	Pooled Random
Flanle, *FE*	4y 4m	-7.42 ± 0.809	400	-9.13 ± 0.375	-11.5 ± 0.233	-5.22 ± 0.209	-1.53 ± 0.115	-0.27 ± 0.0611
Fanle, *Fl*	14	-37.5 ± 1.16	1300	-49.6 ± 0.308	-49.5 ± 0.149	-29.3 ± 0.109	-29.0 ± 0.0767	-28.9 ± 0.0747
Foaf, *FF*	31	-40.3 ± 0	300	-40.3 ± 0	-41.4 ± 0.368	-27.8 ± 0.238	-21.4 ± 0.176	-20.6 ± 0.186
Jeje, *JJ*	14	-36.0 ± 0.559	1300	-48.4 ± 0.154	-47.8 ± 0.16	-29.0 ± 0.124	-27.0 ± 0.0615	-27.3 ± 0.0630
Jire, *Jr*	53*	-26.2 ± 0.441	400	-30.4 ± 1.13	-33.9 ± 0.328	-16.4 ± 0.190	-14.3 ± 0.133	-14.8 ± 0.128
Joya, *Jy*	7	-25.5 ± 0.872	1200	-35.5 ± 0	-35.3 ± 0.239	-19.0 ± 0.148	-21.0 ± 0.0896	-19.6 ± 0.0774
Peley, *PE*	13	-34.9 ± 1.61	1100	-43.5 ± 0.0909	-43.7 ± 0.205	-25.3 ± 0.104	-24.3 ± 0.0779	-24.1 ± 0.0714
Tua, *TA*	54*	-39.4 ± 0.454	1900	-54.2 ± 0.395	-52.6 ± 0.142	-31.7 ± 0.081	-33.3 ± 0.0573	-33.0 ± 0.052

*These individuals were present at the establishment of long-term monitoring of chimpanzees at Bossou in 1976. Ages for these individuals are therefore an estimate.

Table 2. Rules produced through repetition of subroutines. Level-one rules represent the repeating units of corresponding rules. Level-two/three repetitions indicate where level-one rules were compressed successively to produce level-two/three rules with repeating smaller units.

Level—one rule	Level-two/level-three repetitions
[‘grasp NUT’, ‘place NUT’]	[[‘grasp NUT’, ’place NUT’], [‘grasp NUT’, ’place NUT’]]
['grasp NUT', 'place NUT', 'strikeonehand HAMMER']	[['grasp NUT', 'place NUT', 'strikeonehand HAMMER'], ['grasp NUT', 'place NUT', 'strikeonehand HAMMER']]
['grasp KERNEL', 'eat KERNEL']	[['grasp KERNEL', 'eat KERNEL'], ['grasp KERNEL', 'eat KERNEL’]] [[['grasp KERNEL', 'eat KERNEL'], ['grasp KERNEL', 'eat KERNEL']], ['grasp KERNEL', 'eat KERNEL']]
['peelteeth SHELL', 'eat KERNEL']	[['peelteeth SHELL', 'eat KERNEL'],['peelteeth SHELL', 'eat KERNEL’]]

Table 3. Pairs of rules with identical action sequences but differing in hierarchical complexity. Pairs of rules are presented in less hierarchically or more hierarchically complex forms. More complex hierarchical forms include additional instances of actions being nested into subroutines within the wider rule. An explanation of the difference between the rules in each pair is provided in the column 'variation'.

Less Hierarchically Complex Form	More Hierarchically Complex Form	Variation
['grasp NUT', 'place NUT', 'strikeonehand HAMMER']	[['grasp NUT', 'place NUT'], strikeonehand HAMMER]	The first two actions are sometimes compressed as a nested rule.
['peelteeth SHELL', 'eat KERNEL', 'drop SHELL']	[['peelteeth SHELL', 'eat KERNEL'], 'drop SHELL']	
['grasp KERNEL', 'peelteeth SHELL', 'eat KERNEL']	['grasp KERNEL', ['peelteeth SHELL', 'eat KERNEL']]	The final two actions are sometimes compressed as a nested rule.
[['grasp NUT', 'place NUT'], 'grasp HAMMER', 'strikeonehand HAMMER']	[['grasp NUT', 'place NUT'], ['grasp HAMMER', 'strikeonehand HAMMER']]	The final two actions are sometimes compressed as two additional actions, and sometimes added as a nested rule.
[['grasp NUT', 'place NUT', 'strikeonehand HAMMER'] 'touchhand NUT', 'strikeonehand HAMMER']	[['grasp NUT', 'place NUT', 'strikeonehand HAMMER'] ['touchhand NUT', 'strikeonehand HAMMER']]	
['grasp KERNEL', ['peelteeth SHELL', 'eat KERNEL', 'drop SHELL']]	['grasp KERNEL', [['peelteeth SHELL', 'eat KERNEL'],'drop SHELL']]	In the less hierarchically complex form, the latter three rules exist in a single, level-two hierarchical unit. In the more hierarchically complex instance, 'peelteeth SHELL' and 'eat KERNEL' form a nested rule at the third hierarchical level.

Table 4. Rules for each individual that were not readily produced during compression of Markovian or random sequences. Each row corresponds to an individual. The total number of dictionary rules are provided, as well as the number of rules spanning one, two and three hierarchical levels. Presented rules occurred in less than 5% of dictionaries for both types of sequences produced by Markov models, as well as sequences produced by randomization procedures.

Subject	Total Dictionary Rules	Rules in < 5% of dictionaries for all types of simulated and random sequences	% rules in < 5% of dictionaries for all types of simulated and random sequences
Fanle	**20** ***(10)*** ***(9)*** ***(1)***	*Level One* [touchhandNUT', 'strikeonehandHAMMER'] ['flipANVIL', 'placeNUT'] ['graspNUT', 'placeNUT', 'strikeonehandHAMMER'] ['graspKERNEL', 'peelteethSHELL', 'eatKERNEL'] ['graspANVIL', 'reloCATE', 'dropANVIL'] *Level Two* [['graspNUT', 'placeNUT', 'strikeonehandHAMMER'], ['graspKERNEL', 'eatKERNEL']] [['graspNUT', 'placeNUT', 'strikeonehandHAMMER'], 'graspNUT', 'peelteethSHELL', 'eatKERNEL'] [['graspNUT', 'placeNUT', 'strikeonehandHAMMER'], ['touchhandNUT', 'strikeonehandHAMMER']] [['graspKERNEL', 'peelteethSHELL', 'eatKERNEL'], 'dropSHELL'] [['graspNUT', 'placeNUT', 'strikeonehandHAMMER'], 'graspNUT'] [['graspNUT', 'placeNUT', 'strikeonehandHAMMER'], 'graspKERNEL', 'dropKERNEL'] [['graspNUT', 'placeNUT', 'strikeonehandHAMMER'], ['graspKERNEL', 'peelteethSHELL', 'eatKERNEL']] *Level Three* [['graspKERNEL', 'eatKERNEL'], [['graspNUT', 'placeNUT', 'strikeonehandHAMMER'] ['graspKERNEL', 'eatKERNEL']]]	**13/20 (65%)**
Jeje	**24** ***(10)*** ***(9)*** ***(5)***	*Level One* ['graspNUT', 'reorientANVIL', 'placeNUT'] ['graspKERNEL', 'dropKERNEL', 'graspKERNEL'] *Level Two* - *Level Three* [['peelteethSHELL', 'eatKERNEL'], [['peelteethSHELL', 'eatKERNEL'], 'dropSHELL']]	**3/24 (12.5%)**
Joya	**19** ***(14)*** ***(5)*** ***(0)***	*Level One* ['touchhandNUT', 'strikeonehandHAMMER'] ['reorientANVIL', 'flipANVIL'] ['graspNUT', 'placeNUT', 'strikeonehandHAMMER'] ['graspHAMMER', 'placeNUT', 'strikeonehandHAMMER'] *Level Two* ['graspKERNEL', 'peelteethSHELL', 'eatKERNEL']['peelteethSHELL', 'eatKERNEL', 'dropSHELL'] [['graspKERNEL', 'peelteethSHELL', 'eatKERNEL'], 'dropSHELL'] [['graspHAMMER', 'reloCATE'], 'dropHAMMER'] ['strikeonehandHAMMER', ['graspNUT', 'placeNUT', 'strikeonehandHAMMER']] ['dropHAMMER', 'reloCATE', ['graspNUT', 'reloCATE']] *Level Three* -	**10/19 (52.6%)**
Peley	**21** ***(10)*** ***(9)*** ***(2)***	*Level One* ['reorientANVIL', 'supportfootANVIL'] ['graspNUT', 'storeNUT'] ['reorientANVIL', 'supportfootANVIL'] ['peelteethSHELL', 'dropSHELL', 'eatKERNEL'] ['graspNUT', 'placeNUT', 'strikeonehandHAMMER'] *Level Two* [[['graspNUT', 'placeNUT', 'strikeonehandHAMMER'], 'touchhandNUT', 'strikeonehandHAMMER'], 'touchhandNUT', 'strikeonehandHAMMER'] [['graspNUT', 'placeNUT', 'strikeonehandHAMMER'], 'graspNUT'] [['graspNUT', 'placeNUT', 'strikeonehandHAMMER'], ['graspNUT', 'placeNUT', 'strikeonehandHAMMER']] [['graspNUT', 'placeNUT', 'strikeonehandHAMMER'], 'touchhandNUT', 'strikeonehandHAMMER'] [['graspNUT', 'placeNUT', 'strikeonehandHAMMER'], ['graspKERNEL', 'eatKERNEL']] *Level Three* [[['graspKERNEL', 'eatKERNEL'], ['graspKERNEL', 'eatKERNEL']], ['graspKERNEL', 'eatKERNEL']	**10/21 (47.6%)**
Tua	**21** **(13)** **(7)**	*Level One* ['graspNUT', 'placeNUT', 'strikeonehandHAMMER'] ['peelteethSHELL', 'eatKERNEL', 'dropSHELL'] ['graspNUT', 'placeNUT', 'supporthandNUT', 'strikeonehandHAMMER'] ['peelteethSHELL', 'dropSHELL', 'eatKERNEL'] ['dropNUT', 'graspHAMMER'] ['dropHAMMER', 'peelhandSHELL'] *Level Two* [['graspNUT', 'placeNUT', 'strikeonehandHAMMER'], ['graspKERNEL', 'eatKERNEL']] [['peelteethSHELL', 'eatKERNEL'], ['peelteethSHELL', 'eatKERNEL', 'dropSHELL']] [['graspNUT', 'placeNUT', 'strikeonehandHAMMER'], 'touchhandNUT', 'strikeonehandHAMMER'] ['graspKERNEL', ['peelteethSHELL', 'eatKERNEL', 'dropSHELL']]	**11/21 (52.3%)**

	(1)	*Level Three* [[['peelteethSHELL', 'eatKERNEL'], ['peelteethSHELL', 'eatKERNEL', 'dropSHELL']], 'graspHAMMER', 'placeHAMMER', ['graspNUT', 'placeNUT', 'strikeonehandHAMMER']]	

3.8 References

Asano, R., Boeckx, C., 2015. Syntax in language and music: what is the right level of comparison? Front. Psychol. 6, 1–16. https://doi.org/10.3389/fpsyg.2015.00942

Babiszewska, M., Schel, A.M., Wilke, C., Slocombe, K.E., 2015. 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. https://doi.org/10.1002/ajpa.22634

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. Sci. Adv. 7, eabi4883. https://doi.org/10.1126/sciadv.abi4883

Bala, P.C., Eisenreich, B.R., Yoo, S.B.M., Hayden, B.Y., Park, H.S., Zimmermann, J., 2020. Automated markerless pose estimation in freely moving macaques with OpenMonkeyStudio. Nat. Commun. 11, 4560. https://doi.org/10.1038/s41467-020-18441-5

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. Anim. Cogn. 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. Cogn. Dev. Chimpanzees 476–508. https://doi.org/10.1007/4-431-30248-4_28

Boesch, C., Kalan, A.K., Mundry, R., Arandjelovic, M., Pika, S., Dieguez, P., Ayimisin, E.A., Barciela, A., Coupland, C., Egbe, V.E., Eno-Nku, M., Michael Fay, J., Fine, D., Adriana Hernandez-Aguilar, R., Hermans, V., Kadam, P., Kambi, M., Llana, M., Maretti, G., Morgan, D., Murai, M., Neil, E., Nicholl, S., Ormsby, L.J., Orume, R., Pacheco, L., Piel, A., Sanz, C., Sciaky, L., Stewart, F.A., Tagg, N., Wessling, E.G., Willie, J., Kühl, H.S., 2020. Chimpanzee ethnography reveals unexpected cultural diversity. Nat. Hum. Behav. 4, 910–916. https://doi.org/10.1038/s41562-020-0890-1

Bril, B., Dietrich, G., Foucart, J., Fuwa, K., 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? Anim. Cogn. 12, 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. Philos. Trans. R. Soc. B Biol. Sci. 370. https://doi.org/10.1098/rstb.2014.0355

Byrne, R.W., 2007. Culture in great apes: Using intricate complexity in feeding skills to trace the evolutionary origin of human technical prowess. Philos. Trans. R. Soc. B Biol. Sci. 362, 577–585. https://doi.org/10.1098/rstb.2006.1996

Byrne, R.W., Byrne, J.M.E., 1993. Complex leaf-gathering skills of mountain gorillas (Gorilla g. beringei): Variability and standardization. Am. J. Primatol. 31, 241–261.

Byrne, R.W., Corp, N., Byrne, J.M.E., 2001. Estimating the complexity of animal behaviour: How mountain gorillas eat thistles. Behaviour 138, 525–557. https://doi.org/10.1163/156853901750382142

Byrne, R.W., Russon, A.E., 1998. Learning by imitation : A hierarchical approach. Behav. Brain Sci. 21, 667–721.

Byrne, R.W., Sanz, C.M., Morgan, D.B., 2013. Chimpanzees plan their tool use, in: Sanz, C.M., Call, J., Boesch, C. (Eds.), Tool Use in Animals. Cambridge University Press, pp. 48–64. https://doi.org/10.1017/CBO9780511894800.004

Carvalho, S., Cunha, E., Sousa, C., Matsuzawa, T., 2008. Chaînes opératoires and resource-exploitation strategies in chimpanzee (Pan troglodytes) nut cracking. J. Hum. Evol. 55, 148–163. https://doi.org/10.1016/j.jhevol.2008.02.005

Carvalho, S., McGrew, W., 2012. The origins of the Oldowan: Why chimpanzees (Pan troglodytes) still are good models for technological evolution in Africa, in: Domínguez-Rodrigo, M. (Ed.), Stone

Tools and Fossil Bones. Cambridge University Press, pp. 201–221. https://doi.org/10.1017/CBO9781139149327.010
Chomsky, N., 2002. An Elementary Linguistic Theory, in: Syntactic Structures; Second Edition. Berlin ; New York : Mouton de Gruyter, pp. 18–25. https://doi.org/10.1515/9783110218329
Chomsky, N., 1956. Three models for the description of language. IRE Trans. Inf. Theory 2, 113–124.
Clay, Z., Zuberbühler, K., 2009. Food-associated calling sequences in bonobos. Anim. Behav. 77, 1387–1396. https://doi.org/10.1016/j.anbehav.2009.02.016
Corat, C., Siqueira, J., Ottoni, E.B., 2016. Sequential organization and optimization of the nut-cracking behavior of semi-free tufted capuchin monkeys (Sapajus sp.). Primates 57, 113–121. https://doi.org/10.1007/s10329-015-0491-1
Coye, C., Townsend, S., Lemasson, A., 2018. From animal communication to linguistics and back: Insight from combinatorial abilities in monkeys and birds, Origins of Human Language: Continuities and Discontinuities with Nonhuman Primates. https://doi.org/10.3726/b12405
Dawkins, R., 1976. Hierarchical organization: a candidate principle for ethology., in: Growing Points in Ethology. Cambridge University Press.
Dawkins, R., Dawkins, M., 1976. Hierarchical Organization and Postural Facilitation: Rules for Grooming in Flies. Anim. Behav. 24, 739–755. https://doi.org/10.1016/S0003-3472(76)80003-6
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. Am. J. Primatol. 79, e22672. https://doi.org/10.1002/ajp.22672
Fadiga, L., Craighero, L., D'Ausilio, A., 2009. Broca's area in language, action, and music. Ann. N. Y. Acad. Sci. 1169, 448–458. https://doi.org/10.1111/j.1749-6632.2009.04582.x
Ferrigno, S., Cheyette, S.J., Piantadosi, S.T., Cantlon, J.F., 2020. Recursive sequence generation in monkeys, children, U.S. adults, and native Amazonians. Sci. Adv. 6, eaaz1002. https://doi.org/10.1126/sciadv.aaz1002
Fitch, W.T., Hauser, M.D., 2004. Computational Constraints on Syntactic Processing in a Nonhuman Primate. Science 303, 377–380. https://doi.org/10.1126/science.1089401
Fitch, W.T., Martins, M.D., 2014. Hierarchical processing in music, language, and action: Lashley revisited. Ann. N. Y. Acad. Sci. 1316, 87–104. https://doi.org/10.1111/nyas.12406
Fragaszy, D.M., Aiempichitkijkarn, N., Eshchar, Y., Mangalam, M., Izar, P., Resende, B., Visalberghi, E., 2023. The development of expertise at cracking palm nuts by wild bearded capuchin monkeys, Sapajus libidinosus. Anim. Behav. 197, 1–14. https://doi.org/10.1016/j.anbehav.2022.12.008
Friederici, A.D., Bahlmann, J., Friedrich, R., Makuuchi, M., 2011. The Neural Basis of Recursion and Complex Syntactic Hierarchy. Learning 5, 87–104.
Gagniuc, P., 2017. Markov Chains: From Theory to Implementation and Experimentation. https://doi.org/10.1002/9781119387596
Gomez-Marin, A., Stephens, G.J., Brown, A.E.X., 2016. Hierarchical compression of *Caenorhabditis elegans* locomotion reveals phenotypic differences in the organization of behaviour. J. R. Soc. Interface 13, 20160466. https://doi.org/10.1098/rsif.2016.0466
Greenfield, P.M., 1991. Language, tools and brain: The ontogeny and phylogeny of hierarchically organized sequential behavior. Behav. Brain Sci. 531–595.
Gruber, T., Clay, Z., 2016. A Comparison Between Bonobos and Chimpanzees: A Review and Update. Evol. Anthropol. 25, 239–252. https://doi.org/10.1002/evan.21501
Hattori, Y., Tomonaga, M., 2020. Rhythmic swaying induced by sound in chimpanzees (Pan troglodytes). Proc. Natl. Acad. Sci. U. S. A. 117, 936–942. https://doi.org/10.1073/pnas.1910318116
Hauser, M.D., Chomsky, N., Fitch, W.T., 2002. The faculty of language: What is it, who has it, and how did it evolve? Evol. Hum. Lang. Biolinguistic Perspect. 298, 14–42. https://doi.org/10.1017/CBO9780511817755.002
Hayashi, M., 2015. Perspectives on object manipulation and action grammar for percussive actions in primates. Philos. Trans. R. Soc. B Biol. Sci. 370. https://doi.org/10.1098/rstb.2014.0350
Hayashi, M., Takeshita, H., 2022. Hierarchical object combination and tool use in the great apes and human children. Primates. https://doi.org/10.1007/s10329-022-01003-2
Humle, T., Matsuzawa, T., 2002. Ant-dipping among the chimpanzees of Bossou, Guinea, and some comparisons with other sites. Am. J. Primatol. 58, 133–148. https://doi.org/10.1002/ajp.10055
Inoue-Nakamura, N., Matsuzawa, T., 1997. Development of Stone Tool Use by Wild Chimpanzees (Pan troglodytes). J. Comp. Psychol. 111, 159–173. https://doi.org/10.1037/0735-7036.111.2.159

Koelsch, S., Rohrmeier, M., Torrecuso, R., Jentschke, S., 2013. Processing of hierarchical syntactic structure in music. Proc. Natl. Acad. Sci. U. S. A. 110, 15443–15448. https://doi.org/10.1073/pnas.1300272110
Larsson, N.J., Moffat, A., 2000. Off-Line Dictionary-Based Compression. Proc. IEEE 88.
Lashley, K., 1951. The problem of serial order in behavior. Cereb. Mech. Behav. 112–147.
Leroux, M., Schel, Anne M, Wilke, Claudia, Bosco, Chandia, Zuberbühler, Klaus, Slocombe, Katie, Townsend, Simon, 2023. Call combinations and compositional processing in wild chimpanzees. Nat. Commun. 14, 1–8. https://doi.org/10.1038/s41467-023-37816-y
Leroux, M., Townsend, S.W., 2020. Call combinations in great apes and the evolution of syntax. Anim. Behav. Cogn. 7, 131–139. https://doi.org/10.26451/abc.07.02.07.2020
Mangalam, M., Fragaszy, D.M., 2015. Wild Bearded Capuchin Monkeys Crack Nuts Dexterously. Curr. Biol. 25, 1334–1339. https://doi.org/10.1016/j.cub.2015.03.035
Martins, M.J.D., Bianco, R., Sammler, D., Villringer, A., 2019. Recursion in action: An fMRI study on the generation of new hierarchical levels in motor sequences. Hum. Brain Mapp. 40, 2623–2638. https://doi.org/10.1002/hbm.24549
Matsuzawa, T., 2011. Stone Tools for Nut-Cracking, in: The Chimpanzees of Bossou and Nimba. Springer Japan, Tokyo, Japan, pp. 73–84.
Matsuzawa, T., 2001. Primate Foundations of Human Intelligence: A View of Tool Use in Nonhuman Primates and Fossil Hominids, in: Matsuzawa, T. (Ed.), Primate Origins of Human Cognition and Behavior. Springer Japan, Tokyo, pp. 3–25. https://doi.org/10.1007/978-4-431-09423-4_1
Matsuzawa, T., 1996. Chimpanzee intelligence in nature and in captivity: Isomorphism of symbol use and tool use, in: Great Ape Societies. pp. 196–212.
Matsuzawa, T., 1994. Field Experiments on use of Stone Tools in the wild, in: Chimpanzee Cultures. pp. 351–370.
Matsuzawa, T., 1991. Nesting cups and metatools in chimpanzees. Behav. Brain Sci. 14, 570–571. https://doi.org/10.1017/S0140525X00071417
Mielke, A., Carvalho, S., 2022. Chimpanzee play sequences are structured hierarchically as games. PeerJ 10, e14294. https://doi.org/10.7717/peerj.14294
Myowa-Yamakoshi, M., Matsuzawa, T., 1999. Factors influencing imitation of manipulatory actions in chimpanzees (Pan troglodytes). J. Comp. Psychol. 113, 128–136. https://doi.org/10.1037/0735-7036.113.2.128
Nevill-Manning, C., Witten, I., 1997. Identifying Hierarchical Structure in Sequences: A linear-time algorithm. J. Artif. Intell. Res. 7, 67–82.
Nevill-Manning, C.G., Witten, I.H., 2000. On-line and off-line heuristics for inferring hierarchies of repetitions in sequences. Proc. IEEE 88, 1745–1755. https://doi.org/10.1109/5.892710
Pastra, K., Aloimonos, Y., 2012. The minimalist grammar of action. Philos. Trans. R. Soc. B Biol. Sci. 367, 103–117. https://doi.org/10.1098/rstb.2011.0123
Pulvermüller, F., 2014. The syntax of action. Trends Cogn. Sci. 18, 219–220. https://doi.org/10.1016/j.tics.2014.01.001
Read, D.W., 2008. Working Memory: A Cognitive Limit to Non-Human Primate Recursive Thinking Prior to Hominid Evolution. Evol. Psychol. 6, 147470490800600. https://doi.org/10.1177/147470490800600413
Rosenbaum, D.A., Cohen, R.G., Jax, S.A., Weiss, D.J., van der Wel, R., 2007. The problem of serial order in behavior: Lashley's legacy. Hum. Mov. Sci. 26, 525–554. https://doi.org/10.1016/j.humov.2007.04.001
Sainburg, T., Mai, A., Gentner, T.Q., 2022. Long-range sequential dependencies precede complex syntactic production in language acquisition. Proc R Soc B 289:, 2020.08.19.256792. https://doi.org/10.1098
Sainburg, T., Theilman, B., Thielk, M., Gentner, T.Q., 2019. Parallels in the sequential organization of birdsong and human speech. Nat. Commun. 10, 1–11. https://doi.org/10.1038/s41467-019-11605-y
Sanz, C.M., Morgan, D.B., 2010. The Complexity of Chimpanzee Tool-Use Behaviors, in: The Mind of the Chimpanzee: Ecological and Experimental Perspectives. The University of Chicago Press, pp. 127–140.
Sanz, C.M., Morgan, D.B., 2009. Flexible and Persistent Tool-using Strategies in Honey-gathering by Wild Chimpanzees. Int. J. Primatol. 30, 411–427. https://doi.org/10.1007/s10764-009-9350-5

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. Sci. Adv. 5, 1–10. https://doi.org/10.1126/sciadv.aaw0736

Schofield, D.P., 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 Ecol. Evol. 14, 1937–1951. https://doi.org/10.1111/2041-210X.14181

Seeds, A.M., Ravbar, P., Chung, P., Hampel, S., Midgley, F.M., Mensh, B.D., Simpson, J.H., 2014. A suppression hierarchy among competing motor programs drives sequential grooming in Drosophila. eLife 3, e02951. https://doi.org/10.7554/eLife.02951

Sellet, F., 1993. Chaine Operatoire; The Concept and Its Applications. Lithic Technol. 18, 106–112. https://doi.org/10.1080/01977261.1993.11720900

Sirianni, G., Mundry, R., Boesch, C., 2015. When to choose which tool: multidimensional and conditional selection of nut-cracking hammers in wild chimpanzees. Anim. Behav. 100, 152–165. https://doi.org/10.1016/j.anbehav.2014.11.022

Spedicato, G.A., 2017. Discrete Time Markov Chains with R. R J.

Steele, J., Ferrari, P.F., Fogassi, L., 2012. From action to language: Comparative perspectives on primate tool use, gesture and the evolution of human language. Philos. Trans. R. Soc. B Biol. Sci. 367, 4–9. https://doi.org/10.1098/rstb.2011.0295

Stout, D., Chaminade, T., Apel, J., Shafti, A., Faisal, A.A., 2021. The measurement, evolution, and neural representation of action grammars of human behavior. Sci. Rep. 11, 13720. https://doi.org/10.1038/s41598-021-92992-5

Tomasello, M., 1990. Cultural transmission in the tool use and communicatory signaling of chimpanzees?, in: Parker, S.T., Gibson (Eds.), Language and Intelligence in Monkeys and Apes. Cambridge University Press, pp. 274–311.

Tonooka, R., 2001. Leaf-folding behavior for drinking water by wild chimpanzees (Pan troglodytes verus) at Bossou, Guinea. Anim. Cogn. 4, 325–334. https://doi.org/10.1007/s100710100110

Traxler, M.J., Boudewyn, M., Loudermilk, J., 2012. What's Special About Human Language? The Contents of the "Narrow Language Faculty" Revisited. Linguist. Lang. Compass 6, 611–621. https://doi.org/10.1002/lnc3.355

Uddén, J., de Jesus Dias Martins, M., Zuidema, W., Tecumseh Fitch, W., 2020. Hierarchical Structure in Sequence Processing: How to Measure It and Determine Its Neural Implementation. Top. Cogn. Sci. 12, 910–924. https://doi.org/10.1111/tops.12442

Vereijken, B., Whiting, H., 1998. Hoist by their own petard: The constraints of hierarchical models. Behav. Brain Sci. 21, 705–705. https://doi.org/10.1017/S0140525X98451744

Wilson, B., Spierings, M., Ravignani, A., Mueller, J.L., Mintz, T.H., Wijnen, F., van der Kant, A., Smith, K., Rey, A., 2020. Non-adjacent Dependency Learning in Humans and Other Animals. Top. Cogn. Sci. 12, 843–858. https://doi.org/10.1111/tops.12381

Yamakoshi, G., Sugiyama, Y., 1995. Pestle-pounding behavior of wild chimpanzees at Bossou, Guinea: a newly observed tool-using behavior. Primates 36, 489–500.

3.9 Supplementary materials

3.9.1 Behaviour coding and sampled data

Table S1. Action Sequence Data Summary. This table is a replica of Table 1 from Howard-Spink *et al.* (in review): Eight individuals were included in MI decay modelling. 'Time Coded' relates to the total duration of time individuals were seen to be engaging with nuts, nut fragments and stone tools throughout all video footage. An 'Element' is defined as each action coded within a sequence, whereas 'Action Types' represent the different types of coded actions in a sequence (e.g., "Grasp Nut" "Place Nut" "Grasp Nut" – Number of elements: 3, Number of Action Types: 2). 'Nuts Cracked' marks the number of nuts observed to have been cracked by an individual across all available video footage. Mean Sequence Length Per Nut refers to the mean number of elements in a sequence that is directed at cracking open each individual nut. SE for all means were calculated via the normal approximation of the Poisson distribution. Ages marked with * are an estimate, as these individuals were present when long-term monitoring at Bossou began.

Individual	Sex	Age (years)	Time Coded (MM:SS)	Number of Sequences	Sequence Elements (Total)	Mean Sequence Length ± SE	Number of Action Types	Nuts Cracked	Mean Sequence Length Per Nut ± SE
Fanle	F	14	44:55	21	1368	65.1 ± 1.8	34	85	13.9 ± 0.4
Flanle	M	7	24:03	35	453	12.9 ± 0.6	59	1	48
Foaf	M	31	07:22	8	299	37.4 ± 2.2	18	10	31.2 ± 1.8
Jeje	M	14	40:33	18	1373	76.3 ± 2.1	36	39	29.4 ± 0.9
Jire	F	53*	19:27	12	482	40.2 ± 1.8	33	22	16.0 ± 0.9
Joya	F	4	36:52	39	1178	30.2 ± 0.9	55	22	36 ± 1.3
Peley	M	13	34:05	15	1168	77.9 ± 2.3	44	45	21.7 ± 0.7
Tua	M	54*	55:33	15	1940	129.3 ± 2.9	43	79	22.4 ± 0.5
Velu	F	52*	01:07	2	16	8 ± 2	12	0	0

Table S2. Ethogram of different action types, and their descriptions. This table is a replica of Table S2 from Howard-Spink *et al.* (in review): Actions in bold are coded alongside a corresponding object. There are 6 possible corresponding objects: 1. Nut, 2. Hammer, 3. Anvil, 4. Kernel, 5. Shell, 6. Bare Hand. Event codes in italics are used to denote the start and end of observable sequences. Coding commenced when individuals began interacting with stones, nuts, or nut-fragments. Coding ceased when individuals began engaging in a new behaviour e.g. play, grooming, eating oil-palm fruits. On the occasions where an individual moved out of clear sight of the video recording, or actions became obscured by an individual's body position, sequences were terminated with a 'Not Visible' codon, and marked as incomplete.

Action	Description
Bite	Place object in mouth and bite with teeth. Differs from 'Eat' as there is no consumption. Differs from 'Store' as object moves in and out of mouth whilst chimp is stationary. Differs from 'Peel Teeth' as bite applies general force, whereas peel with mouth is to remove shell fragments from kernel dexterously. Differs from 'Kiss' as object enters inside the mouth.
Brush	Brush objects off the anvil.
Drop	Place object(s) on ground.
Eat	Consume object. Differs from bite and store as it requires successful ingestion.
Flip	Flip object over.
Grasp	Grasp an object and move off the ground.
Kick	Apply rapid, hard force on object with the foot, so that the object is displaced.
Kiss	Place object to lips or nose, but not inside of the mouth.
Pass	Pass object between hands.
Peel Hand	Peel shell off of kernel with hands.
Peel Teeth	Peel shell off of kernel with teeth.
Place	Place an object on an anvil.
Provide	Directly hand an object to another individual.
Pull Foot	Pull an object across the ground with foot.
Pull Hand	Pull an object across the ground with hand.
Push Foot	Push an object across the ground with foot.
Push Hand	Push an object across the ground with hand.
Rake Foot	Pull many objects towards oneself using foot/leg.
Rake Hand	Pull many objects towards oneself using hand/arm.
Reorient	Rotate object horizontally.
Roll Foot	Roll object along the floor with foot.
Roll Hand	Roll object along the floor with hand.
Spit	Let object fall from mouth or lips.
Stomp	Whilst standing, apply strong force to object with foot.
Store	Place object(s) in mouth for transportation. Separated from bite, eat, peel teeth as it is followed by transportation across the outdoor laboratory, before then being removed from the mouth intact.
Strike One Hand	Strike with one hand, (and associated object).
Strike Two Hand	Strike with two hands, (and associated object).
Support Foot	Support object with foot.
Support Hand	Support object with hand.
Take	Receive an object directly from another individual.
Throw	Throw object away from self, horizontally or vertically.
Touch Foot	Touch or grasp object without moving it using foot.
Touch Hand	Touch or grasp object without moving it using hand.
Relocate	Stand up and move to a new area; is immediately followed by another coding action.
Start	Start of a sequence.
End Bout	End of a sequence.
Not Visible	Individual moves out of view, and coding cannot continue. Differs from 'End Bout', as there is no evidence the individual has stopped engaging with stones, nuts or nut-fragments.

Table formatting for tables S3-S6.

Each table has the same formatting: ‘rule numbers’ include a two-letter code (AR = acquiring resources, CO = combining objects, PK = processing kernels) as well as a number, providing a unique reference for each rule. Rules are organised based on their hierarchical complexity (1 = all one level, 2 = two levels, 3 = three levels). ‘Rule’ is the combination sequence elements used for dictionary-based compression. ‘Contains rule’ indicates which other rules are contained within a given rule (provided as a list, with rules separated by commas). For rules at hierarchical level three, which contain rules which contain further rules, both the level two rule is provided, along with its internal level-one rules in brackets (see rule CO28 for an example). Rules which appear in other rules are colour coded. ‘Prevalence’ describes whether a rule is universal across all individuals; shared across many (but not all) individuals, or is unique to a single individual. ‘Substitutions for each individual’ indicate how many times a given rule was substituted into the concatenated action sequence for each individual. ‘Number of actions within the rule’ indicates how many actions are contained within a rule, across all hierarchical levels. ‘Unique Action’ indicates where a rule contains an action which is not present in any other rule. These rules are discussed as specific points of interest within the manuscript.

A brief discussion can be found below each table, describing the rules it contains.

Table S3. Dictionary rules associated with acquiring resources.

Rule Number	Rule	Contains Rule	Prevalence	No. Individuals with Rule	Substitutions for each individual					Number of Actions within the Rule	Unique Action?
					fl	jj	jy	pe	ta		
	Hierarchical Level = 1										
AR1	['grasp NUT', 'reloCATE']	-	Shared	3	0	7	9	0	7	2	
AR2	['grasp HAMMER', 'reloCATE']	-	Unique	1	0	0	10	0	0	2	
AR3	['grasp NUT', 'store NUT']	-	Unique	1	0	0	0	9	0	2	
AR4	['grasp ANVIL', 'reloCATE', 'drop ANVIL']	-	Unique	1	4	0	0	0	0	3	
	Hierarchical Level = 2										
AR5	['drop HAMMER', 'reloCATE', ['grasp NUT', 'reloCATE']]	AR1	Unique	1	0	0	3	0	0	**4**	
AR6	[['grasp HAMMER', 'reloCATE'], 'drop HAMMER']	AR2	Unique	1	0	0	5	0	0	**3**	

Six rules were included within the category acquiring resources. One rule was shared, and five rules were unique to individuals. The only shared rule, AR1, occurred in the dictionary of four individuals, and reflected where an individual would gras a nut and carry it across the outdoor lab. Similarly, rules AR2, AR4 and AR6 reflect where individuals would transport tool objects across the outdoor lab.

Rule AR3 involved a unique action type that was not found in any other rule, ‘store NUT’. This action indicates where an individual stores an uncracked nut in their mouth for transportation across the outdoor lab, and was observed in the dictionary of one individual, Peley. The action ‘store NUT’ was present in the action sequences of Tua and Joya also; however for Tua, these five instances were outside of the first 900 actions, and for Joya, one instance was within the first 900 actions, and one was after this point, and therefore was not sampled. However for Peley, who demonstrated this action 19 times in the first 900 actions, the act of storing a nut in the mouth was a far more common behaviour. Therefore, ‘store NUT’ does not reflect an action confined to the behavioural repertoire of Peley; however, its presence in Peley’s dictionary of rules reflects a more common elicitation of this behaviour.

Rules AR5 and AR6 were the only level-2 hierarchical rules, both of which occurred relatively infrequently within the action sequence for Joya. Both of these rules concerned moving across the outdoor lab whilst transporting tool objects and nuts.

Table S4. Dictionary rules associated with combining objects.

Rule Number	Rule	Contains Rule	Prevalence	No. Individuals with Rule	Substitutions for each individual					Number of Actions within the Rule	Unique Action?
					fl	jj	jy	pe	ta		
	Hierarchical Level = 1										
CO1	['grasp NUT', 'place NUT']	-	Universal	5	38	102	24	34	10	2	
CO2	['grasp NUT', 'place NUT', 'strikeonehand HAMMER']	-	Shared	4	74	0	28	61	50	3	
CO3	['grasp HAMMER', 'strikeonehand HAMMER']	-	Shared	3	0	5	10	5	0	2	
CO4	['place NUT', 'strikeonehand HAMMER']	-	Shared	2	20	0	0	0	5	2	
CO5	['touchhand NUT', 'strikeonehand HAMMER']	-	Shared	2	15	0	9	0	0	2	
CO6	['reorient ANVIL', 'place NUT']	-	Shared	2	11	0	0	7	0	2	
CO7	['reorient ANVIL', 'supportfoot ANVIL']	-	Unique	1	0	0	0	5	0	2	
CO8	['grasp NUT', 'place NUT', 'supporthand NUT', 'strikeonehand HAMMER']	-	Unique	1	0	0	0	0	8	4	
CO9	['drop NUT', 'grasp HAMMER']	-	Unique	1	0	0	0	0	6	2	
CO10	['grasp HAMMER', 'drop HAMMER']	-	Unique	1	0	0	13	0	0	2	
CO11	['grasp HAMMER', 'place NUT', 'strikeonehand HAMMER']	-	Unique	1	0	0	7	0	0	3	
CO12	['flip ANVIL', 'place NUT']	-	Unique	1	8	0	0	0	0	2	
CO13	['grasp HAMMER', 'strikeonehand HAMMER', 'drop HAMMER']	-	Unique	1	0	10	0	0	0	3	
CO14	['grasp NUT', 'drop NUT']	-	Unique	1	0	10	0	0	0	2	
CO15	['grasp NUT', 'reorient ANVIL', 'place NUT']	-	Unique	1	0	4	0	0	0	3	
CO16	['reorient ANVIL', 'flip ANVIL']	-	Unique	1	0	0	5	0	0	2	
	Hierarchical Level = 2										
CO17	[['grasp NUT', 'place NUT'], ['grasp NUT', 'place NUT']]	CO1	Shared	3	7	10	0	6	0	4	
CO18	[['grasp NUT', 'place NUT', 'strikeonehand HAMMER'], 'touchhand NUT', 'strikeonehand HAMMER']	CO2*	Shared	2	0	0	0	8	5	5	
CO19	[['grasp NUT', 'place NUT', 'strikeonehand HAMMER'], 'grasp NUT']	CO2	Shared	2	5	0	0	7	0	4	
CO20	[['grasp NUT', 'place NUT', 'strikeonehand HAMMER'], ['grasp NUT', 'place NUT', 'strikeonehand HAMMER']]	CO2	Unique	1	0	0	0	5	0	6	
CO21	['strikeonehand HAMMER', ['grasp NUT', 'place NUT', 'strikeonehand HAMMER']]	CO2	Unique	1	0	0	5	0	0	4	
CO22	['place NUT', ['grasp NUT', 'place NUT']]	CO1	Unique	1	0	0	6	0	0	3	
CO23	[['grasp NUT', 'place NUT'], 'strikeonehand HAMMER']	CO1	Unique	1	0	17	0	0	0	3	
CO24	[['grasp NUT', 'place NUT', 'strikeonehand HAMMER'], ['touchhand NUT', 'strikeonehand HAMMER']]	CO2, CO5*	Unique	1	7	0	0	0	0	5	
CO25	[['grasp NUT', 'place NUT'], 'grasp HAMMER', 'strikeonehand HAMMER']	CO1	Unique	1	0	31	0	0	0	4	
CO26	[['grasp NUT', 'place NUT'], 'supportfoot ANVIL']	CO1	Unique	1	0	5	0	0	0	3	
	Max Hierarchical Level = 3										
CO27	[[['grasp NUT', 'place NUT', 'strikeonehand HAMMER'], 'touchhand NUT', 'strikeonehand HAMMER'], 'touchhand NUT', 'strikeonehand HAMMER']	CO18 (CO1 & CO5)	Unique	1	0	0	0	4	0	7	
CO28	[[['grasp NUT', 'place NUT'], 'grasp HAMMER', 'strikeonehand HAMMER'], 'drop HAMMER']	CO25 (CO1)	Unique	1	0	13	0	0	0	5	
CO29	[[['grasp NUT', 'place NUT'], 'strikeonehand HAMMER'], 'drop HAMMER']	CO23 (CO1)	Unique	1	0	5	0	0	0	4	
CO30	[['grasp NUT', 'place NUT'], [['grasp NUT', 'place NUT'], 'grasp HAMMER', 'strikeonehand HAMMER']]	CO1, CO25 (CO1)	Unique	1	0	6	0	0	0	6	

*Rules CO18 and CO24 contain identical actions, however differ in how they were produced by the compression algorithm. CO18 is made of CO2, which has then been compressed with the actions 'touchhandNUT' and 'strikeonehandHAMMER' (identical actions those that occur in rule CO5). For rule CO24, rules CO2 and CO5 were produced by compression prior to the emergence of rule CO24. Rule CO24 was then produced by compressing these two rules together.

Combining objects contained a total of 30 rules: 16 rules were level one; 10 rules were level two, and four rules were level three. There was one universal rule (CO1), as well as eight shared rules, and 21 unique rules.

One rule contained a unique action: rule CO8 contained the action ‘supporthand NUT’ – this rule occurred 8 times in the sequence of actions used by Tua. The action of supporting the nut by the hand during striking was only seen in one other individual (Fanle, action performed 2 times); however this action was used less frequently compared with Tua (13 occasions). This rule for CO8 is highly similar to the shared rule CO2: ['grasp NUT', 'place NUT', 'strikeonehand HAMMER']. However, in the case of CO8, the additional ‘supporthand NUT’ appears as the third action, producing a 4-gram across one hierarchical level: ['grasp NUT', 'place NUT', 'supporthand NUT', 'strikeonehand HAMMER']. Rule CO2 was seen in the dictionaries of four individuals, including Tua. Thus, the combination of rules CO2 and CO8 in the dictionary of Tua may reflect some behavioural flexibility in nut placement, whereas on rare occasions, Tua uses his hand to hold the nut in position before striking down with the hammer stone.

A similar pattern rules varying due to the presence of a single, central action is seen in three other instances:

(1) Between the shared rule CO3, and the unique rule CO11 (both present in the dictionary for Joya). Often, Joya would grasp a hammer immediately before striking (CO3); however in some circumstances, Joya would grasp the hammer before positioning the nut on the anvil, and then begin striking, indicating a slight variability in the order in which actions were executed.

(2) The universal rule CO1 was combined with a central ‘reorient anvil’ action in rule CO15: ['grasp NUT', 'reorient ANVIL', 'place NUT']. Rule CO15 was confined to the dictionary of Jeje, and was less commonly substituted than CO1.

(3) CO10: ['grasp HAMMER', 'drop HAMMER'] and CO13: ['grasp HAMMER', 'strikeonehand HAMMER', 'drop HAMMER'] differ through the presence of a single ‘strikeonehand HAMMER’ action; however these rules were unique to the dictionaries of different individuals, and thus are less likely to reflect variation in the behaviour of an individual.

Rules CO6, CO7, CO12, and CO16 all involved reorientation of stone tools, and were distributed across the dictionaries of Fanle, Peley and Joya, in the forms of one shared and three unique rules (shared for Fanle and Peley; CO7 for Peley, CO12 for Fanle, and CO16 for Joya).

Four level-one rules were used for the compression of level-two rules:

(1) Two level-two rules involved repetition of a level-one rule (CO17 and CO20).

(2) Two level-two rules had identical action sequences, 'grasp NUT', 'place NUT', 'strikeonehand HAMMER', 'touchhand NUT', 'strikeonehand HAMMER' (CO24 and CO18); however, these rules differed in their hierarchical organisation. CO24 involved the combination of two level-one rules that were already present in the dictionary for Fanle. Whereas in CO18, the rule ['grasp NUT', 'place NUT', 'strikeonehand HAMMER'] was compressed with the actions 'touchhand NUT', 'strikeonehand HAMMER' without these actions being part of a previously compressed rule in the dictionaries for Peley and Tua.

(3) Many of the level-two rules are associated with nuts rolling off of the anvil, and requiring replacement (CO17; CO19; CO20; CO21; CO22). Overall, seven of ten level-two rules were associated with nut positioning on the anvil.

(4) Two rules also include nut repositioning on the anvil, where light ‘touches’ are used between strikes (CO18, CO24).

(5) Rule CO25 includes the universal rule CO1, which is compressed with identical actions to those found in the shared rule CO3: [['grasp NUT', 'place NUT'], 'grasp HAMMER', 'strikeonehand HAMMER']; however similar to the scenario described in (2), this compression occurred in sequences where rule CO3 did not exist, and therefore the actions of ‘grasp HAMMER’ and ‘strikeonehand HAMMER’ are added without their prior combination into a level-one rule.

(6) Rules CO23 and CO26 were produced through the compression of the universal rule, CO1, with another individual action.

CO23 involved the formation of a rule which was identical to the shared rule of CO2; however, in the case of CO23, the actions were split over two hierarchical levels, rather than all contained at the same level in a 3-gram.

Four level-three rules were produced. All level-three rules involved placement of the nut on the anvil, striking with the hammer stone, and either adjusting the position of the nut between strikes, or disposing of hammer stones after striking. Two level-two rules were combined with singular actions to produce a new, level-three rule CO28 & CO29. CO30 involved the compression of two level-two rules.

61 **Table S5. Dictionary rules associated with kernel processing.**

Rule Number	Rule	Contains Rule	Prevalence	No. Individuals with Rule	Substitutions for each individual					Number of Actions within the Rule	Unique Action?
					fl	jj	jy	pe	ta		
	Hierarchical Level = 1										
KP1	['grasp KERNEL', 'eat KERNEL']	-	Universal	5	70	52	32	74	58	2	
KP2	['peelteeth SHELL', 'eat KERNEL']	-	Universal	5	5	56	8	48	44	2	
KP3	['peelteeth SHELL', 'drop SHELL', 'eat KERNEL']	-	Shared	2	0	0	0	6	8	3	
KP4	['peelteeth SHELL', 'eat KERNEL', 'drop SHELL']	-	Shared	2	0	0	10	0	45	3	
KP5	['grasp KERNEL', 'peelteeth SHELL', 'eat KERNEL']	-	Shared	2	21	0	22	0	0	3	
KP6	['peelhand SHELL', 'eat KERNEL']	-	Unique	1	0	0	0	0	10	2	
KP7	['grasp KERNEL', 'drop KERNEL']	-	Unique	1	0	0	0	0	6	2	
KP8	['drop HAMMER', 'peelhand SHELL']	-	Unique	1	0	0	0	0	6	2	
KP9	['drop SHELL', 'eat KERNEL']	-	Unique	1	0	0	7	0	0	2	
KP10	['grasp KERNEL', 'peelteeth SHELL']	-	Unique	1	0	0	0	6	0	2	
KP11	['peelteeth SHELL', 'drop SHELL']	-	Unique	1	0	6	0	0	0	2	
KP12	['grasp KERNEL', 'drop KERNEL', 'grasp KERNEL']	-	Unique	1	0	3	0	0	0	3	
	Hierarchical Level = 2										
KP13	[['grasp KERNEL', 'eat KERNEL'], ['grasp KERNEL', 'eat KERNEL']]	KP1	Shared	4	6	9	0	18	8	4	
KP14	['grasp KERNEL', ['peelteeth SHELL', 'eat KERNEL']]	KP2	Shared	3	0	11	0	14	10	3	
KP15	[['peelteeth SHELL', 'eat KERNEL'], ['peelteeth SHELL', 'eat KERNEL']]	KP2	Shared	2	0	0	0	6	5	4	
KP16	[['peelteeth SHELL', 'eat KERNEL'], 'drop SHELL']	KP2	Shared	2	0	25	0	10	0	3	
KP17	[['grasp KERNEL', 'peelteeth SHELL', 'eat KERNEL'], 'drop SHELL']	KP5	Shared	2	6	0	6	0	0	4	
KP18	[['peelteeth SHELL', 'eat KERNEL'], ['peelteeth SHELL', 'eat KERNEL', 'drop SHELL']]	KP2,KP4	Unique	1	0	0	0	0	12	5	
KP19	['grasp KERNEL', ['peelteeth SHELL', 'eat KERNEL', 'drop SHELL']]	KP4	Unique	1	0	0	0	0	6	4	
KP20	[['grasp KERNEL', 'eat KERNEL'], 'grasp KERNEL']	KP1	Unique	1	0	6	0	0	0	3	
KP21	[['grasp KERNEL', 'eat KERNEL'], 'drop SHELL']	KP1	Unique	1	0	6	0	0	0	3	
	Max Hierarchical Level = 3										
KP22	[[['grasp KERNEL', 'eat KERNEL'], ['grasp KERNEL', 'eat KERNEL']], ['grasp KERNEL', 'eat KERNEL']]	KP1	Unique	1	0	0	0	5	0	6	
KP23	['grasp KERNEL', [['peelteeth SHELL', 'eat KERNEL'], 'drop SHELL']]	KP16 (KP2)	Unique	1	0	10	0	0	0	4	
KP24	[['peelteeth SHELL', 'eat KERNEL'], [['peelteeth SHELL', 'eat KERNEL'], 'drop SHELL']]	KP2, KP16 (KP2)	Unique	1	0	5	0	0	0	5	

62

When organizing rules into hierarchical levels, 12 rules were level one, eight were level two, and three were level three. Two universal rules were included in the category kernel processing, including KP1 & KP2. Two rules included an action which was unique to the dictionary for Tua: 'peelhand SHELL' (rules KP6 & KP8). This may reflect Tua's more frequent use of his hands to peel shells from kernels compared with other individuals. The action 'peelhand SHELL' was also observed in the first 900 actions of Peley (3 times), Jeje (11 times, and 4 times outside of this range), and Joya (10 times). However, for Tua, peelhand SHELL was observed 25 times in his first 900 actions, and 24 times outside of this range. Other than KP6 and KP8, the other 24 rules reflect combinations of a small number of actions, including grasping kernels, peeling shell from kernels with the teeth, dropping shells and kernels, and consuming kernels.

For two pairs of rules, identical subsequences of actions were identified in each pair, however the order in which they were compressed differed. For one rule in the pair, three actions were compressed simultaneously, whereas in the other rule, a shorter rule was initially compressed, before being compressed with the third action, recreating an identical rule over two hierarchical levels. This can be seen in the pair KP5 and KP14. In KP5 (seen in the dictionaries of Flanle and Joya), the actions of grasping a kernel, peeling off a fragment of shell, and eating a kernel are all compressed as a 3-gram with across one hierarchical level; whereas in KP14 (seen in the dictionaries of Jeje, Peley and Tua), the universal rule of peelteeth SHELL and eat KERNEL is compressed with an antecedent 'grasp KERNEL', producing the same subsequence of actions spanning over two hierarchical levels. This is also seen in the action pair KP4 and KP16, where in the instance of KP16, the universal rule [peelteeth SHELL, eat KERNEL] is compressed with the subsequent action 'drop SHELL'; however in the rule KP4, all three actions form one 3-gram across a single hierarchical level.

In addition to pairs of identical subsequences, some rules involved reordering of the same actions. For example, the rules KP3 and KP4 involve the same three actions; however, in KP3, the shell is dropped before the kernel is consumed, whereas in KP4, the kernel is consumed prior to the shell falling from the hand. We believe it to be unlikely that this particular difference represents a notable behavioural distinction within an individual's approach to nut cracking.

Two rules were almost identical to other rules, except for the addition of a central action. Rule KP5 mirrored the universal rule KP1, but with the addition of a single action where the shell is peeled

away from the kernel with the teeth. Additionally, rule KP3 was similar to the universal rule KP2, but with a central action where the shell is discarded by being dropped to the ground.

Two level-two rules were produced by repetition of level-one rules (KP13 and KP15). Four rules involved the combination of a level-one rule with a single action (KP14, KP17, KP19, KP20, KP21). One rule, KP18, involved the combination of two level-one rules into a new rule.

For the three rules with three hierarchical levels, one rule involved the repetition of grasping and eating pieces of kernel (KP22). One rule (KP23) included the compression of an existing level-two rule with an antecedent action ‘grasp KERNEL’; however, this rule was an identical action sequence to rule KP19, which spanned two hierarchical levels. The final level-three rule involved compression of a level-two repetition of the actions ‘peelteeth SHELL, eat KERNEL’ with the subsequent action of dropping a piece of shell.

Table S6. Dictionary rules which span multiple categories.

Rule Number	Rule	Contains Rule	Prevalence	No. Individuals with Rule	Substitutions for each individual					Number of Actions within the Rule	Unique Action?
					fl	jj	jy	pe	ta		
	Hierarchical Level = 2										
CO-KP1	[['grasp NUT', 'place NUT', 'strikeonehand HAMMER'], ['grasp KERNEL', 'eat KERNEL']]	CO2, KP1	Shared	3	30	0	0	12	17	5	
CO-KP2	[['grasp NUT', 'place NUT', 'strikeonehand HAMMER'], 'grasp NUT', 'peelteeth SHELL', 'eat KERNEL']	CO2	Unique	1	5	0	0	0	0	6	
CO-KP3	[['grasp NUT', 'place NUT', 'strikeonehand HAMMER'], 'grasp KERNEL', 'drop KERNEL']	CO2	Unique	1	3	0	0	0	0	5	
CO-KP4	[['grasp NUT', 'place NUT', 'strikeonehand HAMMER'], ['grasp KERNEL', 'peelteeth SHELL', 'eat KERNEL']]	CO2, KP5	Unique	1	5	0	0	0	0	6	
	Max Hierarchical Level = 3										
CO-KP5	[[['peelteeth SHELL', 'eat KERNEL'], ['peelteeth SHELL', 'eat KERNEL', 'drop SHELL']], 'grasp HAMMER', 'place HAMMER', ['grasp NUT', 'place NUT', 'strikeonehand HAMMER']]	KP18 (KP2,KP4), CO2	Unique	1	0	0	0	0	3	10	
CO-KP6	[['grasp KERNEL', 'eat KERNEL'], [['grasp NUT', 'place NUT', 'strikeonehand HAMMER'], ['grasp KERNEL', 'eat KERNEL']]]	KP1, CO-KP1(CO2, KP1)	Unique	1	7	0	0	0	0	7	

Six rules involved the compression of subroutines of actions associated with both the combination of objects, as well as the processing of kernels (CO-KP). Four rules were level-two, and two were level three.

One rule involved the compression of an existing CO-KP rule with the universal rule [‘grasp KERNEL’, ‘eat KERNEL’] (CO-KP6). All rules included the nested rule CO2.

Most rules were unique to the dictionary of Flanle (4/6 rules). One rule was unique to the dictionary of Tua (CO-KP5), and one rule was shared across the dictionaries of Fanle, Peley and Tua (CO-KP1).

Chapter 4

Exploration and Pruning of Action Repertoires During the Development of Chimpanzee Tool-Use

4.1 Abstract

Apes habitually perform a wide variety of tool-use behaviours in the wild, with each behaviour requiring individuals to learn and combine sets of fine-grained actions. Despite evidence that tool-use behaviours are socially transmitted between individuals within communities of wild apes, apes are limited in the extent to which they can imitate sequences of actions performed by others. Instead, apes appear to copy the goals of the behaviours of others (emulation), and must therefore address these aims using independently innovated sequences of actions. However, the pathways through which apes acquire the correct actions to facilitate tool-use in the wild are not clearly understood. We present longitudinal data on the action repertoires of six wild chimpanzees between the ages of one and eight years old, as they learn how to perform a naturally occurring tool-use behaviour - the cracking of hard-shelled nuts with hammer and anvil stones (nut cracking). We report that, as chimpanzees develop tool-use behaviours, the number of actions (and the number of objects actions are performed on) is higher than that of proficient adults, and peaks at the age at which nut cracking is first observed being successfully performed. Following the age at which the skill of nut cracking is acquired, the repertoire size reduces across subsequent years, including into adolescence. We argue that the growth of action repertoires up until the acquisition of nut cracking, and their decay following successful acquisition of this behaviour, are indicative of complementary processes of exploration and pruning. We also report that striking, a key action in nut cracking, emerges early in the repertoires of learners, and at a higher frequency than other methods to exert force. We discuss both of these results in tandem, with specific consideration of a largely asocial process of repertoire acquisition, which is possibly guided by the transmission of particularly frequent and salient actions from experienced individuals to learners.

4.2 Introduction

The repeatable ecological challenges that wild animals encounter can be thought of as recurring tasks (e.g. feeding, navigating, communicating, etc.), and, in the absence of genetically preprogramed behaviours, animals must generate, evaluate and remember effective solutions to such tasks to maximise their fitness. Understanding how animals acquire, refine and store behavioural solutions to recurrent natural tasks is a long-held point of scientific interest (Byrne and Russon, 1998; Dawkins, 1976; Lashley, 1951; Thorndike, 1927). This is particularly true for tasks which involve the organisation of numerous actions into elaborate sequences of behaviours (Dawkins, 1976; Lashley, 1951; Whalen et al., 2015), or involve the manipulation and direction of multiple objects towards a specific target, such as in the case of tool-use (Seed and Byrne, 2010). For behaviours which demand longer sequences of actions, naïve individuals are faced with a number of possible behavioural sequences, that grows supra-exponentially with each additional sequence element, and are challenged with finding the appropriate solution (Whalen et al., 2015). This issue of divining improbable solutions is further compounded by the addition of increasing numbers of objects to behavioural tasks – such as in the case of elaborate tool-use behaviours – where each added object increases the number of possible combinations of objects across space and time, thus increasing the complexity of action organisation (Matsuzawa, 1996). Research into how animals learn and refine solutions to naturally occurring tasks, including those which involve the production and use of tools, is therefore central to understanding how animals produce complex responses to ecological challenges.

Numerous taxa have been documented producing and using tools (Shumaker et al., 2011), and of these groups, the tool-use behaviours of non-human primates (henceforth primates) have been the subject of long-term scientific investigation (Boesch and Boesch, 1990; Chiang, 1967; Goodall, 1964; Matsuzawa, 1994; Ohashi, 2006; Ottoni and Izar, 2008; Sanz and Morgan, 2010; Tan et al., 2015; Van Schaik et al., 1999). Non-human apes (henceforth apes) are renown for exhibiting a number of tool-use behaviours in the wild, especially in the cases of chimpanzees (*Pan troglodytes*) (Boesch and Boesch, 1990; Ohashi, 2006; Sanz and Morgan, 2010) and orangutans (*Pongo* spp.) (Meulman and Van Schaik, 2013; Van Schaik et al., 1996). Both produce and use a wide variety of tools from vegetation, and in the particular case of chimpanzees, multiple populations engage in the use of stone tools (Biro et al., 2003; Boesch and Boesch, 1990; Carvalho and McGrew, 2012; Matsuzawa, 1994). The tool-use behaviours of apes are embedded

within wider operation chains (the *chaîne operatoire*), where individuals must acquire tool objects (including the possible production of tools from raw materials); combine tool objects and substrates, and dispose of tools and waste products following tool-use (Byrne et al., 2013; Carvalho et al., 2008; Sanz and Morgan, 2010). Additionally, many of the tool-use behaviours of apes require individuals to combine multiple different objects, either consecutively or all at once (Matsuzawa, 1996; Sanz and Morgan, 2010). Thus, the tool-use behaviours of apes reflect a complex form of non-human technology.

In addition to their complexity, the tool-use behaviours of apes are also of particular interest as they are central to an on-going debate around culturally transmitted behaviours in primates (Biro et al., 2006, 2003; Boesch et al., 2020; Byrne, 2007; Gruber et al., 2009; Hopper et al., 2007; Koops et al., 2023, 2022; Tennie et al., 2020, 2009; Tennie and Call, 2023; Whiten, 2017; Whiten et al., 2001, 1999). Under the theory of culturally maintained tool-use behaviours, population-level differences in both whether and how apes perform tool use is theorised to be driven through the social transmission of strategies between individuals (Biro et al., 2003; Boesch et al., 2020; Gruber et al., 2015; Matsuzawa, 2001). Apes demonstrate a number of sensitivities to the behaviours of conspecifics when solving novel tasks, such as the copying of end-states of behaviours (goal emulation), possibly including subgoals of behaviours, and the order in which sub-goals must be achieved (program-level imitation) (Byrne and Russon, 1998; Call et al., 2005; Horner and Whiten, 2005; Tennie et al., 2010; Tomasello, 1990), as well as the ability to socially acquire information surrounding both which objects may be used as tools, and which substrates represent profitable targets for tool-use (Biro et al., 2003; Myowa-Yamakoshi and Matsuzawa, 2000, 1999). Several studies have also reported that apes are able to imitate a small number of fine-grained actions following frequent presentation by demonstrators (Custance et al., 1995; Horner and Whiten, 2005; Stoinski et al., 2001; Whiten et al., 1996); possibly reflecting some form of limited, fine-grained action imitation. However, the extent to which apes attend to and imitate even small numbers of actions is still unclear, with several other studies reporting that imitation was not a behaviour readily exhibited by apes under similar experimental paradigms (Hayashi et al., 2005; Stoinski et al., 2001; Subiaul, 2016; Tennie et al., 2012, 2010). Ultimately, whilst the ability for apes to imitate individual or short sequences of actions remains ambiguous, it is unlikely that naïve individuals are able to acquire solutions to tool-use tasks through the imitation of extended action sequences demonstrated by knowledgeable individuals (Hoppitt and Laland, 2013; Whalen et al., 2015).

If apes are not able to imitate the extended sequences of actions used by skilled individuals during tool use, naïve individuals are therefore presented with the challenge of generating and refining successful sequences through predominantly asocial means; this process may be scaffolded by selective forms of social learning, such as goal emulation (including possibly the order of subgoals), stimulus enhancement, or possible copying of isolated, utile actions. The complexity of action sequences for tool use means that sequences are unlikely to be innovated in one or a small number of steps, but rather gradually developed and refined piecemeal over time (Whalen et al., 2015). Therefore, understanding how naïve apes identify appropriate actions for tool use, and construct actions into complex sequences, is central to understanding the endurance of such complex wild behaviours.

We hypothesise that naïve apes may acquire action repertoires for tool use through a process of exploration and pruning. During pathways of exploration and pruning, naïve individuals begin the learning process by experimenting with a growing number of different actions and action combinations (exploration phase). Actions which assist individuals in realising the goals of their behaviour are consequently strengthened and elicited more frequently, whereas actions which fail to address the aims of a behaviour are performed increasingly less frequently, until they are ultimately 'pruned' from the repertoire. Thus, exploration and pruning lead to an initial expansion in repertoire size, which exceeds that of mature repertoires, before reducing down to similar sizes to those observed in experienced individuals. Conversely, this process of expansion and reduction is not predicted under scenarios where individuals are able to copy extended sequences of actions from conspecifics, where individuals may begin performing a behaviour with a socially acquired, 'prepared' repertoire of actions. Under such a scenario, repertoires should rapidly rise to a similar size to experienced individuals, and remain steady over time.

Previous research has suggested that exploration and pruning are likely mechanisms for the acquisition of action sequences for tool-use (Biro et al., 2006, 2003; Inoue-Nakamura and Matsuzawa, 1997); and much of this evidence has come from the study of chimpanzee stone-tool use behaviours. However the precise dynamics of this developmental process require further clarification. For example, a study of the development of chimpanzee nut cracking at Bossou (a behaviour where chimpanzees crack open hard-shelled nuts using stone tools), reported that, for three chimpanzees between the ages of 0.5 and 3.5 years, chimpanzees perform increasingly complex combinations of actions and objects, many of

which are not functionally useful in the context of cracking nuts with hammer stones (e.g. mouthing on uncracked nuts and stones; Inoue-Nakamura and Matsuzawa, 1997). Additional research from the Bossou community reveals that, following the acquisition of nut cracking, chimpanzees become successively more skilled at cracking nuts with the hammer stone, and in adulthood, are able to crack open nuts using fewer blows of the hammer (Biro et al., 2006, 2003), and a similar result is found for the development of nut cracking behaviours by chimpanzees at Tai (Ivory Coast; Boesch et al., 2019).

Both of these factors suggest that, to acquire a tool-use skill such as nut cracking, chimpanzees first use a process of exploration of different actions, and once a skill is acquired, they refine their solutions through pruning, as they iteratively engage in the behaviour. However, previous descriptions of how action repertoires change during nut cracking development cease at the point at which the skill is 'learnt' (around 3.5 years; however for some chimpanzees, this can be as late as seven years old; Matsuzawa, 2011); and whilst chimpanzees become increasingly more efficient in their striking actions with age, it is unclear whether, and if so, how action repertoires are refined to increase efficiency across the entire *chaîne operatoire*. Characterizing how action repertoires change during a wider developmental window – including post-infancy, and following the acquisition of nut cracking – will therefore provide further clarity on this matter.

To fill this knowledge gap, we herein present data on the development of action-repertoires of wild West-African chimpanzees (*Pan troglodytes verus*) used in nut cracking, across an extended developmental window of 1 to 8 years old. Nut cracking is performed by individuals from a small number of wild chimpanzee populations (Biro et al., 2003; Boesch and Boesch, 1990; Carvalho and McGrew, 2012; Matsuzawa, 1994; Ohashi, 2006), with multiple lines of evidence supporting that this behaviour is culturally transmitted through interactions between naïve and skilled individuals (Biro et al., 2006, 2003; Hayashi et al., 2005; Koops, 2020). The process of nut cracking varies between chimpanzee populations, e.g. the chimpanzees of the Bossou forest are unique in their use of portable anvil stones to crack open nuts, whereas other populations rely on immovable anvils (Biro et al., 2006, 2003; Inoue-Nakamura and Matsuzawa, 1997). Among all wild chimpanzee tool-use behaviours, nut cracking is considered to be one of the most complex, as it requires the simultaneous combination of the greatest number of objects at any one time (Matsuzawa, 1996). Experienced nut crackers at Bossou (including many adult, subadult, and

adolescent individuals) are able to successfully complete nut cracking behaviours through the use of a small number of highly frequent actions, which are common across individuals (Howard-Spink et al., in review), suggesting that solutions to tasks are highly similar across individuals, but with a small amount of variation between individuals in how supplementary subroutines of behaviour are employed (see chapter 3). Nut cracking therefore provides an excellent opportunity to study the acquisition of sequential actions to address a complex and culturally scaffolded task in the behaviours of apes.

We longitudinally sampled the action repertoires of six chimpanzees at Bossou between birth and eight years of age – including both the actions used by individuals and the objects manipulated by individuals for each action – and compared both the size and composition of repertoires at each age. We predicted that, if chimpanzees develop repertoires through a process of exploration and pruning, then the repertoire sizes should be higher for individuals who have yet to successfully acquire nut cracking behaviours (reflecting an exploration phase), and once the behaviour is successfully acquired, repertoire sizes should decrease as chimpanzees refine and streamline their behaviours through iterative engagement with nut cracking (pruning phase). We also compare the sizes and composition of repertoires with those of experienced nut crackers (adolescent, subadult, and adult individuals who have previously learnt how to crack nuts using stone tools) to investigate whether the repertoire of individuals at the end of the juvenile phase (eight years old) has developed into a fully matured repertoire, and also to determine when actions and action-object combinations that are frequently performed by experienced individuals emerge in the repertoires of learners.

We report that, for both actions and action-object combinations, the repertoires of chimpanzees undergo a process of expansion and reduction, peaking at the age learners are first observed cracking open nuts using stone tools. Additionally, naive learners exhibit a number of different actions and action-object combinations which are not observed in the repertoires of experienced individuals during nut cracking; however, one of the most frequent actions performed by experienced individuals (striking downwards with a hammer stone) emerged early in the repertoire of learners, including at ages which preceded the acquisition of nut cracking by several years (a result which differs from previous descriptions of this developmental process; Inoue-Nakamura and Matsuzawa, 1997). We present these findings as evidence of a predominantly asocial process of action-repertoire development for chimpanzee tool use;

however, we also discuss possible scenarios of how social observation may influence the exploration and pruning of action repertoires during tool-use acquisition.

4.3 Methods

4.3.1 Study site and data archive

Bossou-Nimba (07° 390' N; 008° 300' W) is one of a small number of field sites focused on research and the conservation of wild West-African chimpanzees (Matsuzawa et al., 2011). Longitudinal research of the Bossou community commenced in 1976, and is ongoing as of 2023. The chimpanzees at Bossou share a home range of approximately 5-6 km^2. During the period of longitudinal research of chimpanzees at Bossou, the community size has greatly reduced from a previously stable size of around 20 individuals, down to four individuals in 2023.

Chimpanzees at Bossou habitually employ a diverse array of tool-use behaviours (Humle, 2011), including those involving plant-based tools (e.g. algae-scooping, ant-dipping, pestle-pounding and leaf-sponging; Humle and Matsuzawa, 2002; Tonooka, 2001; Yamakoshi and Sugiyama, 1995), and stone tools for nut cracking (Biro et al., 2006, 2003; Carvalho et al., 2008; Inoue-Nakamura and Matsuzawa, 1997; Matsuzawa, 1994). Of all tool-use behaviours exhibited by chimpanzees at Bossou, nut cracking is the most complex, as it involves the greatest number of tool objects which must be simultaneously oriented towards a given target (i.e. a nut is placed on an anvil stone [tool 1] before being struck by a hammer stone [tool 2]) (Matsuzawa, 1996).

The nut cracking tool-use behaviours of the Bossou chimpanzees have been studied for several decades through the use of an outdoor laboratory (Biro et al., 2006, 2003; Carvalho et al., 2008; Matsuzawa, 1994). Established in 1988, the outdoor laboratory is a natural clearing in the forest (approx. 7 x 20m), where chimpanzees are presented with piles of oil-palm nuts (*Elaeis guineensis*; a species of nut which occurs naturally within the home range of the Bossou chimpanzees and is the only species cracked by the Bossou community), in addition to the occasional provisioning of coula and panda nuts (*Coula edulis* and *Panda oleosa*; both cracked by chimpanzees at other sites), as well as a selection of approx. 50 stones to be used as hammer and anvil tools. Nuts are provided in a number of piles around the clearing (typically 6-12 piles of 40-50 oil-palm nuts), and in the middle of the clearing, stone tools are placed in a central matrix

in a randomised configuration (see Fig. S1 for diagram of the experimental set-up at the outdoor laboratory). The outdoor laboratory is open to chimpanzees during the dry season (approx. November-February). Chimpanzees are able to enter the outdoor laboratory on three sides of the clearing, and on the fourth side, researchers record the behaviours of chimpanzees from behind a screen of palm fronds using video cameras. In 2011, a second outdoor laboratory was opened in a separate clearing in the Bossou forest; however, the experimental set-up remained identical to the original.

Video footage of chimpanzees engaging in nut cracking at the outdoor laboratory between 1988 and 2023 has recently been collated into a longitudinal video archive (the Bossou Archive; Schofield et al., 2019), with additional years being added as data collection continues at Bossou. The recent production of a longitudinal video archive has permitted researchers to track how individual chimpanzees engage in nut cracking over a period of many years, including the development of nut cracking behaviours during the period between infancy and adulthood.

4.3.2 Sampled individuals: between one and eight years of age

To collect data on how repertoires of actions develop, we collected action sequence data from all individuals whose ages spanned from one to eight years of age (one year into infancy, to end of the juvenile stage) between the 1996 to 2018 sample window (six individuals in total; four males, two females). We chose this window as, for the chimpanzees at Bossou, nut cracking is a behaviour which is acquired between 3 and 7 years of age (Matsuzawa, 2011). Additionally, previous research into the development of actions repertoires for nut cracking at Bossou was conducted between 1992 to 1995, and therefore commencing sampling in 1996 allowed us to collect data on six new individuals. Our study therefore raises the descriptions of action repertoire development from three individuals, to nine.

We first attempted to sample the first 500 actions used by each individual for each field season as individuals aged from one to eight years old (see *Behaviour Coding*). However, an initial period of data collection revealed that for many years, this target exceeded the number of observable actions available for many individuals. Thus, we reduced this target down to the first 400 actions performed by each individual in each year. We sampled videos from the archive chronologically during each field season, and sampled

data for each individual if they were present in a sampled video, and interacted with nuts, nut fragments (i.e. shell or kernel), or stone tools.

To estimate the age at which each individual had successfully acquired nut cracking, we recorded the age of each individual during the field season in which they were first observed to successfully crack open nuts with stone tools. The exact point at which individuals acquired nut cracking may have occurred before this point, as nut cracking is a behaviour habitually performed by the chimpanzees at Bossou outside of the active field seasons at the outdoor laboratory. However, by estimating the age at which nut cracking is acquired using field seasons, we were still able to parse data into repertoires collected 'before' and 'after' each individual learnt how to successfully crack open nuts using stone tools.

4.3.3 Sampled individuals: experienced tool-users

To understand how chimpanzees who were experienced in nut cracking performed this behaviour, we sampled the first 400 actions used by all experienced tool-users in the years 1999, 2004, 2008, and 2012. We define experienced tool-users as those individuals who are older than eight years old (and thus, have reached adolescence, sub adulthood, or adulthood) and, prior to this age, had successfully learnt how to crack nuts with stone tools.

4.3.4 Behaviour coding

To code the actions used by focal individuals during each field season, we used an ethogram adapted from previous studies investigating the nut cracking behaviours of chimpanzees at Bossou (Inoue-Nakamura and Matsuzawa, 1997; Howard-Spink et al, in review). We included 34 distinct action types in the ethogram (see Table S1), and, where relevant, we coded each action along with one of five possible corresponding suffixes, which indicated if objects were manipulated as part of the action, including: 'Stone', 'Nut' (uncracked), 'Shell' (defined as inedible parts of cracked nuts); 'Kernel' (defined as the edible interior fragments of a cracked nut); and when no object was used, we included 'Hand' to reflect an action was performed in the absence of an object (e.g. when an individual strikes downwards using an open palm). In contrast to previous studies of nut cracking behaviours which focussed primarily on the behaviours of adults (Howard-Spink et al, in review), we included both hammer and anvil tools as simply 'Stones', as for

individuals who are inexperienced or naïve to nut cracking, stone tools lack the consistent functional distinction to be clearly labelled as either hammer or anvil (Myowa-Yamakoshi and Yamakoshi, 2011). One action, 'relocate', indicated that individuals moved across the outdoor laboratory during a continuous period of engagement with nuts and stone tools (e.g. when moving from one set of tools to another), and was the only action to be systematically coded without an object suffix.

The coding of actions alongside corresponding objects allows for the behaviour of individuals to be characterised by both the function of the action performed by an individual (e.g. Grasp), with the additional option to include the target of the action (e.g. Stone) to produce a unitary description of both the operation performed by an individual, as well as the object manipulated by a given operation (e.g. 'Grasp Stone'). For our analysis, we analysed both the unique types of actions used by focal individuals (e.g. 'Grasp', 'Drop', 'Strikeonehand', etc.) as well as the unique action-object combinations recorded (e.g. 'Grasp Stone', 'Drop Nut', 'Strikeonehand Hand', etc.).

Behaviour coding commenced when an individual began interacting with nuts, nut fragments (i.e. pieces of shell or kernel), or stone tools. Behaviour coding ceased when an individual stopped engaging with nuts or stone tools to engage in another behaviour (e.g. grooming, eating oil-palm fruits, etc.); dropped all relevant objects and rested for longer than one minute; or if they became obstructed from clear view in the video (e.g. through the camera panning away from an individual, or if another individual sat in the direct line of site of the focal individual, thus obstructing observation of their actions). If behaviour coding ceased when an individual was no longer clearly visible, coding recommenced when that individual returned into clear view, so long as they were still interacting with tool objects, nuts or nut fragments.

Behaviour coding was conducted by EHS (archive years 2008, 2009 and 2012), MB (1997-1999, 2001-2004), AA (2005, 2008, 2010, 2014-2018) and JH (2007 and 2013). No data was collected for the years 2000 and 2006, as, due to an outbreak of Ebola, and year of political instability in guinea, these field seasons were not conducted. All behaviour coding was performed using BORIS (Friard and Gamba, 2016), and during behaviour coding, videos were visualised on monitors that were between 13" and 15" in diagonal length. To ensure that observers were coding behaviours consistently, all observers completed an inter-observer reliability exercise, which involved all observers coding a five-minute clip of an encounter from the 2012 field season. Observers coded all actions performed by all individuals during this encounter. Pairwise

comparisons of sampled coded behaviours by the four observers revealed that observers had a mean agreement across 76% of actions, and 75% of action-object combinations (see supplementary materials for further information on how inter-observer reliability was calculated across all four observers).

4.3.5 Repertoire size: actions and action-object combinations

At each age between one and eight years old, we counted the total number of unique actions and action-object combinations performed by individuals within their first 400 actions. If the total number of actions sampled for individuals at a certain age was fewer than 400, we omitted data for that individual at that particular age from our analysis. This allowed us to sample repertoire sizes using a standardised number of actions from each individual at each age. We then compared the total size of the repertoire (including actions and action-object combinations) across individuals at each age between one and eight years old.

Chimpanzees at Bossou vary in the age at which they successfully acquire the skill of nut cracking (between approx. 3.5 and 7 years old). To control for this difference, we also compared repertoire size at ages which were standardised to the age at which individuals were first observed to crack open a nut using stone tools. Standardised ages were calculated by taking the age at which an individual was first observed to successfully crack open a nut (e.g. 4 years old) and subtracting this age from all ages between 1 and 8 to produce a 'relative' age (e.g. 3-4 = -1, therefore, for this hypothetical individual, 3 years old is equivalent to -1 years from the age at which they were first observed successfully cracking nuts using stone tools).

We also compared whether individuals established a repertoire size which was similar to those of experienced chimpanzees. The number of actions and action-object combinations used by each experienced individual during their first 400 actions was counted in the years 1999, 2004, 2008 and 2012, and the mean repertoire size was estimated across experienced individuals within each year. To estimate overall mean repertoire size across years for experienced individuals, we took the means from each year, and calculated an average to produce a single mean-of-means, with accompanying standard error (*SE*) for the mean between years (estimated through the normal approximation for Poisson distributed data: $\lambda/\sqrt{n}$, where λ is the mean, and n = 4). This mean and standard error were used to produce a 95% confidence interval (CI) for the mean repertoire size for experienced individuals in each year, where we estimated $CI_{95\%}$ using the 'mean of means' $\pm$ 1.96 times the standard error.

4.3.6 Actions and action-object combinations within repertoires

To characterise which actions individuals employ as they acquire the repertoire of actions for nut cracking, we calculated the rate at which individuals perform different actions and action-object combinations at the ages between one and eight years old. To estimate these rates, we first counted the total number of unique actions and action-object combinations performed by all individuals across all years (including all individuals above and below the age of eight years). This allowed us to produce a list of all observed actions and action-object combinations from our sampled data. Using the data collected from each individual, for each age that they were sampled, we calculated the proportion of actions performed by that individual which belonged to each unique type of action, and calculated the same for all sampled action-object combinations, using the formula:

$$(1)\ \ p(A) = \frac{n_a}{N_i}$$

where p(A) is the proportion of the total corpus of data sampled for an individual at a given age that is made up of a specific action or action-object combination; n_a is the number of times a specific action or action-object combination was recorded for an individual at that age, and N_i was the total number of actions sampled from an individual at a given age. We used all available actions coded for each individual at each age, up to a maximum of 400 individual actions.

As well as estimating how repertoires change for individuals, we also compared data across individuals during the years before and after the age they were first observed successfully cracking open nuts with stone tools. We standardised ages in the same way as we did for the repertoire analysis, and pooled all actions sampled from all individuals at each standardised age. We then calculated the proportion of each action type, and each action-object combination, in the pooled corpus as each standardised age, using the equation:

$$(2)\ \ p(A) = \frac{\sum n(a)}{N_{Age}}$$

where N_{Age} is the total corpus size for a standardised age, and $\sum n(a)$ relates to the total number of times a given action, or action-object combination, occurred across all individuals in this age category.

We compared these proportions to the rate at which experienced individuals performed different actions and action-object combinations. We took the first 400 actions performed by each experienced

individual in the 1999, 2004, 2008, and 2012 field seasons. We estimated the rate at which different actions and action-object combinations were performed by each of these individuals using the same method as for individuals below the age of eight years old (see equation 1), but with N_i representing the total corpus size for an experienced individual in one of the four sampled years. We also estimated the rate at which actions and action-object combinations were performed across all experienced individuals in each year (a metric for how frequently different behaviours were performed in the environments of individuals below the age of eight). We pooled the total number of instances each action and action-object combination occurred within the sampled data for all experienced individuals within a given year, and calculated the proportion of sampled data which belonged to each unique type of action and action-object combinations using a similar equation to equation 2:

$$(3)\ \ p(A) = \frac{\sum n(a)}{N_{Year}}$$

where N_{year} is the total number of actions or action-object combinations sampled across all experienced individuals in a given year, and $\sum n(a)$ relates to the total number of times a given action, or action-object combination, occurred across all experienced individuals in that year.

4.4 Results

Between the years 1996 and 2018, we sampled 13,804 individual actions and action-object combinations performed by six chimpanzees between the ages of one and eight years of age (see Table 1 for summary of sampled data for each individual at each age). For these individuals, the age at which nut cracking was first observed varied between three and seven years of age. We also sampled 11,515 actions and action-object combinations from 11 individuals above the age of eight years old across the years 1999, 2004, 2008, and 2012 (sample size of actions and action-object combinations across all individuals per year: mean = 2879, SD = 673; number of individuals sampled per year: mean = 8; SD = 1.6; see Table S4 for summary of sampled data for individuals over eight years old).

Across all individuals both above and below the age of eight years, we recorded a total of 34 unique actions, and 87 unique action-object combinations (see Figs. 2 & 3).

4.4.1 Repertoire size

Across individuals, the sizes of the repertoires of actions and action-object combinations increased across the first few years of life, with the median (M) number of unique actions and action-object combinations in the repertoire of sampled individuals reaching a peak at between three and five years old, before undergoing a reduction over subsequent years (Actions: $M_{one-year}$= 20.5, $M_{three-years}$= 25, $M_{eight-years}$= 19; Action-Object Combinations: $M_{one-year}$= 30, $M_{five-years}$= 31, $M_{eight-years}$= 25.5; see Fig. 1a and Table 2).

When standardising the ages of individuals relative to the age at which they were first observed successfully cracking open nuts using stone tools, the median number of unique action types peaked at the age individuals were first observed cracking nuts ($M_{-5} = 18, M_0 = 22, M_{+5} = 19$), as did the median number of unique action-object combinations across the repertoires of individuals ($M_{-5} = 24, M_0 = 32, M_{+5} = 25$, see Fig. 1b and Table 2).

The mean repertoire size of experienced individuals was stable across years for both actions (mean = 13.4 actions; 95% CI_{upper} = 15.4; CI_{lower} = 11.4), and action-object combinations (mean = 20.6 action-object combinations; 95% CI_{upper} = 23.2; CI_{lower} = 17.9). Of all individuals below the age of eight, only one individual, Fanwaa, exhibited a repertoire size which was contained within the 95% CI for experienced individuals, and this was only the case for the final age at which data was collected for Fanwaa (seven years old; +3 years from first observed nut crack). For all other individuals, the repertoire size at the maximum age sampled between 1 and 8 years old remained higher than the 95% confidence interval for experienced individuals, and this trend applied to both the number of actions and action-object combinations.

Three individuals for whom we sampled data between the ages of 1 and 8 years were also sampled again at ages older than 8 years old, as these individuals were sampled as part of the experienced cohort in the 2008 and 2012 field seasons (Fanle, Jeje and Peley, whose ages were 11, 11, and 10 years, respectively, in 2008, and 15, 15, and 14 in 2012). For two of these individuals (Fanle and Jeje), repertoire sizes were highly similar to other experienced individuals (a cohort of almost exclusively adults) when sampled in 2008 and 2012 (action repertoire size; mean for experienced individuals: 2008 = 12.4, 2012 = 14.8; Fanle: 2008 = 12, 2012 = 11; Jeje: 2008 = 10, 2012 = 13; repertoire size for action-object

combinations; mean for experienced individuals: 2008 = 18.9, 2012 = 24.5; Fanle: 2008 = 17, 2012 = 17; Jeje: 2008 = 16, 2012 = 23). This similarity extended to the mean number of actions and action-object combinations performed by experienced individuals in 1999 (mean action = 12.9; action-object combinations = 20.3) and 2004 (actions = 13.3; action-object combinations = 18.5), confirming that the similarity in repertoire size between Fanle and Jeje, and all other experienced individuals, was not an artefact of their data being used to estimate mean repertoire sizes across experienced individuals in 2008 and 2012 (see Tables S5 and S6 for repertoire sizes of experienced individuals across sampled years). The third individual who aged into the 'experienced' category – Peley – still demonstrated repertoire sizes which were comparatively larger than other experienced individuals when sampled at ages above eight years old (actions: 2008 = 17, 2012 = 19; action-object combinations: 2008 = 27, 2012 = 33).

4.4.2 Actions and action-object combinations within repertoires: experienced individuals

Experienced individuals performed nut cracking through the use of approximately six highly frequent actions, supplemented by a small number of less frequent actions. The most frequent actions performed by experienced individuals were striking with the stone using one hand (Strikeonehand = 28.2-31.3% of sampled actions across all individuals for each year), grasping objects (Grasp = 29.3-26%), eating (Eat = 11.5-14.1%), and placing objects on the anvil (Place = 10.6-13.3%). The separation of kernels from shells by peeling with the teeth was also a frequently observed behaviour (Peelteeth = 4.6-5.8%), as was the placement of objects on the ground (Drop = 4.3-7.1%).

Most actions performed by experienced individuals were associated with the manipulation of a specific object, e.g. striking downwards onto an object was only ever performed using a hammer stone. The exceptions to this were the actions 'Grasp' and 'Drop', which were performed on stones, nuts, kernels and shells as individuals moved through the process of placing nuts on anvils, grasping hammer stones for striking, grasping kernels for consumption, and disposing of objects no longer needed, such as shells, and sometimes tools once nuts were cracked. The rates at which different actions and action-object combinations were performed by experienced chimpanzees were stable across years (see Fig. 3 & Table S9) as well as across individuals within years (see Figs. S3 & S4). The only exception to this was Velu, for whom only 16 actions and action-object combinations could be sampled in 2012. We anticipate that the

difference between the proportion of actions and action-object combinations performed by Velu in 2012 compared to other individuals, and the data for Velu in previously sampled years, was likely due to this extremely small sample size for 2012. The proportion of actions and action-object combinations performed by Velu in other years was similar to other individuals.

4.4.3 Actions and action-object combinations within repertoires: individuals below eight years old

Prior to the age at which individuals were first observed successfully cracking nuts, a diverse number of actions were used by different individuals, including many which were not common to the repertoires of individuals who were experienced in nut cracking. These actions included rolling objects along the ground; biting objects; and pushing and pulling objects across the ground (see Figs. 2 & 3). The most common manipulatory actions performed by individuals at the youngest ages was the touching of stones, nuts and nut fragments with the hands and feet (distinguished from grasping, placing, rolling, etc. as touching does not lead to any change in the physical position of an object). Across all individuals, the percentage of total actions which involved touching objects with hands at ages before nut cracking was first observed ranged from between 13.6%-41.2%, with a peak at -4 years relative to the age nut cracking was first observed. For touching with the feet, this range was lower at 0.2-18.8%, also with a peak at a relative age of -4 years. For touching behaviours with both the hands and feet, this proportion was much higher than seen in experienced individuals (ranges across years: touchhand = 2.2-4.1%; touchfeet = 0.04-0.08%) and this behaviour reduced in frequency as individuals aged, including across ages which preceded the age at which individuals were first observed successfully cracking nuts. Touching behaviours endured into ages following the acquisition of successful nut cracking, especially in the case of touching objects with the hands. However, their frequency continued to reduce once individuals had begun successfully cracking nuts with stone tools (see Figs. 2 & 3, as well as supplementary Figs. S4 & S5 and Table S17).

For many individuals, the action of striking downwards with either an object or a bare hand emerged several years prior to the first instance individuals were observed successfully cracking nuts. Prior to the acquisition of nut cracking, most striking was performed using a stone; however, all individuals also performed this behaviour using their bare hands (see Fig. S5 for all heatmaps of action-object combinations for all individuals, and Tables S11-S16 for underlying data). For two individuals, one-handed striking was

an action which became highly frequent during this period, either through the use of stones or using a bare hand (see Fig. 2). For Fanwaa, up to 17% of actions performed at 2 years of age was striking with the bare hand, and for Flanle, 24-25% of actions at ages two and three involved striking with a stone.

Three individuals (Flanle, Joya and Peley) were observed performing a two-handed strike using a stone tool (an action which was not observed in the sampled actions for experienced nut crackers, who always perform one-handed strikes; see Fig. 3); for Joya, this was observed at an age after she had been documented successfully cracking nuts at the outdoor laboratory (age at two-handed strike = four years; age at first nut cracked: = three); whereas for Flanle and Peley, this behaviour was observed at three and one years old respectively, several years before either individual was first observed cracking nuts with stone tools (four years old). One individual, Fanle, was observed performing a two-handed strike using a nut at the same age she was first observed successfully cracking; however this was only performed once. Striking with two hands was, on the whole, less common than the use of one-handed striking (see Figs 2 & 3).

Four of the six individuals were observed stomping on objects, including nuts (Fanle and Jeje) and stones (Fanle, Flanle, Jeje, and Joya) between one and four years of age. Most instances of stomping occurred at ages prior to the age individuals were first observed successfully cracking nuts; however, at one year following the first observation of successful nut cracking, Joya was observed stomping on stones, and Flanle on stones and nuts. During the following years (+2 years from first observed nut crack and onwards) neither of these individuals were observed performing stomping behaviours. Across all ages, instances of stomping were rare: stomping on stones constituted between 0-9.3% of repertoires for individuals of any given year, with most individuals performing this behaviour in less than 1% of action-object combinations (see tables S11-S16); for stomping on nuts, this range was 0-0.51%. Thus, stomping reflects an infrequent approach to exerting percussive force on nuts and stone tools which was never observed in the data sampled from experienced nut crackers, likely as it never resulted in the cracking open of nuts, and is therefore restricted to the repertoires of younger individuals; the frequency with which stomping is performed then decreases to zero following the acquisition of nut cracking.

Three individuals (Fanle, Flanle and Jeje) were observed placing nuts on the anvil at ages preceding the age at which nut cracking was first observed, and for all other individuals, this action was first observed only at the age individuals began successfully cracking nuts. Additionally, two individuals (Fanle

and Jeje) were observed peeling shells from kernels using their teeth prior to the age at which they first successfully cracked nuts, as they processed fragments of kernel produced by experienced nut crackers at the outdoor laboratory. All other individuals were observed peeling shells with their teeth either on or after the age at which they had successfully acquired the behaviour of nut cracking. Peeling shell with the teeth reached a similar level to experienced individuals by +5 years after acquiring nut cracking (6% of all action-object combinations); however, this relative age contained data from only one individual (Joya). Prior to this age, peeling shell using the teeth was a less common action than what is seen in experienced individuals, suggesting that on the whole, this is an action which is performed less commonly by chimpanzees as they first acquire nut cracking behaviours (between 1-2% of actions across relative years 0 to +4).

Following the successful acquisition of nut cracking, the proportion of actions and action-object combinations demonstrated across individuals was more similar to that of experienced tool-users than before this age. The most common action-object combination was one-handed striking using a stone, which increased from 14.6% of actions across all individuals at the age nut cracking was first observed, to between 33.8-24.2% at the relative ages of +3-5 years. The second most common action was placing objects on anvil stones, which nearly always occurred in instances where nuts were placed on anvils, and remained between 8.2-13.2% of repertoires between the relative ages of 0 and +5. Similarly to experienced nut crackers, the grasping and dropping of several different types of objects was also common during nut cracking, as individuals moved through the necessary process of acquiring and disposing of objects (see Fig. 3; see Table S17).

4.5 Discussion

Chimpanzees habitually perform a number of complex tool-use behaviours in the wild. Understanding how chimpanzees acquire the solutions to naturally reoccurring tool-use tasks is central to understanding how these behaviours persist within wild populations, with possible implications for understanding the mechanisms which drive inter-population differences in tool-use techniques. This is a key line of research in the debate surrounding the existence of socially learnt traditions and material cultures among wild apes. In particular, prior research into social learning by chimpanzees suggest that they may not be capable of

imitating long sequences of fine-grained actions through observations of conspecifics (Hayashi et al., 2005; Stoinski et al., 2001; Subiaul, 2016; Tennie et al., 2012, 2010). Instead, chimpanzees are more likely to be successful emulators of behaviour, copying goals and subgoals which they then address through generating sequences of actions through largely asocial means (Call et al., 2005; Horner and Whiten, 2005; Tennie et al., 2010; Tomasello, 1990). This presents the question of how chimpanzees are able to derive the appropriate sequences of actions necessary for tool-use. We predicted that, to derive a repertoire of actions which are useful for tool-use, chimpanzees undergo phases of exploration and pruning, where they first explore a large number of possible solutions to a tool-use task, before refining the number of actions used based on the success with which they allow naive tool-users to address the goals of their behaviours. To investigate this prediction, we longitudinally sampled over 13,000 actions used by six wild chimpanzees as they developed from their first year of life, up until adolescence (eight years of age), when engaging with nuts and stone tools at an outdoor laboratory at Bossou, Guinea. During sampling, we recorded both the actions used by individuals and the objects which chimpanzees used for different types of actions. We compared this data with 11,515 actions (including associated objects of actions) sampled from 'experienced' nut crackers at four time points (1999, 2004, 2008 and 2012). This allowed us to examine how repertoires of actions for nut cracking change throughout the infancy and juvenile period of wild chimpanzees, and to compare this process with the mature repertoires of competent tool-users.

Our data reveals that between the ages of one and eight years old, chimpanzees undergo an initial expansion in the repertoire of actions used when interacting with nuts and stone tools (including in both actions, and combinations of actions applied to different objects), which peaks at the age individuals are first observed successfully cracking open nuts using stone tools, before gradually decreasing over subsequent years. At ages prior to when individuals 'solve' the task of nut cracking - where individuals had not yet learnt how to successfully crack open nuts using stone tools - chimpanzees were observed performing a number of different actions which were rare or absent from the repertoires of experienced individuals, including alternative methods of manipulating objects (e.g. rolling objects along the floor; and pushing and pulling objects across the ground) and of applying force to objects (e.g. biting, stomping, two-handed striking). Younger individuals also engaged in more 'touching' behaviours, where they would place hands and feet on objects but not move them. The increased number of action-object combinations was

likely driven by this increase in the number of unique action types used by younger individuals, and by the fact that for many of these action types, younger chimpanzees combined actions with multiple different objects (e.g. younger individuals frequently 'touched' stones, nuts, shells and kernels with the hands and feet). However, younger individuals also performed a number of actions which were frequently used by experienced tool-users, but in novel action-object combinations. For example, many individuals performed striking actions from a young age; however, they would do so without an object in their hand, and would therefore strike downwards with an open palm. Alternatively, other individuals were observed performing striking behaviours using nuts. These combinations also contributed to increased repertoire sizes for action-object combinations at younger ages.

Only one individual exhibited a repertoire size for actions and action-object combinations which was similar to that of experienced nut crackers at the oldest year of sampling (Fanwaa, age 8). Additionally, behaviours which were commonly performed by experienced nut crackers (e.g. peeling shells using the teeth), did not emerge until the very end of the juvenile stage, and remained at low frequency. This suggests that nut cracking is a skill which chimpanzees continue to refine throughout early adolescence. This conclusion is supported when examining the repertoires of Jeje, Fanle and Peley, three individuals who were sampled longitudinally between 1997 and 2005, but were also sampled as experienced individuals in 2008 and 2012. When sampled at eight years old, all of these individuals had repertoire sizes which were greater than the upper limit of the 95% confidence interval for experienced individuals; however, by the age of 11 (sample year 2008), both Jeje and Fanle performed nut cracking using repertoires which were highly similar to other experienced individuals sampled in both the same year and other years. Peley (aged 10 in 2008, and 14 in 2012), however, still demonstrated a repertoire which was much larger than other experienced individuals across both of these years. This suggests that whilst the refinement of actions is a process which continues after the juvenile stage and into adolescence in wild chimpanzees, the rate at which actions are refined is not necessarily equal across individuals. Due to the disappearance of Peley from the Bossou community in September 2013, we are unable to determine whether his repertoire of behaviours would have continued to be refined after the age of 14, or if Peley's repertoire would have persisted with a greater number of actions, suggesting that Peley had derived an approach to nut cracking which required a greater diversity of behavioural elements.

The process of repertoire expansion and reduction is expected if chimpanzees follow a process of testing out multiple different actions when innovating a solution to nut cracking, and at the point at which a chimpanzee successfully acquires the behaviour, they refine their repertoire through a process of pruning. During subsequent iterations of stone-tool use, effective actions and action-object combinations are strengthened and retained, whereas those which are less effective become less likely to be elicited, and are eventually pruned from the repertoire. The combined processes of exploration and pruning reflect a method of asocial learning which reoccurs across many different taxa, and spans levels of biological organisation. Within animal systems, exploration and pruning can be observed both at the level of behaviours (Byrne et al., 2017; Guillette et al., 2009; Gultekin and Hage, 2017; Hobaiter and Byrne, 2011; Qin and Wheeler, 2007; Renner, 1988; Rosenberg et al., 2021), and at the level of neurological organisation (Bock and Braun, 1999; De Bot, 2006; Faust et al., 2021; Huttenlocher, 1979; Jones and Schallert, 1992; Sakai, 2020). As such, exploration and pruning have been frequently described through experimental paradigms where animals must solve complex tasks, and have been documented in a variety of taxa, including mammals (Gultekin and Hage, 2017; Renner, 1988; Rosenberg et al., 2021), birds (Guillette et al., 2009), and invertebrates (Qin and Wheeler, 2007). In extension, the processes of exploration and pruning have also been demonstrated as mechanisms through which slime moulds (*Physarum* sp.) establish transport networks as they grow across experimentally designed substrates, demonstrating their utility in non-animal systems of cognition (Nakagaki et al., 2000; Reid, 2023; Tero et al., 2010), as well as highly utile processes for constructing effective systems of artificial intelligence, through the process of refining neural network structures (Averbeck, 2022; Faghihi et al., 2022; Hoefler et al., 2021). Ultimately, exploration and pruning are recurring complementary processes associated with organisms learning to construct complex, organizationally improbable structures from smaller units.

The prevalence of exploration and pruning as a system for constructing complex biological phenomena across taxa, as well as its role in refining synaptic connections during animal learning, reinforces the argument that the expansion and reduction observed in chimpanzee repertoires during the development of nut cracking is likely governed by a similar process. Additionally, exploration and pruning does not necessarily reflect sophisticated cognition, as it may instead be driven by reinforcement learning during iterative exposure to a task. The reinforcement may come from access to a particular resource (in

this case an edible kernel) or through some internal mental or affective process, triggered through the realisation of a behavioural goal or subgoal. Within primates, processes of exploration and pruning have been documented in how chimpanzees and gorillas develop mature repertoires of communicative gestures (Byrne et al., 2017; Genty et al., 2009; Hobaiter and Byrne, 2011) and how monkeys refine the sets of vocal calls used from an immature to an adult repertoire (Gultekin and Hage, 2017; Seyfarth and Cheney, 1986). Moreover, exploration and pruning are behaviours readily observed during human learning, including during the processes of primary and second language acquisition (Benjamin et al., 2023; Brown, 1972; De Bot, 2006). Thus, the observation of similar developmental processes in both the adjacent taxa of chimpanzees, as well as in alternative domains of behaviour, reinforces our argument that such processes are prominent in the development of complex sequences of actions used by wild chimpanzees during tool-use.

Our observations do not preclude the use of social learning to guide the processes of action repertoire development in wild chimpanzees; however, they do suggest that a substantial part of this process is performed asocially. Nut cracking is a behaviour which is difficult to learn for adult chimpanzees (Hayashi et al., 2005), and field experiments in the wild suggest that this is a behaviour which is not readily innovated by chimpanzees who are not able to observe the tool-use behaviours of knowledgeable individuals (Koops et al., 2022). What is most likely informative to apes during social observation are the goals and subgoals of behaviours, and to address these goals, apes must organise their own actions into solutions (Byrne and Russon, 1998; Call et al., 2005; Horner and Whiten, 2005; Tennie et al., 2010; Tomasello, 1990). This presents a challenge to young individuals, where an extended period of exploration may offer no reward to naive individuals. The 'Education by Master Apprenticeship' model of social learning suggests that naive learners are motivated not by food rewards, but by a desire to copy the behaviours of their mothers and other adults, and during this period mothers - as well as unrelated groupmates - are highly tolerant of young chimpanzees' close observation of their tool use (Matsuzawa, 2001); however, the question of what naive learners are able to copy from knowledgeable individuals, including the nature of higher-order goals; the relationships between tool objects and substrates; or the sampling of individual actions to use in exploration, remain open questions.

It is possible that socially acquired information may shape the process of action exploration for juvenile chimpanzees through biassing individuals to explore particular actions. Such a process may occur

through goal emulation, where individuals explore actions which they judge to be most likely to result in a specific outcome (e.g. to apply force, I should stomp, or bite, or strike), or through response facilitation, where actions commonly performed by observed individuals being copied and employed by naive individuals during the exploration process (Byrne, 2005). A number of processes have been suggested for how actions used by demonstrators may bias naive individuals to perform the similar behaviours, of which several do not require learners to construct explicit mental representations of the action (see Byrne, 2005 for a discussion of possible mechanisms). Our data is not suitable for comparisons with the nuanced hypothesised mechanisms through which an action may pass from knowledgeable to naive individual; however, data on the frequency with which actions are performed by skilled tool-users, and the order of their emergence in the repertoire, may offer some insight into whether social observation could be a force which influences the order in which actions emerge in repertoires.

Our analysis revealed that striking, one of the actions most commonly performed by individuals who were experienced in nut cracking, was a behaviour which emerged early in the repertoires of learners. Additionally, striking with one hand, and with the use of a stone, was common for many individuals before they acquired the skill of nut cracking; however, many instances also involved striking without an object, through the use of bare hands. Striking is a particularly conspicuous action required for nut cracking, where an object moves at a fast rate, and an audible sound is produced when a hammer stone collides with nut and anvil. Additionally, striking is an action which is proximate in time to grasping and eating of fragments of kernel following successful cracking. Striking may therefore be an action which readily attracts the attention of learners, and is quickly associated with kernel consumption through the observation of knowledgeable individuals. Infant chimpanzees have been anecdotally reported replicating striking actions when observing the percussive tool-use behaviours of conspecifics (Fuhrmann et al., 2014), and experimental paradigms have suggested that chimpanzees will more readily imitate actions which involve the manipulation of objects compared to actions performed without an object (Myowa-Yamakoshi and Matsuzawa, 1999), something which is salient in the striking motion of hammer stones. It is therefore possible that striking reflects an action which juveniles are likely to imitate when observing the nut cracking behaviours of experienced individuals. Such a conclusion is supported through computational models of action sequence acquisition in great ape behaviours, which suggest that the process of infrequently

sampling an action demonstrated by skilled individuals offers naive learners an accelerated pathway to establishing canonical, effective action sequences, even if the majority of the learning process remains asocial (Whalen et al., 2015). However, we are unable to provide a conclusive argument in favour of social learning leading to the early emergence of striking in young chimpanzee stone-tool manipulation. Striking was not the only action performed by naive individuals to exert force (biting and stomping were also performed), meaning that striking may emerge at an early age as one of multiple strategies used by learners to meet the emulated goal of exerting a force on an object; though, this explanation does not account for why striking was more common than alternative strategies.

Understanding whether social observation guides exploration and refinement of action repertoires during the development of tool-use behaviours in wild apes is central to understanding how population-level differences emerge in tool-use techniques (see Boesch et al., 2020, for a recent example of population-level differences in the termite-fishing behaviours of chimpanzees). The sampling of frequently demonstrated actions to guide exploration may act as a homogenising force within populations; however, environmental differences between populations may also present a scaffold through which individuals converge on similar approaches to tool use, as particular aspects of the environment determine which solutions are most efficient, and therefore should not be pruned from repertoires (Byrne, 2005; Tomasello, 1990). Understanding how both social and physical environments influence the actions which apes explore during their learning therefore remains a key question for researchers seeking to understand the dynamics of ape material culture.

How animals learn and refine solutions to complex tasks is a question at the forefront of behavioural research. We have herein identified that the development of one of the most complex nonhuman technological behaviours observed in nature - chimpanzee nut cracking - exhibits a signature of expansion and reduction which can be explained through a process of behavioural exploration, and the refinement of tool-use strategies through pruning. This explanation for our data is highly parsimonious, given the taxonomic breadth of such developmental and learning processes, as well as the complementary processes identified during the construction of neural architectures. This result suggests that the process through which apes acquire actions for tool use is not the imitation of sequences of actions, but independent exploration. However, we do not rule out the possibility that isolated actions may transfer from

knowledgeable to naive individuals, with the possibility of them also guiding further exploration. Further research in this area must now examine how social learning may guide processes of repertoire development in chimpanzees, including during the exploration and pruning phase. This research could be performed through longitudinal data collection on juvenile chimpanzees, which also tracks their social observations, such as through the construction of an observation network (Dasaratha and He, 2021). This research will provide key insight into how cultural traditions described in wild apes are adopted by individuals, and transmitted across generations.

4.6 Figures

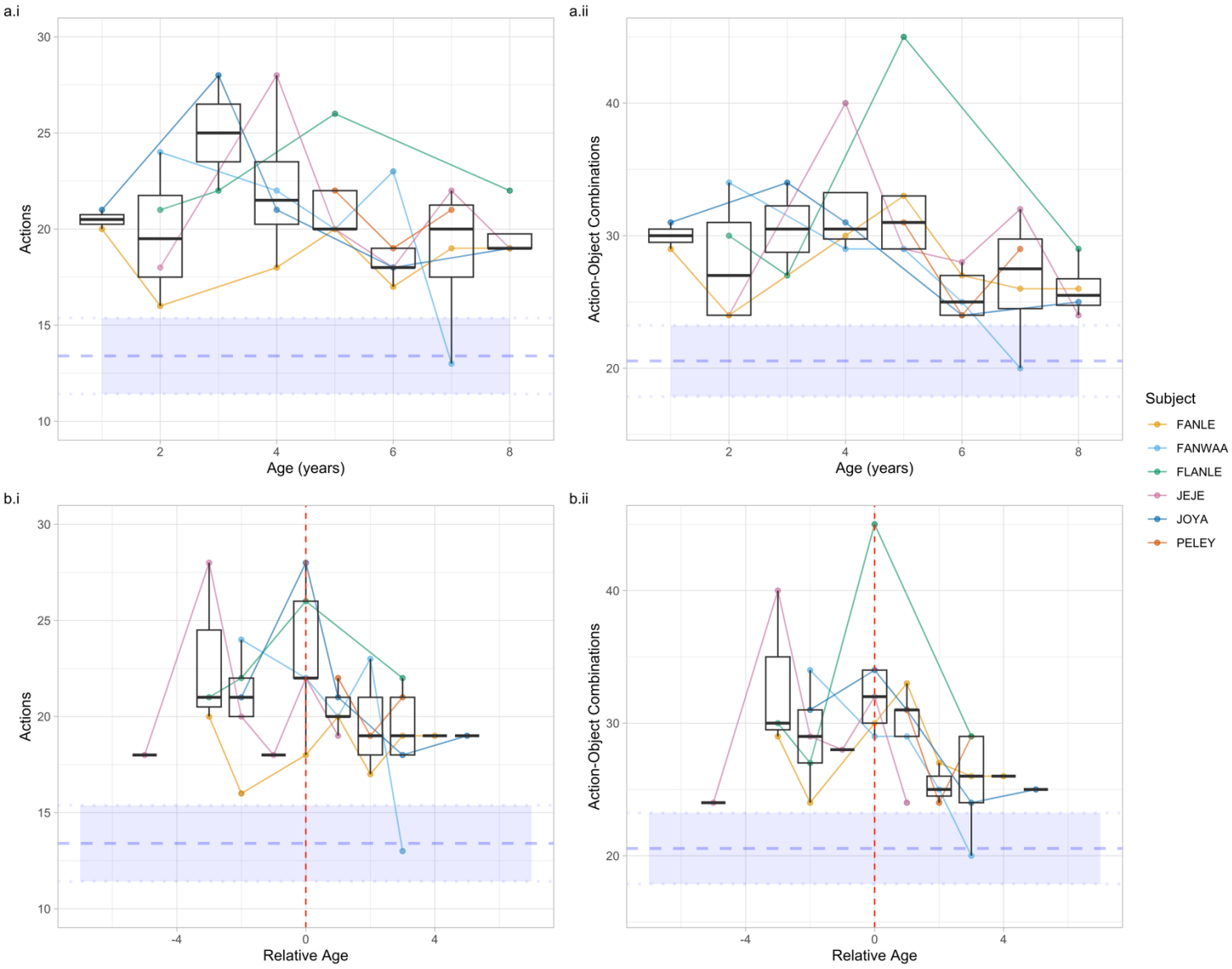


Figure 1. Repertoire size for actions and action-object combinations across ages. Coloured points and lines reflect data for specific individuals. Boxplots describe data across individuals at a particular age point. (a) Repertoire sizes across ages between one and eight years old, including (ai) actions and (aii) action-object combinations. (b) Repertoire sizes across ages standardised to the age individuals were first observed cracking open nuts using stone tools (indicated by the vertical red dashed line, at relative age zero). Plot (bi) describes the repertoire sizes for actions, and (bii) for action-object combinations.

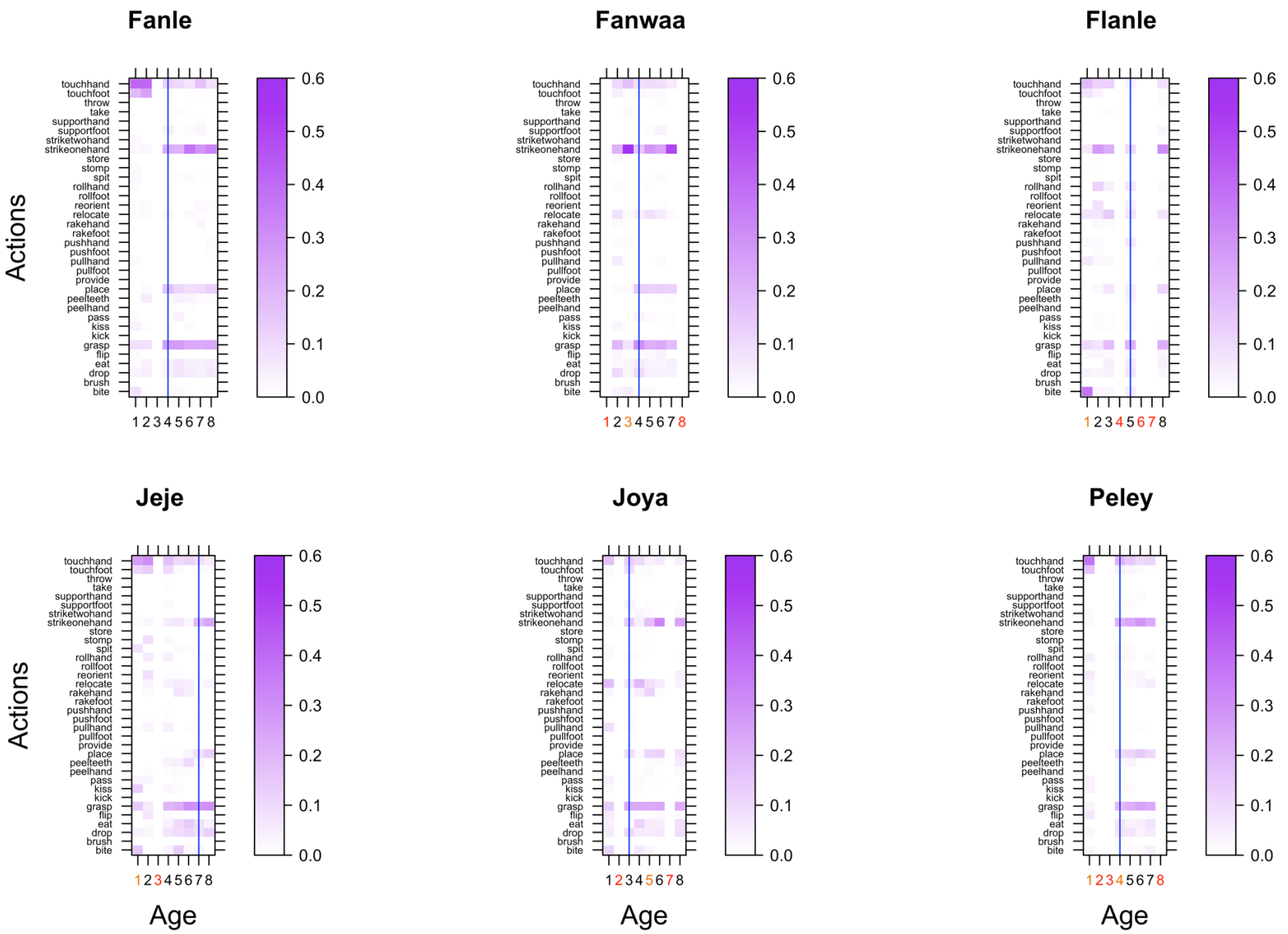


Figure 2. Actions used by individuals between the ages of one and eight years old. On each x-axis, ages are colour coded based on sample size: red numbers indicate no actions were sampled at this age; orange indicates fewer than 400 actions; black indicates 400 actions. Darker actions are more frequent. Vertical blue lines indicate the age at which each individual was first observed cracking open nuts using stone tool

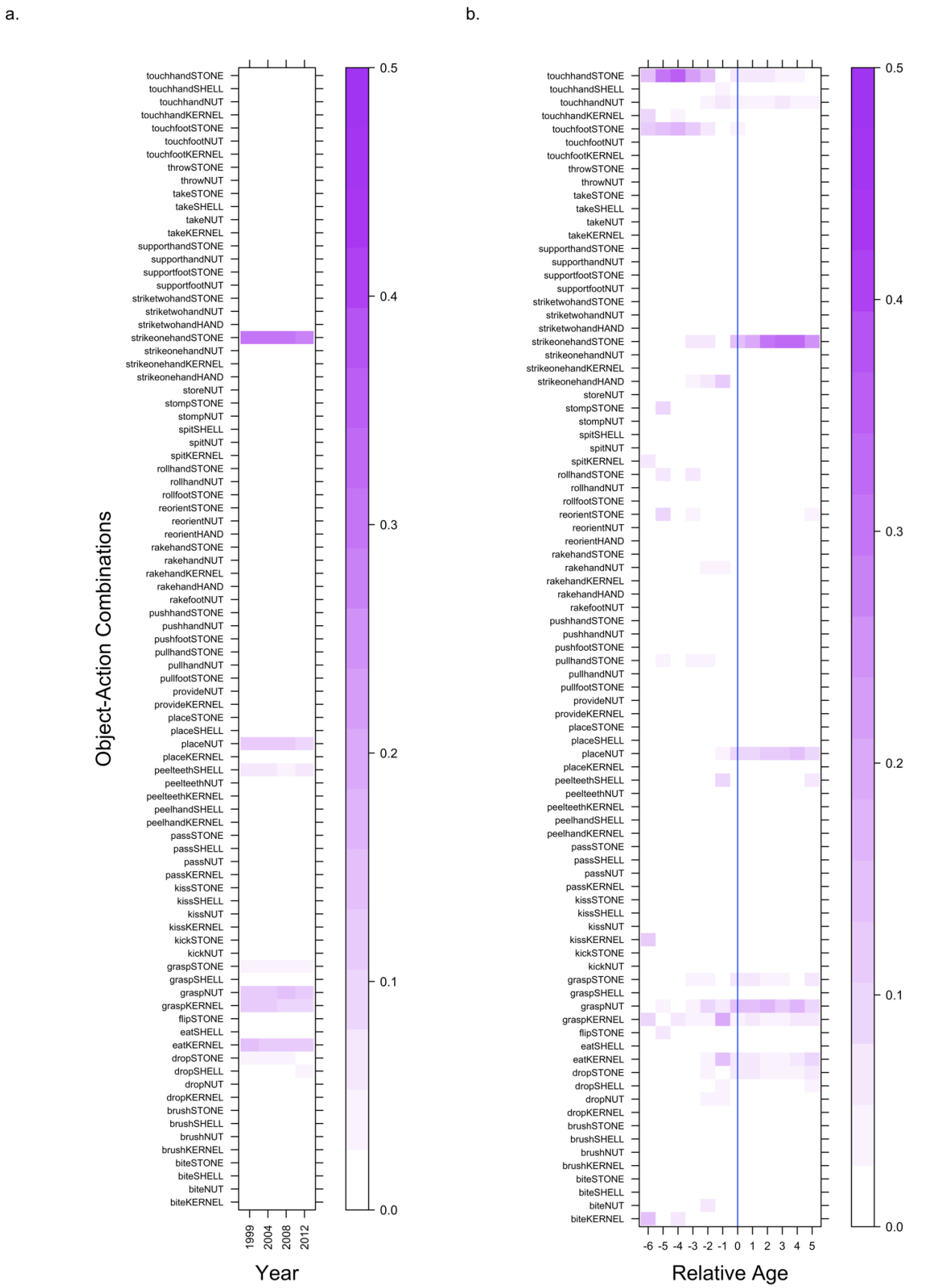


Figure 3. Action-object combinations used by experienced and naïve individuals. Darker squares indicate that action-object combinations were more frequently performed. (a) A heatmap of all actions performed by experienced individuals across sampled field seasons. (b) A heatmap of all action-object combinations performed by individuals sampled between the ages of 1 and 8 years old, with ages scaled to the first age at which they were observed cracking nuts with stone tools.

4.7 Tables

Table 1. Longitudinal sampling of chimpanzees between one and eight years old. Numbers in the different age columns (1-8) relate to the number of actions and action-object combinations sampled.

Subject	Sex	Years	Age (Years)								Age Range Sampled (years)	Age Nut Cracking First Observed (years)
			1	2	3	4	5	6	7	8		
FANLE (Fl)	F	1998-2005	**400**	**400**	0	**400**	**400**	**400**	**400**	**400**	1-8	4
FANWAA (FW)	M	2012-2018	0	**400**	80	**400**	**400**	**400**	**400**	0	2-7	4
FLANLE (FE)	M	2008-2015	195	**400**	**400**	0	**400**	0	0	**400**	1-8	5
JEJE (JJ)	M	1998-2005	247	**400**	0	**400**	**400**	**400**	**400**	**400**	1-8	7
JOYA (Jy)	F	2005-2012	**400**	0	**400**	**400**	133	**400**	0	**400**	1-8	3
PELEY (PE)	M	1999-2006	105	0	0	244	**400**	**400**	**400**	0	1-7	4
TOTAL			1347	1600	880	1844	2133	2000	2000	2000		

Table 2. Repertoire sizes at ages relative to the age at which nut cracking was first observed. Data on actions and action-object combinations are provided. Horizontal lines indicate where fewer than 400 actions were available for an individual at a particular age, and therefore we excluded data for that individual in that age category. The mean (with standard error of the mean in brackets) and median (with interquartile range in brackets) are provided.

		Age Relative to First Observed Instance of Cracking Nuts with Stone Tools (Years)										
Sample Type	**Subject**	-5	-4	-3	-2	-1	0	1	2	3	4	5
Actions												
	FANLE	-	-	20	16	-	18	20	17	19	19	-
	FANWAA	-	-	-	24	-	22	20	23	13	-	-
	FLANLE	-	-	21	22	-	26	-	-	22	-	-
	JEJE	18	-	28	20	18	22	19	-	-	-	-
	JOYA	-	-	-	21	-	28	21	-	18	-	19
	PELEY	-	-	-	-	-	-	22	19	21	-	-
	Mean (SE)	18	-	23 (2.52)	20.6 (1.33)	18	23.2 (1.74)	20.4 (0.51)	19.6 (1.76)	18.6 (1.57)	19	19
	Median (IQR)	18	-	21 (8)	21 (5)	18	22 (7)	20 (2)	19 (6)	19 (6)	19	19
Action-Object Combinations												
	FANLE	-	-	29	24	-	30	33	27	26	26	-
	FANWAA	-	-	-	34	-	29	29	25	20	-	-
	FLANLE	-	-	30	27	-	45	-	-	29	-	-
	JEJE	24	-	40	29	28	32	24	-	-	-	-
	JOYA	-	-	-	31	-	34	31	-	24	-	25
	PELEY	-	-	-	-	-	-	31	24	29	-	-
	Mean (SE)	24	-	33 (3.51)	29 (1.7)	28	34 (2.88)	29.6 (1.54)	25 (0.88)	25.6 (1.69)	26	25
	Median (IQR)	24	-	30 (11)	29 (7)	28	30 (4.5)	31 (5.5)	25 (3)	26 (7)	26	25

4.8 References

Averbeck, B.B., 2022. Pruning recurrent neural networks replicates adolescent changes in working memory and reinforcement learning. Proc. Natl. Acad. Sci. 119, e2121331119. https://doi.org/10.1073/pnas.2121331119

Benjamin, L., Fló, A., Al Roumi, F., Dehaene-Lambertz, G., 2023. Humans parsimoniously represent auditory sequences by pruning and completing the underlying network structure. eLife 12, e86430. https://doi.org/10.7554/eLife.86430

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. Anim. Cogn. 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. Cogn. Dev. Chimpanzees 476–508. https://doi.org/10.1007/4-431-30248-4_28

Bock, J., Braun, K., 1999. Filial imprinting in domestic chicks is associated with spine pruning in the associative area, dorsocaudal neostriatum. Eur. J. Neurosci. 11, 2566–2570. https://doi.org/10.1046/j.1460-9568.1999.00713.x

Boesch, C., Boesch, H., 1990. Tool Use and Tool Making in Wild Chimpanzees. Folia Primatol. (Basel) 54, 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. Sci. Rep. 9, 1515. https://doi.org/10.1038/s41598-018-38392-8

Boesch, C., Kalan, A.K., Mundry, R., Arandjelovic, M., Pika, S., Dieguez, P., Ayimisin, E.A., Barciela, A., Coupland, C., Egbe, V.E., Eno-Nku, M., Michael Fay, J., Fine, D., Adriana Hernandez-Aguilar, R., Hermans, V., Kadam, P., Kambi, M., Llana, M., Maretti, G., Morgan, D., Murai, M., Neil, E., Nicholl, S., Ormsby, L.J., Orume, R., Pacheco, L., Piel, A., Sanz, C., Sciaky, L., Stewart, F.A., Tagg, N., Wessling, E.G., Willie, J., Kühl, H.S., 2020. Chimpanzee ethnography reveals unexpected cultural diversity. Nat. Hum. Behav. 4, 910–916. https://doi.org/10.1038/s41562-020-0890-1

Brown, D., 1972. Cognitive Pruning and Second Language Acquisition. Mod. Lang. J. 56, 218–222.

Byrne, R., 2005. Detecting, Understanding, and Explaining Imitation by Animals, in: Hurley, S.L., Chater, N. (Eds.), Perspectives on Imitation: From Neuroscience to Social Science. MIT Press, Cambridge, Mass, pp. 225–242.

Byrne, R.W., 2007. Culture in great apes: Using intricate complexity in feeding skills to trace the evolutionary origin of human technical prowess. Philos. Trans. R. Soc. B Biol. Sci. 362, 577–585. https://doi.org/10.1098/rstb.2006.1996

Byrne, R.W., Cartmill, E., Genty, E., Graham, K.E., Hobaiter, C., Tanner, J., 2017. Great ape gestures: intentional communication with a rich set of innate signals. Anim. Cogn. 20, 755–769. https://doi.org/10.1007/s10071-017-1096-4

Byrne, R.W., Russon, A.E., 1998. Learning by imitation : A hierarchical approach. Behav. Brain Sci. 21, 667–721.

Byrne, R.W., Sanz, C.M., Morgan, D.B., 2013. Chimpanzees plan their tool use, in: Sanz, C.M., Call, J., Boesch, C. (Eds.), Tool Use in Animals. Cambridge University Press, pp. 48–64. https://doi.org/10.1017/CBO9780511894800.004

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). Anim. Cogn. 8, 151–163. https://doi.org/10.1007/s10071-004-0237-8

Carvalho, S., Cunha, E., Sousa, C., Matsuzawa, T., 2008. Chaînes opératoires and resource-exploitation strategies in chimpanzee (Pan troglodytes) nut cracking. J. Hum. Evol. 55, 148–163. https://doi.org/10.1016/j.jhevol.2008.02.005

Carvalho, S., McGrew, W., 2012. The origins of the Oldowan: Why chimpanzees (Pan troglodytes) still are good models for technological evolution in Africa, in: Domínguez-Rodrigo, M. (Ed.), Stone Tools and Fossil Bones. Cambridge University Press, pp. 201–221. https://doi.org/10.1017/CBO9781139149327.010

Chiang, M., 1967. Use of Tools by Wild Macaque Monkeys in Singapore. Nature 214, 1258–1259. https://doi.org/10.1038/2141258a0

Custance, D.M., Whiten, A., Bard, K.A., 1995. Can Young Chimpanzees (Pan Troglodytes) Imitate Arbitrary Actions? Hayes & Hayes (1952) Revisited. Behaviour 132, 837–859. https://doi.org/10.1163/156853995X00036

Dasaratha, K., He, K., 2021. Network structure and social learning. ACM SIGecom Exch. 19, 62–67. https://doi.org/10.1145/3505156.3505163

Dawkins, R., 1976. Hierarchical organization: a candidate principle for ethology., in: Growing Points in Ethology. Cambridge University Press.

De Bot, K., 2006. The Plastic Bilingual Brain: Synaptic Pruning or Growth? Commentary on Green, et al.: *Plastic Bilingual Brain*. Lang. Learn. 56, 127–132. https://doi.org/10.1111/j.1467-9922.2006.00358.x

Faghihi, F., Alashwal, H., Moustafa, A.A., 2022. A Synaptic Pruning-Based Spiking Neural Network for Hand-Written Digits Classification. Front. Artif. Intell. 5, 680165. https://doi.org/10.3389/frai.2022.680165

Faust, T.E., Gunner, G., Schafer, D.P., 2021. Mechanisms governing activity-dependent synaptic pruning in the developing mammalian CNS. Nat. Rev. Neurosci. 22, 657–673. https://doi.org/10.1038/s41583-021-00507-y

Friard, O., Gamba, M., 2016. BORIS: a free, versatile open-source event-logging software for video/audio coding and live observations. Methods Ecol. Evol. 7, 1325–1330. https://doi.org/10.1111/2041-210X.12584

Fuhrmann, D., Ravignani, A., Marshall-Pescini, S., Whiten, A., 2014. Synchrony and motor mimicking in chimpanzee observational learning. Sci. Rep. 4, 5283. https://doi.org/10.1038/srep05283

Genty, E., Breuer, T., Hobaiter, C., Byrne, R.W., 2009. Gestural communication of the gorilla (Gorilla gorilla): repertoire, intentionality and possible origins. Anim. Cogn. 12, 527–546. https://doi.org/10.1007/s10071-009-0213-4

Goodall, J., 1964. Tool-Using and Aimed Throwing in a Community of Free-Living Chimpanzees. Nature 201, 1264–1266. https://doi.org/10.1038/2011264a0

Gruber, T., Muller, M.N., Strimling, P., Wrangham, R., Zuberbühler, K., 2009. Wild Chimpanzees Rely on Cultural Knowledge to Solve an Experimental Honey Acquisition Task. Curr. Biol. 1806–1810. https://doi.org/10.1016/j.cub.2009.08.060

Gruber, T., Zuberbühler, K., Clément, F., van Schaik, C., 2015. Apes have culture but may not know that they do. Front. Psychol. 6, 1–14. https://doi.org/10.3389/fpsyg.2015.00091

Guillette, L.M., Reddon, A.R., Hurd, P.L., Sturdy, C.B., 2009. Exploration of a novel space is associated with individual differences in learning speed in black-capped chickadees, Poecile atricapillus. Behav. Processes 82, 265–270. https://doi.org/10.1016/j.beproc.2009.07.005

Gultekin, Y.B., Hage, S.R., 2017. Limiting parental feedback disrupts vocal development in marmoset monkeys. Nat. Commun. 8, 14046. https://doi.org/10.1038/ncomms14046

Hayashi, M., Mizuno, Y., Matsuzawa, T., 2005. How does stone-tool use emerge? Introduction of stones and nuts to naïve chimpanzees in captivity. Primates 46, 91–102. https://doi.org/10.1007/s10329-004-0110-z

Hobaiter, C., Byrne, R.W., 2011. Serial gesturing by wild chimpanzees: Its nature and function for communication. Anim. Cogn. 14, 827–838. https://doi.org/10.1007/s10071-011-0416-3

Hoefler, T., Alistarh, D., Ben-Nun, T., Dryden, N., 2021. Sparsity in Deep Learning: Pruning and growth for efficient inference and training in neural networks. J. Mach. Learn. Res. 23.

Hopper, L.M., Spiteri, A., Lambeth, S.P., Schapiro, S.J., Horner, V., Whiten, A., 2007. Experimental studies of traditions and underlying transmission processes in chimpanzees. Anim. Behav. 73, 1021–1032. https://doi.org/10.1016/j.anbehav.2006.07.016

Hoppitt, W., Laland, K., 2013. Social Learning: An Introduction to Mechanisms, Methods and Models, Social Learning: An Introduction to Mechanisms, Methods, and Models. Princeton University Press. https://doi.org/10.1515/9781400846504

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

Humle, T., 2011. The Tool Repertoire of Bossou Chimpanzees, in: The Chimpanzees of Bossou and Nimba. Springer Japan, Tokyo, Japan, pp. 61–72.

Humle, T., Matsuzawa, T., 2002. Ant-dipping among the chimpanzees of Bossou, Guinea, and some comparisons with other sites. Am. J. Primatol. 58, 133–148. https://doi.org/10.1002/ajp.10055

Huttenlocher, P.R., 1979. Synaptic density in human frontal cortex — Developmental changes and effects of aging. Brain Res. 163, 195–205. https://doi.org/10.1016/0006-8993(79)90349-4
Inoue-Nakamura, N., Matsuzawa, T., 1997. Development of Stone Tool Use by Wild Chimpanzees (Pan troglodytes). J. Comp. Psychol. 111, 159–173. https://doi.org/10.1037/0735-7036.111.2.159
Jones, T.A., Schallert, T., 1992. Overgrowth and pruning of dendrites in adult rats recovering from neocortical damage. Brain Res. 156–160.
Koops, K., 2020. Chimpanzee termite fishing etiquette. Nat. Hum. Behav. 4, 887–888. https://doi.org/10.1038/s41562-020-0895-9
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. Anim. Behav. Cogn. 10, 163–168. https://doi.org/10.26451/abc.10.02.05.2023
Koops, K., Soumah, A.G., Van Leeuwen, K.L., Camara, H.D., Matsuzawa, T., 2022. Field experiments find no evidence that chimpanzee nut cracking can be independently innovated. Nat. Hum. Behav. 6, 487–494. https://doi.org/10.1038/s41562-021-01272-9
Lashley, K., 1951. The problem of serial order in behavior. Cereb. Mech. Behav. 112–147.
Matsuzawa, T., 2011. Stone Tools for Nut-Cracking, in: The Chimpanzees of Bossou and Nimba. Springer Japan, Tokyo, Japan, pp. 73–84.
Matsuzawa, T., 2001. Primate Foundations of Human Intelligence: A View of Tool Use in Nonhuman Primates and Fossil Hominids, in: Matsuzawa, T. (Ed.), Primate Origins of Human Cognition and Behavior. Springer Japan, Tokyo, pp. 3–25. https://doi.org/10.1007/978-4-431-09423-4_1
Matsuzawa, T., 1996. Chimpanzee intelligence in nature and in captivity: Isomorphism of symbol use and tool use, in: Great Ape Societies. pp. 196–212.
Matsuzawa, T., 1994. Field Experiments on use of Stone Tools in the wild, in: Chimpanzee Cultures. pp. 351–370.
Matsuzawa, T., Hulme, T., Sugiyama, Y., 2011. The Chimpanzees of Bossou and Nimba.
Meulman, E.J.M., Van Schaik, C.P., 2013. Orangutan tool use and the evolution of technology, in: Sanz, C.M., Call, J., Boesch, C. (Eds.), Tool Use in Animals. Cambridge University Press, pp. 176–202. https://doi.org/10.1017/CBO9780511894800.012
Myowa-Yamakoshi, M., Matsuzawa, T., 2000. Imitation of intentional manipulatory actions in chimpanzees (Pan troglodytes). J. Comp. Psychol. 114, 381–391. https://doi.org/10.1037/0735-7036.114.4.381
Myowa-Yamakoshi, M., Matsuzawa, T., 1999. Factors influencing imitation of manipulatory actions in chimpanzees (Pan troglodytes). J. Comp. Psychol. 113, 128–136. https://doi.org/10.1037/0735-7036.113.2.128
Myowa-Yamakoshi, M., Yamakoshi, G., 2011. Play Behaviors Involving the Use of Objects in Young Chimpanzees at Bossou, in: The Chimpanzees of Bossou and Nimba. Springer Japan, Tokyo, pp. 231–240.
Nakagaki, T., Yamada, H., Tóth, Á., 2000. Maze-solving by an amoeboid organism. Nature 407, 470–470. https://doi.org/10.1038/35035159
Ohashi, G., 2006. Behavioral Repetoire of Tool Use in the Wild Chimpanzees at Bossou, in: Matsuzawa, T., Tomonaga, M., Masayuki, T. (Eds.), Cognitive Development in Chimpanzees. Springer-Verlag Tokyo, Tokyo, Japan, pp. 439–451.
Ottoni, E.B., Izar, P., 2008. Capuchin monkey tool use: Overview and implications. Evol. Anthropol. Issues News Rev. 17, 171–178. https://doi.org/10.1002/evan.20185
Qin, J., Wheeler, A.R., 2007. Maze exploration and learning in C. elegans. Lab Chip 7, 186–192. https://doi.org/10.1039/B613414A
Reid, C.R., 2023. Thoughts from the forest floor: a review of cognition in the slime mould Physarum polycephalum. Anim. Cogn. https://doi.org/10.1007/s10071-023-01782-1
Renner, M.J., 1988. Learning During Exploration: The Role of Behavioral Topography During Exploration in Determining Subsequent Adaptive Behavior in the Sprague-Dawley Rat (Rattus norvegicus). Int. J. Comp. Psychol. 2. https://doi.org/10.46867/C45303
Rosenberg, M., Zhang, T., Perona, P., Meister, M., 2021. Mice in a labyrinth show rapid learning, sudden insight, and efficient exploration. eLife 10, e66175. https://doi.org/10.7554/eLife.66175

Sakai, J., 2020. How synaptic pruning shapes neural wiring during development and, possibly, in disease. Proc. Natl. Acad. Sci. 117, 16096–16099. https://doi.org/10.1073/pnas.2010281117

Sanz, C.M., Morgan, D.B., 2010. The Complexity of Chimpanzee Tool-Use Behaviors, in: The Mind of the Chimpanzee: Ecological and Experimental Perspectives. The University of Chicago Press, pp. 127–140.

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. Sci. Adv. 5, 1–10. https://doi.org/10.1126/sciadv.aaw0736

Seed, A., Byrne, R., 2010. Animal Tool-Use. Curr. Biol. 20, R1032–R1039. https://doi.org/10.1016/j.cub.2010.09.042

Seyfarth, R.M., Cheney, D.L., 1986. Vocal development in vervet monkeys. Anim. Behav. 34, 1640–1658. https://doi.org/10.1016/S0003-3472(86)80252-4

Shumaker, R., Walkup, K., Beck, B., 2011. Animal Tool Behavior: The Use and Manufacture of Tools by Animals. The John Hopkins University Press, Baltimore, Maryland, USA.

Stoinski, T.S., Wrate, J., Whiten, A., 2001. Imitative learning by captive western lowland gorillas (Gorilla gorilla gorilla) in a simulated food-processing task. J. Comp. Psychol. 115, 272–281. https://doi.org/10.1037/0735-7036.115.3.272

Subiaul, F., 2016. What's Special about Human Imitation? A Comparison with Enculturated Apes. Behav. Sci. 6, 13. https://doi.org/10.3390/bs6030013

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, 1–25. 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 and Philosophy. Springer Netherlands. https://doi.org/10.1007/s10539-020-09769-9

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." Anim. Behav. Cogn. 10, 89–94. https://doi.org/10.26451/abc.10.01.05.2023

Tennie, C., Call, J., Tomasello, M., 2012. Untrained Chimpanzees (Pan troglodytes schweinfurthii) Fail to Imitate Novel Actions. PLoS ONE 7, e41548. https://doi.org/10.1371/journal.pone.0041548

Tennie, C., Call, J., Tomasello, M., 2010. Evidence for Emulation in Chimpanzees in Social Settings Using the Floating Peanut Task. PLoS ONE 5, e10544. https://doi.org/10.1371/journal.pone.0010544

Tennie, C., Call, J., Tomasello, M., 2009. Ratcheting up the ratchet: on the evolution of cumulative culture. Philos. Trans. R. Soc. B Biol. Sci. 364, 2405–2415. https://doi.org/10.1098/rstb.2009.0052

Tero, A., Takagi, S., Saigusa, T., Ito, K., Bebber, D.P., Fricker, M.D., Yumiki, K., Kobayashi, R., Nakagaki, T., 2010. Rules for Biologically Inspired Adaptive Network Design. Science 327, 439–442. https://doi.org/10.1126/science.1177894

Thorndike, E.L., 1927. The Law of Effect. Am. J. Psychol. 39, 212. https://doi.org/10.2307/1415413

Tomasello, M., 1990. Cultural transmission in the tool use and communicatory signaling of chimpanzees?, in: Parker, S.T., Gibson (Eds.), Language and Intelligence in Monkeys and Apes. Cambridge University Press, pp. 274–311.

Tonooka, R., 2001. Leaf-folding behavior for drinking water by wild chimpanzees (Pan troglodytes verus) at Bossou, Guinea. Anim. Cogn. 4, 325–334. https://doi.org/10.1007/s100710100110

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. J. Hum. Evol. 36, 719–741. https://doi.org/10.1006/jhev.1999.0304

Van Schaik, C.P., Fox, E.A., Sitompul, A.F., 1996. Manufacture and use of tools in wild Sumatran orangutans: Implications for human evolution. Naturwissenschaften 83, 186–188. https://doi.org/10.1007/BF01143062

Whalen, A., Cownden, D., Laland, K., 2015. The learning of action sequences through social transmission. Anim. Cogn. 18, 1093–1103. https://doi.org/10.1007/s10071-015-0877-x

Whiten, A., 2017. Social Learning and Culture in Child and Chimpanzee. Annu. Rev. Psychol. 68, 129–154. https://doi.org/10.1146/annurev-psych-010416-044108

Whiten, A., Custance, D.M., Gomez, J.-C., Teixidor, P., Bard, K.A., 1996. Imitative learning of artificial fruit processing in children (Homo sapiens) and chimpanzees (Pan troglodytes). J. Comp. Psychol. 110, 3–14. https://doi.org/10.1037/0735-7036.110.1.3

Whiten, A., Goodall, J., Mcgrew, W.C., Nishida, T., Reynolds, V., Sugiyama, Y., Tutin, E.G., Wrangham, R.W., Boesch, C., 2001. Charting Cultural Variation in Chimpanzees. Behaviour 138, 1481–1516.

Whiten, A., Goodall, J., Mcgrew, W.C., Nishida, T., Reynoldsk, V., Sugiyama, Y., Tutin, C.E.G., Wrangham, R.W., Boesch, C., 1999. Cultures in chimpanzees. Nature 399, 682–685.

Yamakoshi, G., Sugiyama, Y., 1995. Pestle-pounding behavior of wild chimpanzees at Bossou, Guinea: a newly observed tool-using behavior. Primates 36, 489–500.

4.9 Supplementary Materials

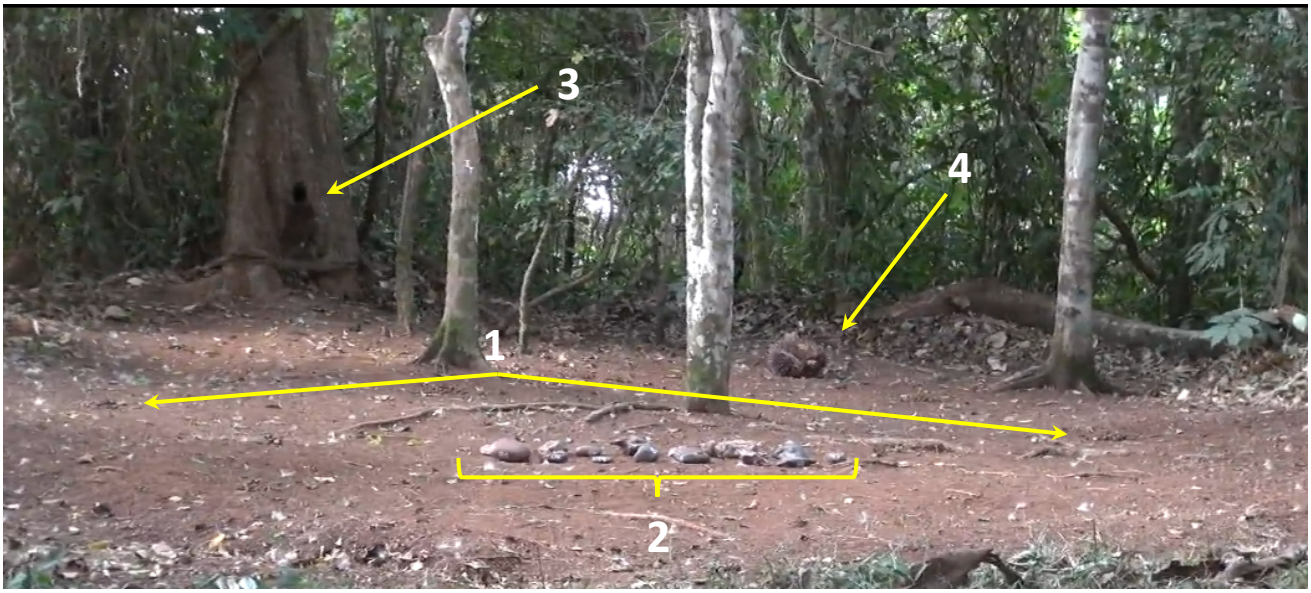


***Figure S1. The outdoor laboratory, Bossou (The Bureau)**. Key features of the Bureau are: 1. Provided piles of oil-palm nuts (two piles are indicated; typically, a total of 6-12 piles of 40-50 nuts each were provided), 2. Central matrix of available stone tools, 3. Water point, 4. Raceme of oil-palm fruits.

* This figure and parts of this legend are identical to figure S1 and corresponding legend in the supplementary materials for Chapter 2

Table S1. Ethogram of codable actions for observations of nut-cracking behaviours. Actions in bold are coded alongside a corresponding object. There are 5 possible corresponding objects: 1. Nut, 2. Stone, 3. Kernel, 4. Shell, 5. Bare Hand. Event codes in italics are used to denote the start and end of observable sequences. Coding commenced when individuals began interacting with stones, nuts, or nut-fragments. Coding ceased when individuals began engaging in a new behaviour e.g. play, grooming, eating oil-palm fruits. On the occasions where an individual moved out of clear sight of the video recording, or actions became obscured by an individual's body position, sequences were terminated with a 'Not Visible' codon, and marked as incomplete.

Action	Description
Bite	Place object in mouth and bite with teeth. Differs from 'Eat' as there is no consumption. Differs from 'Store' as object moves in and out of mouth whilst chimp is stationary. Differs from 'Peel Teeth' as bite applies general force, whereas peel with mouth is to remove shell fragments from kernel dexterously. Differs from 'Kiss' as object enters inside the mouth.
Brush	Brush objects off the anvil.
Drop	Place object(s) on ground.
Eat	Consume object. Differs from bite and store as it requires successful ingestion.
Flip	Flip object over.
Grasp	Grasp an object and move off the ground.
Kick	Apply rapid, hard force on object with the foot, so that the object is displaced.
Kiss	Place object to lips or nose, but not inside of the mouth.
Pass	Pass object between hands.
Peel Hand	Peel shell off of kernel with hands.
Peel Teeth	Peel shell off of kernel with teeth.
Place	Place an object on an anvil.
Provide	Directly hand an object to another individual.
Pull Foot	Pull an object across the ground with foot.
Pull Hand	Pull an object across the ground with hand.
Push Foot	Push an object across the ground with foot.
Push Hand	Push an object across the ground with hand.
Rake Foot	Pull many objects towards oneself using foot/leg.
Rake Hand	Pull many objects towards oneself using hand/arm.
Reorient	Rotate object horizontally.
Roll Foot	Roll object along the floor with foot.
Roll Hand	Roll object along the floor with hand.
Spit	Let object fall from mouth or lips.
Stomp	Whilst standing, apply strong force to object with foot.
Store	Place object(s) in mouth for transportation. Separated from bite, eat, peel teeth as it is followed by transportation across the outdoor laboratory, before then being removed from the mouth intact.
Strike One Hand	Strike with one hand, (and associated object).
Strike Two Hand	Strike with two hands, (and associated object).
Support Foot	Support object with foot.
Support Hand	Support object with hand.
Take	Receive an object directly from another individual.
Throw	Throw object away from self, horizontally or vertically.
Touch Foot	Touch or grasp object without moving it using foot.
Touch Hand	Touch or grasp object without moving it using hand.
Relocate	Stand up and move to a new area; is immediately followed by another coding action.
Start	Start of a sequence.
End Bout	End of a sequence.
Not Visible	Individual moves out of view, and coding cannot continue. Differs from 'End Bout', as there is no evidence the individual has stopped engaging with stones, nuts or nut-fragments.

* This table, and parts of this legend, are identical to table S2 and corresponding legend in the supplementary materials for chapter 2.

Inter-Observer Reliability Analysis

To test for inter-observer reliability, all observers coded the same five-minute clip from the 2012 field season. For each observer, 50 coded behaviours were randomly sampled (including different sets of actions and action-object combinations for each observer), and the time stamps recorded. For each of the 50 behaviours sampled for each focal observer, we identified whether an identical behaviour was coded in the recorded actions of the other three observers, within a window of ± 4 s. If an identical behaviour was present within this window, we recorded that observers agreed that the sampled behaviour occurred at this point in the video.

Using all comparisons between observers, we estimated the proportion of comparisons where observers agreed:

p(Agree) = Number of Agreed Actions between two observers ÷ Total Number of Comparisons

Where the total number of comparisons was 50.

To estimate the mean agreement between a focal observer and all other observers, we summed the total number of agreements recorded between the focal observer and all other observers, and divided this number by the total number of comparisons (150).

To find the mean rate of inter-observer reliability across all observers, we took the mean proportions of agreements between focal observers and all other observers, and found a mean of means.

Table S2. Interobserver reliability for coded actions. The total number of actions coded within the five-minute clip for each observer are provided. Proportions reflect the rate at which sampled actions coded by the focal observer were found in the corpus of actions coded by each other observer, within a window of ± 4 s.

Focal Observer	Total Actions Coded	EHS	MB	AA	JH	Mean
EHS	125		0.96 (48)	0.94 (47)	0.48 (24)	0.79 (119)
MB	142	0.82 (41)		0.9 (45)	0.56 (28)	0.76 (114)
AA	143	0.82 (41)	0.88 (44)		0.5 (25)	0.73 (110)
JH	76	0.74 (37)	0.76 (38)	0.8 (40)		0.77 (115)
Mean						0.76

Table S3. Interobserver reliability for coded action-object combinations. The total number of action-object combinations coded within the five-minute clip for each observer are provided. Proportions reflect the rate at which sampled action-object combinations coded by the focal observer were found in the corpus of behaviours coded by each other observer, within a window of ± 4 s.

Observer	Total Object-Action Combinations Coded	EHS	MB	AA	JH	Mean
EHS	125		0.96 (48)	0.94 (47)	0.44 (22)	0.78 (117)
MB	142	0.8 (40)		0.9 (45)	0.48 (24)	0.73 (109)
AA	143	0.8 (40)	0.88 (44)		0.42 (21)	0.7 (105)
JH	76	0.74 (37)	0.76 (38)	0.8 (40)		0.77 (115)
Mean						0.75

Table S4. Sampled data for proficient nut crackers between 1999-2012. Horizontal lines indicate where an individual was not eligible to be sampled in a given year, either through being too young (in the case of Peley, Jeje, and Fanle for 1999 and 2004, as well as Yolo for 1999), or if they were no longer present in the population (in the case of Yolo for 2012, and Kai from 2004 onwards).

			Year			
Subject	Sex	Year of Birth	1999	2004	2008	2012
FANA	F	1956*	**400**	**400**	**400**	0
FANLE	F	1997	-	-	**400**	**400**
FOAF	M	1980	**400**	**400**	**400**	299
JEJE	M	1997	-		**400**	**400**
JIRE	F	1958*	**400**	**400**	**400**	**400**
KAI	F	1950*	**400**	-	-	-
PELEY	M	1998	-	-	**400**	**400**
TUA	M	1957*	**400**	**400**	**400**	**400**
VELU	F	1959*	**400**	**400**	**400**	16
YO	F	1961*	**400**	0	**400**	0
YOLO	M	1991	-	**400**	**400**	-
TOTAL			2800	**2400**	**4000**	2315

*These individuals were present at Bossou at the beginning of longitudinal study, so exact DOB is an estimate.

Table S5. The number of actions in the repertoire of proficient nut crackers between 1999-2012. For each year, the number of unique actions present in the first 400 sampled actions for each individual is provided. For each year, the mean number of unique actions across individuals is provided. A mean of means (averaging the average repertoire size across the years) is provided (with standard error of the mean in brackets). Horizontal lines indicate where data was not sampled for an individual in a particular year (see table S4). All values given to three significant figures.

	Year				Mean of Means
Subject	1999	2004	2008	2012	
FANA	13	13	11	-	
FANLE	-	-	12	11	
FOAF	11	10	11	-	
JEJE	-	-	10	13	
JIRE	12	14	14	-	
KAI	13	-	-	-	
PELEY	-	-	17	19	
TUA	12	15	12	16	
VELU	12	10	14	-	
YO	17	-	12	-	
YOLO	-	18	11	-	
Mean (SE)	12.9	13.3	12.4	14.8	13.4 (1.01)

Table S6. The number of action-object combinations in the repertoire of proficient nut crackers between 1999-2012. For each year, the number of unique action-object combinations present in the first 400 sampled actions for each individual is provided. For each year, the mean number of unique action-object combinations across individuals is provided. A mean of means (averaging the average repertoire size across the years) is provided (with standard error of the mean in brackets). Horizontal lines indicate where data was not sampled for an individual in a particular year (see table S4). All values given to three significant figures.

	Year				Mean of means
Subject	1999	2004	2008	2012	
FANA	19	17	16	-	
FANLE	-	-	17	17	
FOAF	18	14	15	-	
JEJE	-	-	16	23	
JIRE	18	21	20	-	
KAI	23	-	-	-	
PELEY	-	-	27	33	
TUA	18	22	21	25	
VELU	19	15	20	-	
YO	27	-	19	-	
YOLO	-	22	18	-	
Mean (SE)	20.3	18.5	18.9	24.5	20.6 (1.37)

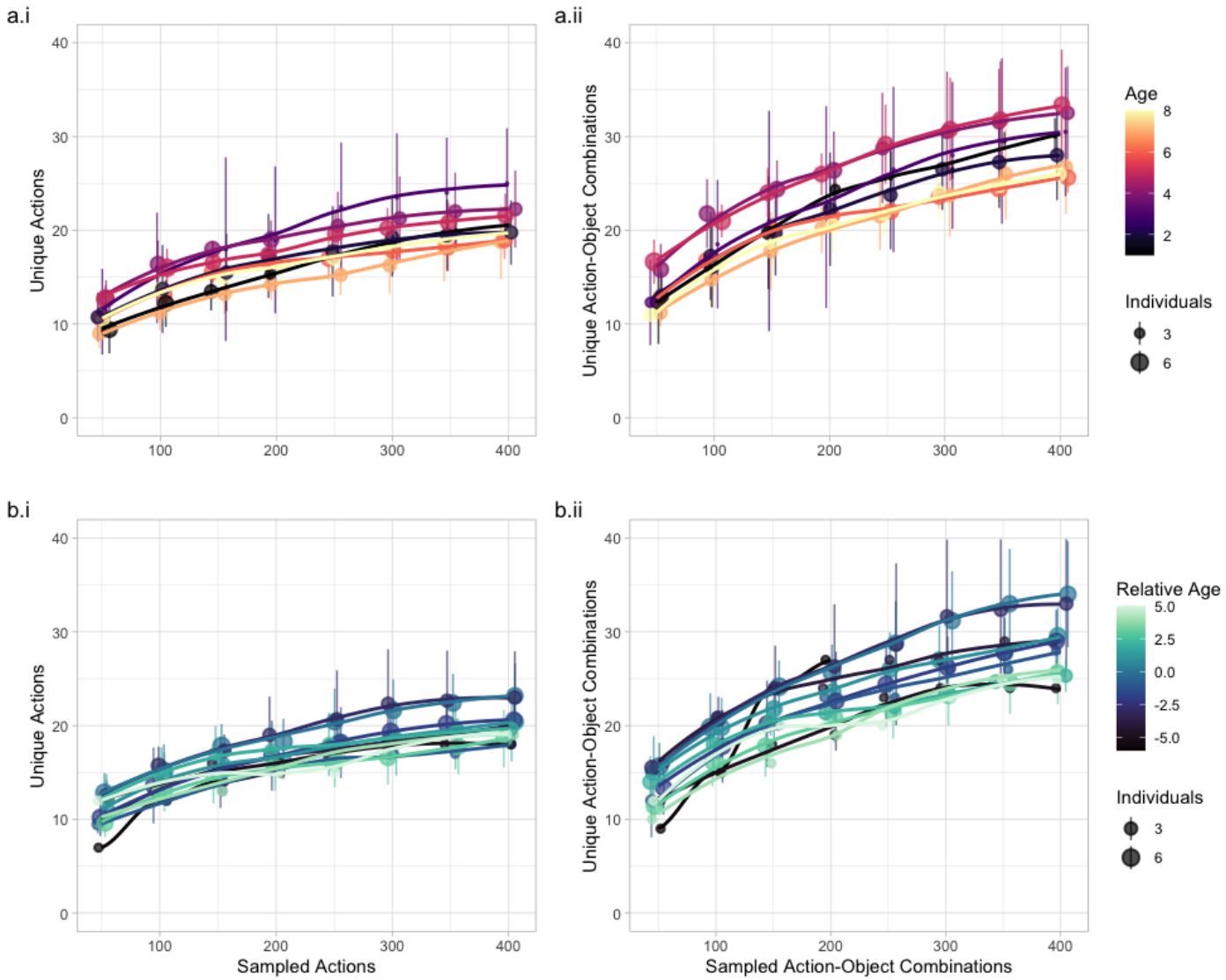
Table S7. Number of unique actions sampled from individuals between the ages of one and eight years old. Data reflects the first 400 sampled actions at each age, where numbers describe the number of unique action types recorded for an individual at a particular age. Horizontal lines indicate that fewer than 400 actions were observed for that individual at a particular age, and therefore we excluded their data from our analysis. The mean (with standard error in brackets) and median (with interquartile range in brackets) are provided for each age.

	Age (Years)							
Subject	1	2	3	4	5	6	7	8
FANLE	20	16	-	18	20	17	19	19
FANWAA	-	24	-	22	20	23	13	-
FLANLE	-	21	22	-	26	-	-	22
JEJE	-	18		28	20	18	22	19
JOYA	21	-	28	21	-	18		19
PELEY	-	-	-	-	22	19	21	-
Mean (SE)	20.5 (0.5)	19.8 (1.75)	25 (3)	22.3 (2.1)	21.6 (1.16)	19 (1.05)	18.8 (2.02)	19.8 (0.75)
Median (IQR)	20.5	19.5 (5.5)	25	21.5 (5.5)	20 (4)	18 (3.5)	20 (5.5)	19 (1.5)

Table S8. Number of unique action-object combinations sampled from individuals between the ages of one and eight years old. Data reflects the first 400 sampled action-object combinations at each age, where numbers describe the number of unique action-object combinations recorded for an individual at a particular age. Horizontal lines indicate that fewer than 400 action-object combinations were observed for that individual at a particular age, and therefore we excluded their data from our analysis. The mean (with standard error in brackets) and median (with interquartile range in brackets) are provided for each age.

	Age (Years)							
Subject	1	2	3	4	5	6	7	8
FANLE	29	24	-	30	33	27	26	26
FANWAA	-	34	-	29	29	25	20	-
FLANLE	-	30	27	-	45	-	-	29
JEJE	-	24	-	40	29	28	32	24
JOYA	31	-	34	31	-	24	-	25
PELEY	-	-	-	-	31	24	29	-
Mean (SE)	30 (1)	28 (2.45)	30.5 (3.5)	32.5 (2.53)	33.4 (2.99)	25.6 (0.81)	26.8 (2.56)	26 (1.08)
Median (IQR)	30	27 (8)	30.5	30.5 (6)	31 (10)	25 (3.5)	27.5 (7.5)	25.5 (3)

Fig. S2. Sample size vs repertoire size for actions and action-object combinations. (a) Colours represent different ages (darkest = youngest, lightest = oldest). Fig. ai shows the relationship between sample size and number of unique actions detected, and Fig. aii shows the relationship between sample size and object-action combinations. (b) The same relationships are shown as seen in Fig a; however, data is organised by ages that are relative to the age at which individuals were first observed cracking open nuts with stone tools: Fib. bi shows how sample size influences the size of action repertoires for each age category, and Fib. bii shows the relationship between sample size and the number of unique action-object combinations.



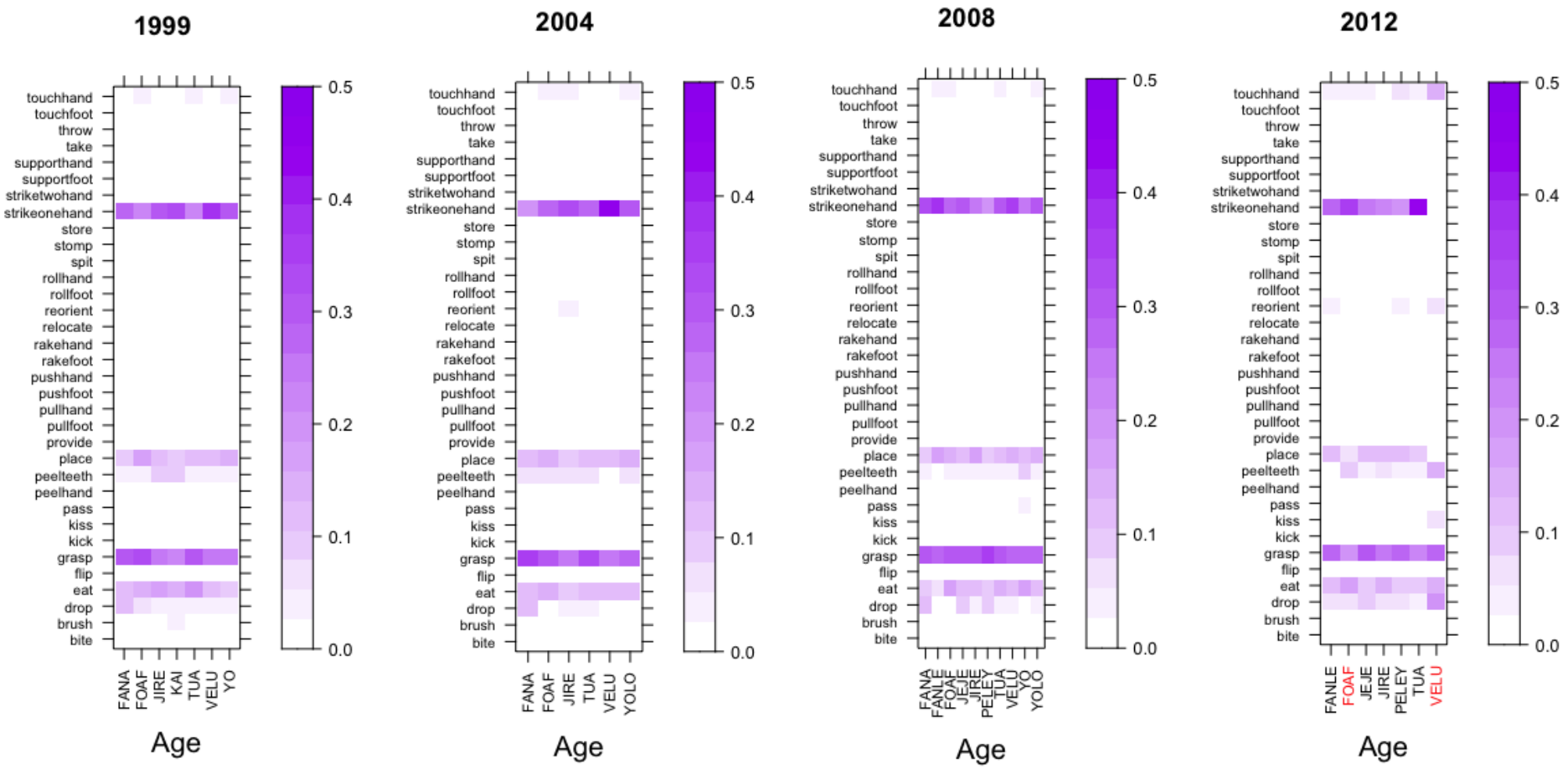


Fig S3. Heatmaps of the proportion of instances each action was sampled during data collection for individuals who were proficient in nut cracking. Proficiency is defined as an individual who is over the age of eight years old, and has successfully learnt the skill of nut cracking. Heatmaps are panelled by sampled year. For each individual in each year, darker squares indicate that actions were more frequently performed. Names in red indicate that, for these individuals, fewer than 400 actions were sampled in a particular year (see Foaf and Velu in 2012).

Table S9. Actions used by individuals who were proficient in nut cracking in each sampled year (1999-2012). Numbers represent the proportion of actions of each unique action type that were performed in a given year, when data is pooled across all proficient tool-users in that year.

Actions	Year			
	1999	2004	2008	2012
bite	0	0.00166667	0.00025	0.00129814
brush	0.01142857	0.00708333	0.0065	0.00173085
drop	0.05107143	0.04375	0.05175	0.07053224
eat	0.14071429	0.11541667	0.11975	0.12289052
flip	0.00142857	0.00125	0.00275	0.0064907
grasp	0.27214286	0.29208333	0.29325	0.26006058
kick	0	0	0	0.00086543
kiss	0.00285714	0.00375	0.00125	0.00389442
pass	0.00428571	0.00083333	0.00375	0.00043271
peelhand	0.00142857	0	0.003	0.00692341
peelteeth	0.05821429	0.05791667	0.046	0.05408914
place	0.12535714	0.12	0.13325	0.105582
provide	0.00035714	0	0.00025	0
pullfoot	0	0	0	0
pullhand	0	0.00333333	0.00025	0
pushfoot	0	0	0.00025	0
pushhand	0.00035714	0	0	0
rakefoot	0	0	0	0
rakehand	0	0.00041667	0.0025	0.00173085
relocate	0	0	0	0
reorient	0.005	0.01041667	0.01	0.01601039
rollfoot	0	0	0	0
rollhand	0	0.00041667	0.00025	0.00432713
spit	0.00214286	0.00041667	0.00175	0.00778884
stomp	0	0	0	0
store	0	0	0	0.0034617
strikeonehand	0.29178571	0.3125	0.292	0.28212895
striketwohand	0	0	0	0
supportfoot	0.00142857	0.00291667	0.00325	0.00692341
supporthand	0	0.0025	0	0.00129814
take	0	0	0	0
throw	0	0	0	0
touchfoot	0.00071429	0.00083333	5.00E-04	0.00043271
touchhand	0.02928571	0.0225	0.0275	0.04110775

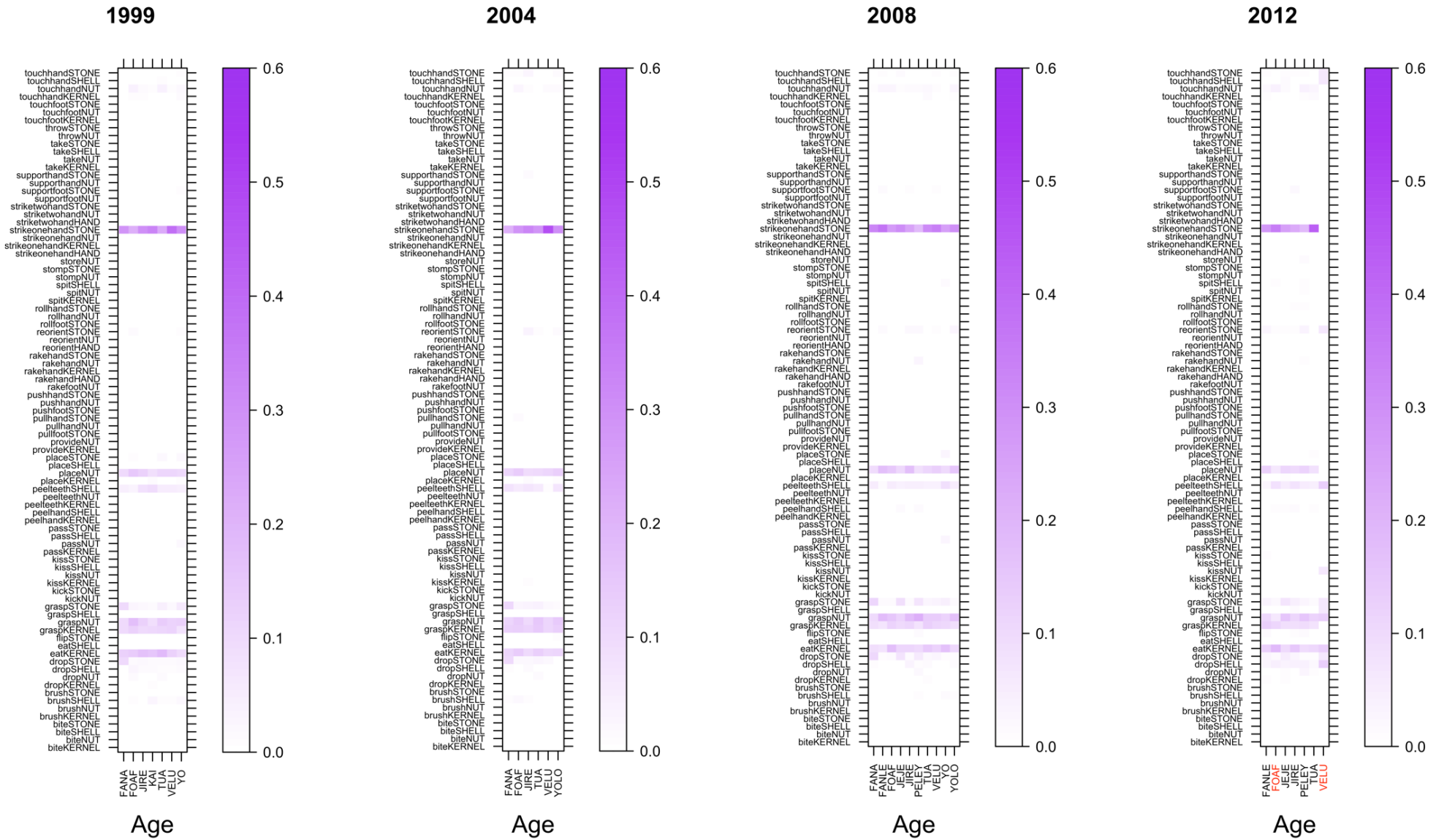


Fig S4. Heatmaps of the proportion of instances each action-object combination was sampled during data collection for individuals who were proficient in nut cracking. Proficiency is defined as an individual who is over the age of eight years old, and has successfully learnt the skill of nut cracking. Heatmaps are panelled by sampled year. For each individual in each year, darker squares indicate that action-object combinations were more frequently performed. Names in red indicate that, for these individuals, fewer than 400 action-object combinations were sampled in a particular year (see Foaf and Velu in 2012).

Table S10. Action-object combinations used by individuals who were proficient in nut cracking in each sampled year (1999-2012). Numbers represent the proportion of action-object combinations of each unique type that were performed in a given year, when data is pooled across all proficient tool-users in that year

Action-object combination	Year			
	1999	2004	2008	2012
biteKERNEL	0	0.00166667	0	0.00043271
biteNUT	0	0	0.00025	0.00043271
biteSHELL	0	0	0	0.00043271
biteSTONE	0	0	0	0
brushKERNEL	0	0.00041667	0	0
brushNUT	0.00035714	0	0.00025	0.00086543
brushSHELL	0.01107143	0.00666667	0.00625	0.00086543
brushSTONE	0	0	0	0
dropKERNEL	0.00321429	0.0025	0.003	0.00432713
dropNUT	0.00535714	0.0025	0.004	0.00865426
dropSHELL	0.01357143	0.00625	0.00975	0.03375162
dropSTONE	0.02892857	0.0325	0.035	0.02379922
eatKERNEL	0.14035714	0.11541667	0.11975	0.12289052
eatSHELL	0.00035714	0	0	0
flipSTONE	0.00142857	0.00125	0.00275	0.0064907
graspKERNEL	0.10714286	0.12708333	0.1	0.09736045
graspNUT	0.12321429	0.12416667	0.15025	0.12159238
graspSHELL	0	0.00083333	0	0.00475984
graspSTONE	0.04178571	0.04	0.043	0.0363479
kickNUT	0	0	0	0
kickSTONE	0	0	0	0.00086543
kissKERNEL	0.00142857	0.00375	5.00E-04	0.00129814
kissNUT	0.00035714	0	0.00025	0.00086543
kissSHELL	0.00035714	0	0	0
kissSTONE	0.00071429	0	5.00E-04	0.00173085
passKERNEL	0	0.00041667	0	0
passNUT	0.00321429	0	0.00275	0
passSHELL	0	0	0	0
passSTONE	0.00107143	0.00041667	0.001	0.00043271
peelhandKERNEL	0	0	0.00025	0
peelhandSHELL	0.00142857	0	0.00275	0.00692341
peelteethKERNEL	0	0	0.00025	0
peelteethNUT	0	0	0	0
peelteethSHELL	0.05821429	0.05791667	0.04575	0.05408914
placeKERNEL	0.00535714	0.00583333	0.002	0.00216357
placeNUT	0.1125	0.11375	0.12775	0.10038944
placeSHELL	0	0	0	0.00043271
placeSTONE	0.0075	0.00041667	0.0035	0.00259628
provideKERNEL	0.00035714	0	0.00025	0
provideNUT	0	0	0	0
pullfootSTONE	0	0	0	0
pullhandNUT	0	0	0.00025	0
pullhandSTONE	0	0.00333333	0	0
pushfootSTONE	0	0	0.00025	0
pushhandNUT	0.00035714	0	0	0
pushhandSTONE	0	0	0	0
rakefootNUT	0	0	0	0
rakehandHAND	0	0	0	0
rakehandKERNEL	0	0	0	0
rakehandNUT	0	0	0.0025	0.00129814
rakehandSTONE	0	0.00041667	0	0.00043271
reorientHAND	0	0	0	0
reorientNUT	0	0	0	0.00043271
reorientSTONE	0.005	0.01041667	0.01	0.01557767
rollfootSTONE	0	0	0	0
rollhandNUT	0	0	0	0.00086543
rollhandSTONE	0	0.00041667	0.00025	0.0034617
spitKERNEL	0.00035714	0.00041667	0	0
spitNUT	0	0	0	0.00259628
spitSHELL	0.00178571	0	0.00175	0.00519256
stompNUT	0	0	0	0
stompSTONE	0	0	0	0
storeNUT	0	0	0	0.0034617
strikeonehandHAND	0	0	0	0
strikeonehandKERNEL	0	0	0	0
strikeonehandNUT	0	0	0	0
strikeonehandSTONE	0.29178571	0.3125	0.292	0.28212895
striketwohandHAND	0	0	0	0
striketwohandNUT	0	0	0	0
striketwohandSTONE	0	0	0	0
supportfootNUT	0	0	0.00025	0
supportfootSTONE	0.00142857	0.00291667	0.003	0.00692341
supporthandNUT	0	0	0	0.00129814
supporthandSTONE	0	0.0025	0	0
takeKERNEL	0	0	0	0
takeNUT	0	0	0	0
takeSHELL	0	0	0	0
takeSTONE	0	0	0	0
throwNUT	0	0	0	0
throwSTONE	0	0	0	0
touchfootKERNEL	0	0	0	0
touchfootNUT	0	0	0	0
touchfootSTONE	0.00071429	0.00083333	5.00E-04	0.00043271
touchhandKERNEL	0.00535714	0	0.00425	0.00735612
touchhandNUT	0.02	0.01125	0.01625	0.02336651
touchhandSHELL	0.00142857	0	0.00125	0.0034617
touchhandSTONE	0.0025	0.01125	0.00575	0.00692341

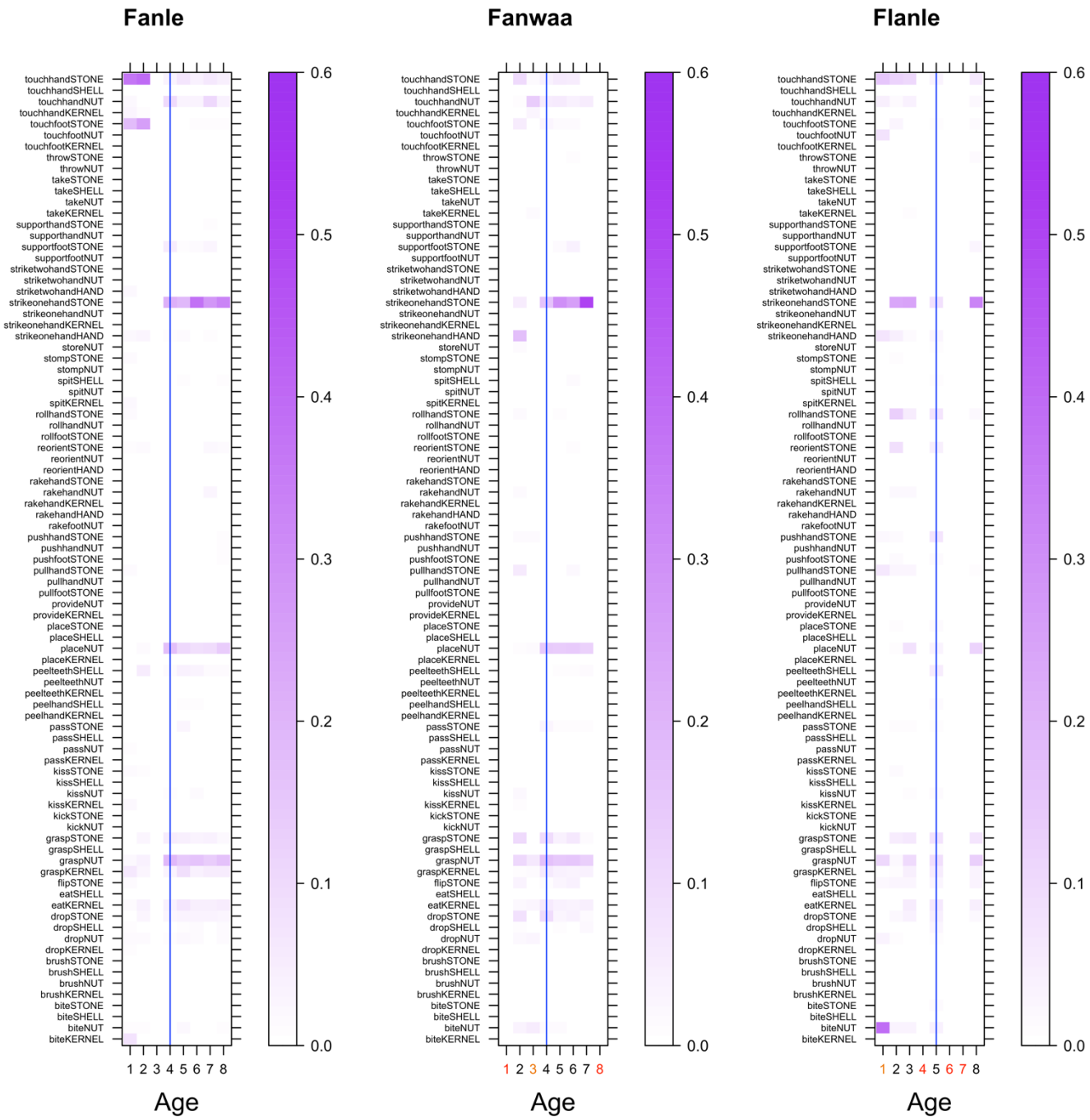


Fig S5. (part 1) Action-object combinations performed by individuals between the ages of one and eight years old. Numbers for ages are colour coded based on sample size: red numbers indicate no actions were sampled at this age; orange indicates fewer than 400 actions; black indicates 400 actions. Darker actions are more frequent. Vertical blue lines indicate the age at which each individual was first observed cracking open nuts using stone tools.

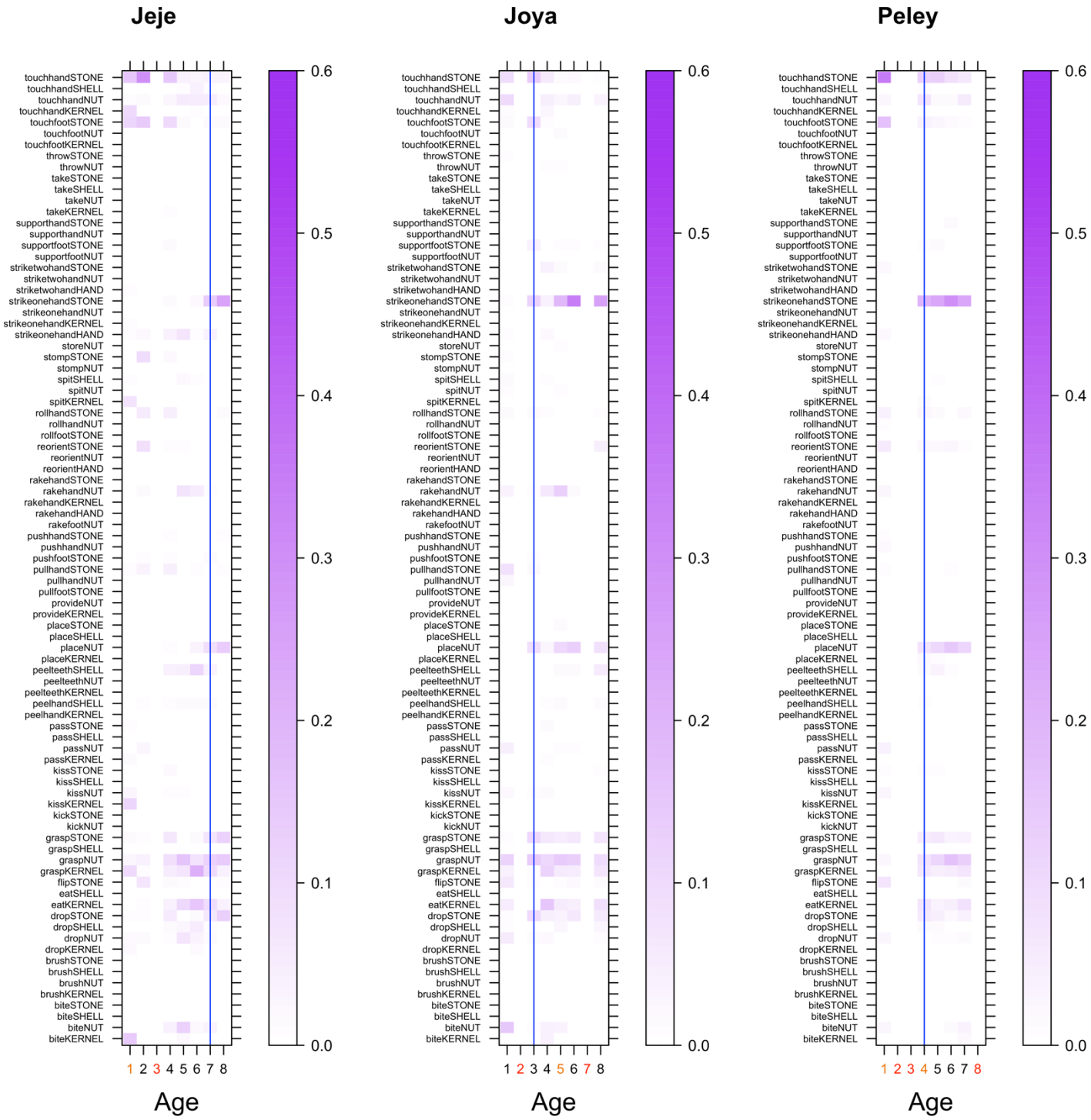


Fig S5. (Part 2) Action-object combinations performed by individuals between the ages of one and eight years old. Numbers for ages are colour coded based on sample size: red numbers indicate no actions were sampled at this age; orange indicates fewer than 400 actions; black indicates 400 actions. Darker actions are more frequent. Vertical blue lines indicate the age at which each individual was first observed cracking open nuts using stone tools.

Table S11. Proportion of action-object combinations sampled for Fanle at each age.

Action	Age							
	1	2	3	4	5	6	7	8
biteKERNEL	0.07304786	0	0	0.00257732	0	0.00255102	0	0
biteNUT	0.00755668	0.01017812	0	0.00515464	0.02261307	0.00255102	0	0.01007557
biteSHELL	0	0	0	0	0	0	0	0
biteSTONE	0	0	0	0	0	0	0	0
brushKERNEL	0	0	0	0.00257732	0	0	0	0
brushNUT	0.00251889	0	0	0.00515464	0	0	0	0
brushSHELL	0	0	0	0	0	0.00255102	0	0
brushSTONE	0	0	0	0	0	0	0.00252525	0
dropKERNEL	0.01007557	0.00508906	0	0	0.00502513	0.00255102	0.00252525	0.00251889
dropNUT	0.01259446	0.01526718	0	0.00773196	0.02261307	0.0127551	0.00505051	0.01259446
dropSHELL	0.01007557	0.00508906	0	0.00515464	0.01005025	0.0127551	0.00252525	0.01763224
dropSTONE	0	0.02544529	0	0.0257732	0.03266332	0.03061224	0.03282828	0.0302267
eatKERNEL	0.01259446	0.03816794	0	0.03865979	0.0678392	0.04591837	0.04545455	0.05289673
eatSHELL	0	0	0	0	0	0	0	0
flipSTONE	0.01511335	0.00508906	0	0	0	0	0.00505051	0.00251889
graspKERNEL	0.06297229	0.02544529	0	0.03092784	0.08542714	0.04081633	0.0530303	0.05289673
graspNUT	0.02267003	0.04071247	0	0.19072165	0.14572864	0.16071429	0.13888889	0.16372796
graspSHELL	0	0	0	0	0	0	0	0
graspSTONE	0	0.02544529	0	0.04896907	0.04271357	0.03571429	0.04040404	0.02267003
kickNUT	0	0	0	0	0	0	0	0
kickSTONE	0	0	0	0	0	0	0	0.00251889
kissKERNEL	0.02015113	0	0	0	0	0	0	0
kissNUT	0.00503778	0	0	0.01030928	0.00502513	0.01785714	0	0.00251889
kissSHELL	0	0	0	0	0	0	0	0
kissSTONE	0.01259446	0.01017812	0	0	0	0	0.00505051	0
passKERNEL	0	0	0	0	0.00502513	0	0	0
passNUT	0.01007557	0	0	0.00257732	0.00502513	0	0	0
passSHELL	0	0	0	0	0	0	0	0
passSTONE	0	0	0	0.00257732	0.02763819	0	0.00252525	0
peelhandKERNEL	0	0	0	0	0	0	0	0
peelhandSHELL	0	0.00254453	0	0.00515464	0.00753769	0.00765306	0	0
peelteethKERNEL	0	0	0	0	0	0	0	0
peelteethNUT	0	0	0	0	0	0	0	0
peelteethSHELL	0.00503778	0.05089059	0	0.01546392	0.04020101	0.03571429	0.01262626	0.01511335
placeKERNEL	0.00251889	0	0	0	0	0.00255102	0.00252525	0
placeNUT	0	0.01526718	0	0.17010309	0.1080402	0.08673469	0.0959596	0.13350126
placeSHELL	0	0	0	0	0	0	0	0
placeSTONE	0	0	0	0.00257732	0.00251256	0	0	0
provideKERNEL	0	0	0	0	0	0	0	0
provideNUT	0	0	0	0	0	0	0	0
pullfootSTONE	0	0	0	0	0	0	0	0
pullhandNUT	0	0	0	0	0	0	0	0
pullhandSTONE	0.01511335	0	0	0	0	0	0.00252525	0
pushfootSTONE	0	0	0	0	0.00251256	0	0	0.00755668
pushhandNUT	0	0	0	0	0	0	0	0.00755668
pushhandSTONE	0	0	0	0	0	0	0	0.01007557
rakefootNUT	0	0	0	0	0	0	0	0
rakehandHAND	0	0	0	0	0	0	0	0
rakehandKERNEL	0	0	0	0	0	0	0	0
rakehandNUT	0	0	0	0	0	0	0.03030303	0
rakehandSTONE	0	0	0	0	0	0	0	0
reorientHAND	0	0	0	0	0	0	0	0
reorientNUT	0	0	0	0	0	0	0	0
reorientSTONE	0.00755668	0.0178117	0	0	0.00502513	0	0.02020202	0.01259446
rollfootSTONE	0	0	0	0	0	0	0	0
rollhandNUT	0	0	0	0	0	0.00255102	0	0
rollhandSTONE	0.01763224	0	0	0.00515464	0	0	0.00252525	0.00503778
spitKERNEL	0.02015113	0	0	0	0	0.00510204	0	0
spitNUT	0	0	0	0	0	0.00255102	0	0
spitSHELL	0	0	0	0	0.01005025	0.00510204	0	0.01007557
stompNUT	0	0	0	0.00515464	0	0	0	0
stompSTONE	0.01511335	0	0	0.00257732	0.00502513	0	0	0
storeNUT	0	0	0	0	0	0.00510204	0	0
strikeonehandHAND	0.02015113	0.02544529	0	0.01030928	0.01256281	0	0.00757576	0
strikeonehandKERNEL	0	0	0	0	0	0	0	0

strikeonehandNUT	0	0	0	0.00257732	0	0	0	0
strikeonehandSTONE	0	0.00254453	0	0.21391753	0.19095477	0.38010204	0.28030303	0.32997481
striketwohandHAND	0.02267003	0	0	0	0.00502513	0	0	0
striketwohandNUT	0	0	0	0	0.00251256	0	0	0
striketwohandSTONE	0	0	0	0	0	0	0	0
supportfootNUT	0	0	0	0	0	0	0	0
supportfootSTONE	0	0.00254453	0	0.04896907	0.01005025	0.0127551	0.02777778	0.00251889
supporthandNUT	0	0	0	0	0	0	0	0
supporthandSTONE	0	0	0	0	0	0	0.00757576	0
takeKERNEL	0	0.00254453	0	0.00257732	0.00251256	0	0	0
takeNUT	0	0	0	0	0.00251256	0	0	0
takeSHELL	0	0	0	0	0.00251256	0	0	0
takeSTONE	0	0	0	0	0	0	0	0
throwNUT	0	0	0	0	0	0	0	0
throwSTONE	0	0	0	0	0	0	0	0
touchfootKERNEL	0.00251889	0	0	0	0	0	0	0
touchfootNUT	0.00251889	0	0	0.00257732	0	0	0	0
touchfootSTONE	0.17884131	0.25699746	0	0.00515464	0.00502513	0.00765306	0.00757576	0.00755668
touchhandKERNEL	0.02770781	0.00763359	0	0	0.00502513	0.00255102	0	0.00503778
touchhandNUT	0.02015113	0.00508906	0	0.09793814	0.03517588	0.03571429	0.10353535	0.03778338
touchhandSHELL	0	0.00508906	0	0	0	0	0	0
touchhandSTONE	0.36523929	0.39949109	0	0.03092784	0.0678392	0.04081633	0.06313131	0.04282116

Table S12. Proportion of action-object combinations sampled for Fanwaa at each age.

Action	Age							
	1	2	3	4	5	6	7	8
biteKERNEL	0	0.00273224	0	0	0	0	0	0
biteNUT	0	0.03551913	0.05063291	0.01308901	0.01648352	0.00527704	0.00508906	0
biteSHELL	0	0	0	0.0026178	0	0	0	0
biteSTONE	0	0	0	0	0	0	0	0
brushKERNEL	0	0	0	0	0	0	0	0
brushNUT	0	0	0	0	0	0	0	0
brushSHELL	0	0	0	0	0.00274725	0	0	0
brushSTONE	0	0	0	0	0	0	0	0
dropKERNEL	0	0	0	0.0052356	0.00274725	0	0	0
dropNUT	0	0.02185792	0.02531646	0	0.00549451	0	0	0
dropSHELL	0	0.00819672	0	0	0.00824176	0	0.02035623	0
dropSTONE	0	0.07923497	0	0.09162304	0.02747253	0.04221636	0.01272265	0
eatKERNEL	0	0.02185792	0.02531646	0.06020942	0.03846154	0.03166227	0.04580153	0
eatSHELL	0	0	0	0	0	0	0	0
flipSTONE	0	0.03278689	0	0.0078534	0.02472527	0.03957784	0.00254453	0
graspKERNEL	0	0.01092896	0.01265823	0.05759162	0.04120879	0.03166227	0.03816794	0
graspNUT	0	0.10655738	0.06329114	0.16492147	0.1510989	0.1530343	0.13231552	0
graspSHELL	0	0	0	0	0.00274725	0	0	0
graspSTONE	0	0.1010929	0	0.09424084	0.03846154	0.06332454	0.01272265	0
kickNUT	0	0	0	0	0	0	0	0
kickSTONE	0	0	0	0	0	0	0	0
kissKERNEL	0	0.00819672	0	0	0	0	0.00254453	0
kissNUT	0	0.02185792	0	0.0052356	0	0.00263852	0.00508906	0
kissSHELL	0	0	0	0	0	0	0	0
kissSTONE	0	0.00273224	0	0	0	0	0	0
passKERNEL	0	0	0	0.0026178	0.00274725	0	0	0
passNUT	0	0	0	0.0052356	0.00549451	0	0.00254453	0
passSHELL	0	0	0	0	0	0	0	0
passSTONE	0	0	0	0.02617801	0.01098901	0.01055409	0.00763359	0
peelhandKERNEL	0	0	0	0	0	0	0	0
peelhandSHELL	0	0.00273224	0	0.0026178	0	0.00263852	0	0
peelteethKERNEL	0	0	0	0	0	0	0.00508906	0
peelteethNUT	0	0	0	0	0	0	0	0
peelteethSHELL	0	0	0	0.0052356	0.00824176	0.00791557	0.01272265	0
placeKERNEL	0	0	0	0	0	0	0	0
placeNUT	0	0.01092896	0.01265823	0.14397906	0.13736264	0.13984169	0.12722646	0
placeSHELL	0	0	0	0	0	0	0	0
placeSTONE	0	0.00273224	0	0	0	0	0	0
provideKERNEL	0	0	0	0	0	0	0	0
provideNUT	0	0	0	0	0	0	0	0
pullfootSTONE	0	0.00273224	0	0	0	0	0	0
pullhandNUT	0	0	0	0	0	0	0	0
pullhandSTONE	0	0.05464481	0	0.0052356	0.00549451	0.01846966	0	0
pushfootSTONE	0	0.00546448	0	0.0026178	0	0.00527704	0	0

pushhandNUT	0	0.00273224	0	0	0	0	0	0
pushhandSTONE	0	0.0136612	0.01265823	0.0052356	0	0.00263852	0	0
rakefootNUT	0	0	0	0	0	0	0	0
rakehandHAND	0	0	0	0	0	0	0	0
rakehandKERNEL	0	0	0	0	0	0	0	0
rakehandNUT	0	0.0136612	0	0	0	0	0	0
rakehandSTONE	0	0	0	0	0	0	0	0
reorientHAND	0	0	0	0	0	0	0	0
reorientNUT	0	0	0	0	0	0	0	0
reorientSTONE	0	0.00273224	0	0	0.00274725	0.00791557	0	0
rollfootSTONE	0	0.00273224	0	0	0	0	0	0
rollhandNUT	0	0	0	0	0	0	0	0
rollhandSTONE	0	0.01639344	0	0.0026178	0.00824176	0.00527704	0	0
spitKERNEL	0	0	0	0	0	0	0	0
spitNUT	0	0.00273224	0	0.0026178	0	0	0	0
spitSHELL	0	0	0	0	0.00549451	0.01319261	0	0
stompNUT	0	0	0	0	0	0	0	0
stompSTONE	0	0	0	0	0	0	0	0
storeNUT	0	0.01639344	0	0.0026178	0	0	0	0
strikeonehandHAND	0	0.17213115	0.60759494	0	0.00549451	0	0	0
strikeonehandKERNEL	0	0	0	0	0	0	0	0
strikeonehandNUT	0	0	0	0	0	0	0.00254453	0
strikeonehandSTONE	0	0.05191257	0	0.16230366	0.3021978	0.25593668	0.50636132	0
striketwohandHAND	0	0	0	0	0	0	0	0
striketwohandNUT	0	0	0	0	0	0	0	0
striketwohandSTONE	0	0	0	0	0	0	0	0
supportfootNUT	0	0	0	0	0	0	0	0
supportfootSTONE	0	0.00546448	0	0.0026178	0.01373626	0.03957784	0	0
supporthandNUT	0	0	0	0	0	0	0	0
supporthandSTONE	0	0	0	0	0.00274725	0.00263852	0	0
takeKERNEL	0	0.00546448	0.01265823	0	0.00274725	0	0	0
takeNUT	0	0	0	0	0	0	0	0
takeSHELL	0	0	0	0	0	0	0	0
takeSTONE	0	0	0	0	0	0	0	0
throwNUT	0	0	0	0.0026178	0	0	0	0
throwSTONE	0	0	0	0.0026178	0	0.01055409	0	0
touchfootKERNEL	0	0	0	0	0	0	0	0
touchfootNUT	0	0	0	0	0	0	0	0
touchfootSTONE	0	0.04918033	0	0.02617801	0.01373626	0.01319261	0.00254453	0
touchhandKERNEL	0	0	0.02531646	0	0	0	0	0
touchhandNUT	0	0.01092896	0.13924051	0.05235602	0.05494505	0.04221636	0.05343511	0
touchhandSHELL	0	0	0	0	0	0	0	0
touchhandSTONE	0	0.1010929	0.01265823	0.04188482	0.05769231	0.05277045	0.00254453	0

Table S13. Proportion of action-object combinations sampled for Flanle at each age.

Action	Age							
	1	2	3	4	5	6	7	8
biteKERNEL	0	0	0	0	0	0	0	0
biteNUT	0.39226519	0.03225806	0.03216374	0	0.03773585	0	0	0.00268817
biteSHELL	0	0	0	0	0.00539084	0	0	0
biteSTONE	0	0	0	0	0.01617251	0	0	0
brushKERNEL	0	0	0	0	0	0	0	0
brushNUT	0	0	0	0	0	0	0	0
brushSHELL	0	0	0	0	0.00269542	0	0	0
brushSTONE	0	0	0	0	0	0	0	0.00537634
dropKERNEL	0	0	0	0	0	0	0	0
dropNUT	0.03314917	0.00806452	0.00292398	0	0.00808625	0	0	0.00268817
dropSHELL	0	0	0	0	0.02425876	0	0	0
dropSTONE	0	0.0188172	0.04093567	0	0.04312668	0	0	0.0188172
eatKERNEL	0	0.00537634	0.0497076	0	0.06469003	0	0	0.04569892
eatSHELL	0	0	0	0	0	0	0	0
flipSTONE	0.02209945	0.02688172	0.02631579	0	0.02425876	0	0	0.03225806
graspKERNEL	0	0.00806452	0.04678363	0	0.04851752	0	0	0.03494624
graspNUT	0.10497238	0.0188172	0.0994152	0	0.08625337	0	0	0.13172043
graspSHELL	0	0	0	0	0.00808625	0	0	0
graspSTONE	0	0.05107527	0.06140351	0	0.07816712	0	0	0.06989247
kickNUT	0	0	0	0	0	0	0	0
kickSTONE	0	0	0	0	0.00269542	0	0	0
kissKERNEL	0	0	0	0	0.00539084	0	0	0.00268817
kissNUT	0.00552486	0.00537634	0.00877193	0	0.01347709	0	0	0.00537634

kissSHELL	0	0	0	0	0.00269542	0	0	0
kissSTONE	0	0.01344086	0	0	0.00539084	0	0	0.00268817
passKERNEL	0	0	0	0	0.00269542	0	0	0
passNUT	0	0.00537634	0	0	0	0	0	0
passSHELL	0	0	0	0	0.00269542	0	0	0
passSTONE	0	0.01075269	0.01169591	0	0.01078167	0	0	0
peelhandKERNEL	0	0	0	0	0	0	0	0
peelhandSHELL	0	0	0.00292398	0	0.01617251	0	0	0
peelteethKERNEL	0	0	0	0	0	0	0	0
peelteethNUT	0	0	0	0	0	0	0	0
peelteethSHELL	0	0.00268817	0.00584795	0	0.04851752	0	0	0.00537634
placeKERNEL	0	0	0.00292398	0	0.00269542	0	0	0
placeNUT	0.00552486	0.01075269	0.07894737	0	0.03234501	0	0	0.1155914
placeSHELL	0	0	0	0	0	0	0	0
placeSTONE	0	0.01075269	0	0	0.01347709	0	0	0.00268817
provideKERNEL	0	0	0	0	0	0	0	0
provideNUT	0	0	0	0	0.00269542	0	0	0
pullfootSTONE	0	0	0	0	0	0	0	0
pullhandNUT	0	0	0	0	0	0	0	0
pullhandSTONE	0.06629834	0.02688172	0.02631579	0	0	0	0	0.01075269
pushfootSTONE	0	0.01612903	0	0	0.01617251	0	0	0.00537634
pushhandNUT	0	0	0	0	0	0	0	0
pushhandSTONE	0.02209945	0.01612903	0.00584795	0	0.06738544	0	0	0
rakefootNUT	0	0	0	0	0	0	0	0
rakehandHAND	0	0	0	0	0	0	0	0
rakehandKERNEL	0	0	0	0	0	0	0	0
rakehandNUT	0	0.02150538	0.02046784	0	0	0	0	0
rakehandSTONE	0	0	0	0	0	0	0	0
reorientHAND	0	0	0	0	0.00269542	0	0	0
reorientNUT	0	0	0	0	0	0	0	0
reorientSTONE	0	0.08870968	0	0	0.0458221	0	0	0.00537634
rollfootSTONE	0	0	0	0	0	0	0	0.00268817
rollhandNUT	0	0	0	0	0.00269542	0	0	0
rollhandSTONE	0	0.13172043	0.0497076	0	0.07008086	0	0	0.02419355
spitKERNEL	0	0	0	0	0.00269542	0	0	0
spitNUT	0	0	0	0	0	0	0	0
spitSHELL	0	0	0	0	0.00808625	0	0	0.00268817
stompNUT	0	0	0	0	0	0	0	0
stompSTONE	0	0.00806452	0	0	0	0	0	0
storeNUT	0	0	0.00292398	0	0.00808625	0	0	0
strikeonehandHAND	0.0718232	0.04569892	0.01461988	0	0.02425876	0	0	0
strikeonehandKERNEL	0	0	0	0	0	0	0	0
strikeonehandNUT	0	0.00537634	0	0	0	0	0	0
strikeonehandSTONE	0	0.24193548	0.24561404	0	0.08355795	0	0	0.33064516
striketwohandHAND	0	0	0	0	0.00269542	0	0	0
striketwohandNUT	0	0	0	0	0	0	0	0
striketwohandSTONE	0	0.00537634	0	0	0	0	0	0
supportfootNUT	0	0	0	0	0	0	0	0
supportfootSTONE	0	0	0.00292398	0	0.00269542	0	0	0.02688172
supporthandNUT	0	0	0	0	0	0	0	0
supporthandSTONE	0	0	0.00292398	0	0	0	0	0
takeKERNEL	0	0	0.00877193	0	0	0	0	0
takeNUT	0	0	0	0	0	0	0	0
takeSHELL	0	0	0	0	0	0	0	0
takeSTONE	0	0	0	0	0.00269542	0	0	0
throwNUT	0	0	0	0	0	0	0	0
throwSTONE	0	0	0	0	0	0	0	0.01344086
touchfootKERNEL	0	0	0	0	0	0	0	0
touchfootNUT	0.07734807	0.00537634	0	0	0	0	0	0
touchfootSTONE	0	0.02956989	0.00292398	0	0.01078167	0	0	0.01344086
touchhandKERNEL	0	0	0	0	0	0	0	0
touchhandNUT	0.0441989	0.01344086	0.04093567	0	0.00269542	0	0	0.02150538
touchhandSHELL	0	0	0	0	0.00539084	0	0	0.00268817
touchhandSTONE	0.15469613	0.1155914	0.10526316	0	0.03234501	0	0	0.06182796

Table S14. Proportion of action-object combinations sampled for Jeje at each age.

Action	Age							
	1	2	3	4	5	6	7	8
biteKERNEL	0.1417004	0	0	0.00260417	0.01861702	0	0	0
biteNUT	0.00404858	0	0	0.0390625	0.125	0.02094241	0.03291139	0.00259067

biteSHELL	0	0	0	0	0	0	0	0
biteSTONE	0	0	0	0	0	0	0	0
brushKERNEL	0	0	0	0	0	0	0	0
brushNUT	0	0	0	0	0	0.0026178	0	0
brushSHELL	0.00404858	0	0	0	0	0	0	0
brushSTONE	0	0	0	0	0	0.0052356	0	0
dropKERNEL	0.02024291	0	0	0.00260417	0.00531915	0.01570681	0.00506329	0
dropNUT	0.01619433	0.01808786	0	0.0078125	0.06914894	0.03403141	0.01265823	0.00259067
dropSHELL	0	0.00258398	0	0.01302083	0.02659574	0.05235602	0.01012658	0.00518135
dropSTONE	0.00809717	0.01033592	0	0.0546875	0	0.01308901	0.06329114	0.12953368
eatKERNEL	0	0.00775194	0	0.04166667	0.10638298	0.15183246	0.09113924	0.04145078
eatSHELL	0	0	0	0	0	0	0	0
flipSTONE	0.00404858	0.07235142	0	0.015625	0.0106383	0.0026178	0.00506329	0.00777202
graspKERNEL	0.09716599	0.00775194	0	0.04947917	0.07180851	0.21727749	0.09873418	0.04145078
graspNUT	0.0242915	0.03875969	0	0.08854167	0.15957447	0.07853403	0.12658228	0.14507772
graspSHELL	0.00404858	0	0	0.00520833	0.00265957	0.0026178	0	0
graspSTONE	0.01619433	0.01033592	0	0.06510417	0	0.01570681	0.06835443	0.12435233
kickNUT	0	0	0	0	0	0	0	0
kickSTONE	0	0	0	0.00260417	0	0	0	0
kissKERNEL	0.10931174	0	0	0	0	0	0.00506329	0
kissNUT	0.0242915	0.00258398	0	0.01041667	0.0106383	0	0	0
kissSHELL	0	0	0	0	0	0	0	0
kissSTONE	0.00404858	0	0	0.01822917	0.00531915	0	0	0
passKERNEL	0.01619433	0.00258398	0	0.00260417	0.00531915	0	0	0
passNUT	0	0.02583979	0	0	0.00265957	0	0.00253165	0
passSHELL	0	0	0	0.00260417	0	0	0.00253165	0
passSTONE	0.00809717	0	0	0	0	0	0	0
peelhandKERNEL	0	0	0	0	0	0	0	0
peelhandSHELL	0	0.00775194	0	0.01041667	0.01595745	0.01308901	0.01518987	0.00259067
peelteethKERNEL	0	0	0	0	0.00531915	0	0	0.00259067
peelteethNUT	0	0	0	0	0	0	0	0
peelteethSHELL	0	0.00516796	0	0.0390625	0.04521277	0.10994764	0.03544304	0.00259067
placeKERNEL	0	0	0	0	0	0	0	0
placeNUT	0	0	0	0.0078125	0.00265957	0.03141361	0.08607595	0.13471503
placeSHELL	0	0	0	0	0	0	0	0
placeSTONE	0	0	0	0.00260417	0	0	0	0
provideKERNEL	0	0	0	0	0	0	0	0
provideNUT	0	0	0	0	0	0	0	0
pullfootSTONE	0	0	0	0.00520833	0	0	0	0.00259067
pullhandNUT	0	0	0	0	0	0	0	0
pullhandSTONE	0.00809717	0.03617571	0	0.046875	0.00531915	0.0104712	0.00253165	0.00777202
pushfootSTONE	0	0.00775194	0	0.0078125	0.00265957	0	0.01518987	0.00259067
pushhandNUT	0	0	0	0	0	0	0	0
pushhandSTONE	0	0	0	0.01041667	0	0	0	0.00777202
rakefootNUT	0	0	0	0	0	0	0	0
rakehandHAND	0	0	0	0	0	0	0	0
rakehandKERNEL	0	0	0	0	0	0	0	0
rakehandNUT	0	0.01550388	0	0.00520833	0.07712766	0.04973822	0.00759494	0
rakehandSTONE	0	0	0	0	0	0	0	0
reorientHAND	0	0	0	0	0	0	0	0
reorientNUT	0	0	0	0	0	0	0	0
reorientSTONE	0.00404858	0.0878553	0	0.0078125	0.0106383	0.0026178	0.00506329	0.00259067
rollfootSTONE	0	0	0	0.00260417	0	0	0.00253165	0
rollhandNUT	0	0	0	0	0	0	0	0
rollhandSTONE	0	0.05684755	0	0.04427083	0	0	0	0.01554404
spitKERNEL	0.07287449	0	0	0	0	0	0	0
spitNUT	0	0	0	0	0	0	0.00506329	0
spitSHELL	0.00809717	0	0	0.00520833	0.01861702	0.0104712	0	0.00259067
stompNUT	0.00404858	0	0	0	0	0	0	0
stompSTONE	0	0.09302326	0	0.0234375	0	0	0	0
storeNUT	0	0	0	0	0	0	0	0
strikeonehandHAND	0.00809717	0.02325581	0	0.0390625	0.07180851	0.0078534	0.04050633	0
strikeonehandKERNEL	0.00809717	0	0	0	0	0	0	0
strikeonehandNUT	0	0	0	0	0	0	0.00506329	0
strikeonehandSTONE	0	0.00516796	0	0.015625	0	0.02094241	0.13924051	0.24611399
striketwohandHAND	0.00809717	0	0	0	0	0	0	0
striketwohandNUT	0	0	0	0	0	0	0	0
striketwohandSTONE	0	0	0	0	0	0	0	0
supportfootNUT	0	0	0	0	0	0	0	0
supportfootSTONE	0	0	0	0.01302083	0	0.0026178	0.00253165	0
supporthandNUT	0	0	0	0	0	0	0	0

supporthandSTONE	0	0	0	0	0	0	0	0
takeKERNEL	0	0	0	0.0078125	0.00531915	0	0.00253165	0
takeNUT	0	0	0	0	0	0	0	0
takeSHELL	0	0	0	0	0	0	0	0
takeSTONE	0	0	0	0	0	0	0	0
throwNUT	0	0	0	0	0	0	0	0
throwSTONE	0	0	0	0.00260417	0	0	0	0
touchfootKERNEL	0	0	0	0	0	0	0	0
touchfootNUT	0	0	0	0	0	0	0	0
touchfootSTONE	0.11336032	0.14470284	0	0.1015625	0.01329787	0.0026178	0.01772152	0.01554404
touchhandKERNEL	0.10121457	0	0	0.00520833	0	0.0078534	0.00253165	0
touchhandNUT	0.00809717	0.01550388	0	0.02864583	0.05851064	0.05235602	0.05063291	0.02331606
touchhandSHELL	0	0	0	0	0.00797872	0.03926702	0.01012658	0
touchhandSTONE	0.15384615	0.30232558	0	0.14583333	0.03989362	0.02617801	0.03037975	0.03108808

Table S15. Proportion of action-object combinations sampled for Joya at each age.

Action	Age							
	1	2	3	4	5	6	7	8
biteKERNEL	0	0	0	0.04012346	0	0	0	0
biteNUT	0.14589666	0	0.01126761	0.03703704	0.03305785	0.00263852	0	0
biteSHELL	0	0	0	0	0	0	0	0
biteSTONE	0	0	0	0.00308642	0	0	0	0
brushKERNEL	0	0	0	0	0	0	0	0
brushNUT	0	0	0.0028169	0	0	0	0	0
brushSHELL	0	0	0	0	0	0	0	0
brushSTONE	0	0	0	0	0	0	0	0
dropKERNEL	0	0	0	0	0	0.00263852	0	0
dropNUT	0.05775076	0	0.01408451	0.02160494	0	0	0	0.01038961
dropSHELL	0.00911854	0	0.0028169	0	0.02479339	0.00263852	0	0.02857143
dropSTONE	0.00607903	0	0.09859155	0.04320988	0.03305785	0.06068602	0	0.05974026
eatKERNEL	0.04863222	0	0.0028169	0.15432099	0.05785124	0.04485488	0	0.09090909
eatSHELL	0	0	0	0	0	0	0	0
flipSTONE	0.06079027	0	0.01126761	0.00308642	0.00826446	0.0237467	0	0.01818182
graspKERNEL	0.03951368	0	0.01126761	0.11728395	0.05785124	0.05013193	0	0.06753247
graspNUT	0.11550152	0	0.14084507	0.10802469	0.14049587	0.13192612	0	0.09350649
graspSHELL	0.00303951	0	0	0	0	0	0	0.0025974
graspSTONE	0.00911854	0	0.10704225	0.0617284	0.04958678	0.06332454	0	0.06753247
kickNUT	0	0	0	0	0	0	0	0
kickSTONE	0	0	0	0	0	0	0	0
kissKERNEL	0	0	0	0	0	0	0	0
kissNUT	0.0212766	0	0.0084507	0.0154321	0	0	0	0
kissSHELL	0	0	0	0	0	0	0	0
kissSTONE	0.00303951	0	0	0.00308642	0	0	0	0.00779221
passKERNEL	0	0	0	0.00925926	0	0	0	0
passNUT	0.04559271	0	0.0028169	0	0.00826446	0.00791557	0	0
passSHELL	0	0	0	0	0	0	0	0
passSTONE	0	0	0.0056338	0.01234568	0	0.00263852	0	0.0025974
peelhandKERNEL	0	0	0	0	0	0	0	0
peelhandSHELL	0	0	0	0.00925926	0.01652893	0.00527704	0	0.01558442
peelteethKERNEL	0	0	0	0	0	0	0	0
peelteethNUT	0	0	0	0	0	0	0	0
peelteethSHELL	0.00303951	0	0	0	0.01652893	0.01583113	0	0.05714286
placeKERNEL	0	0	0	0	0	0	0	0.0025974
placeNUT	0.00303951	0	0.09014085	0.02777778	0.10743802	0.1292876	0	0.08311688
placeSHELL	0	0	0	0	0	0	0	0
placeSTONE	0	0	0.0056338	0	0.01652893	0	0	0
provideKERNEL	0	0	0	0	0	0	0	0
provideNUT	0	0	0	0	0	0	0	0
pullfootSTONE	0	0	0.0056338	0	0	0	0	0
pullhandNUT	0.02735562	0	0	0	0	0	0	0
pullhandSTONE	0.07902736	0	0.01971831	0.00308642	0	0	0	0
pushfootSTONE	0	0	0.0084507	0	0	0.00263852	0	0
pushhandNUT	0.00303951	0	0	0	0	0	0	0
pushhandSTONE	0	0	0.0028169	0.00308642	0	0.00263852	0	0
rakefootNUT	0	0	0.0028169	0	0	0	0	0
rakehandHAND	0	0	0	0	0	0	0	0
rakehandKERNEL	0	0	0	0	0	0	0	0
rakehandNUT	0.03343465	0	0.0084507	0.0617284	0.1322314	0.01319261	0	0.00519481
rakehandSTONE	0	0	0	0	0	0	0	0
reorientHAND	0	0	0	0	0	0	0	0

reorientNUT	0	0	0	0	0	0	0	0
reorientSTONE	0	0	0.0028169	0	0	0	0	0.04415584
rollfootSTONE	0	0	0.0028169	0	0	0	0	0
rollhandNUT	0	0	0	0	0	0	0	0
rollhandSTONE	0.01519757	0	0.01690141	0.00925926	0	0	0	0.00779221
spitKERNEL	0	0	0	0	0	0	0	0
spitNUT	0.00911854	0	0.0028169	0	0.00826446	0	0	0
spitSHELL	0.01215805	0	0	0.00617284	0	0.00527704	0	0.0025974
stompNUT	0	0	0	0	0	0	0	0
stompSTONE	0.00607903	0	0	0.00308642	0	0	0	0
storeNUT	0	0	0.0056338	0	0.00826446	0	0	0
strikeonehandHAND	0.00911854	0	0	0.02160494	0	0	0	0
strikeonehandKERNEL	0	0	0	0	0	0	0	0
strikeonehandNUT	0	0	0	0	0	0	0	0
strikeonehandSTONE	0.00607903	0	0.11830986	0.03703704	0.19008264	0.35092348	0	0.25194805
striketwohandHAND	0	0	0	0	0	0	0	0
striketwohandNUT	0	0	0	0	0	0	0	0
striketwohandSTONE	0	0	0	0.03703704	0.01652893	0	0	0.01818182
supportfootNUT	0	0	0	0	0	0	0	0
supportfootSTONE	0	0	0.03661972	0	0.00826446	0.01055409	0	0.01038961
supporthandNUT	0	0	0	0	0	0	0	0
supporthandSTONE	0	0	0.0028169	0	0	0	0	0
takeKERNEL	0	0	0	0	0	0	0	0
takeNUT	0	0	0	0	0	0	0	0
takeSHELL	0	0	0	0	0	0	0	0
takeSTONE	0.00303951	0	0	0	0	0	0	0
throwNUT	0	0	0	0.00617284	0.00826446	0	0	0
throwSTONE	0.00911854	0	0.0028169	0.00308642	0	0	0	0
touchfootKERNEL	0	0	0	0	0	0	0	0
touchfootNUT	0	0	0.0056338	0	0.01652893	0	0	0
touchfootSTONE	0.01519757	0	0.09577465	0.00925926	0	0.00263852	0	0.00519481
touchhandKERNEL	0.00607903	0	0	0.02777778	0	0.00263852	0	0
touchhandNUT	0.10030395	0	0.0056338	0.0462963	0.02479339	0.0474934	0	0.03636364
touchhandSHELL	0	0	0	0	0	0	0	0
touchhandSTONE	0.09422492	0	0.13802817	0.05864198	0.01652893	0.01846966	0	0.01038961

Table S16. Proportion of action-object combinations sampled for Peley at each age.

Action	Age							
	1	2	3	4	5	6	7	8
biteKERNEL	0	0	0	0	0.00254453	0	0.01842105	0
biteNUT	0.02941176	0	0	0	0.00508906	0.0129199	0.03157895	0
biteSHELL	0	0	0	0	0	0	0	0
biteSTONE	0	0	0	0	0	0	0	0
brushKERNEL	0	0	0	0	0	0	0	0
brushNUT	0	0	0	0	0	0	0	0
brushSHELL	0	0	0	0.00411523	0	0	0	0
brushSTONE	0	0	0	0.00411523	0.00254453	0	0.00263158	0
dropKERNEL	0	0	0	0	0	0.00258398	0.00263158	0
dropNUT	0.02941176	0	0	0	0.00763359	0.01033592	0.01315789	0
dropSHELL	0	0	0	0.01234568	0.01526718	0	0.00526316	0
dropSTONE	0	0	0	0.05761317	0.04580153	0.02325581	0.03947368	0
eatKERNEL	0	0	0	0.06995885	0.03307888	0.04392765	0.07894737	0
eatSHELL	0	0	0	0	0	0	0	0
flipSTONE	0.06862745	0	0	0.00411523	0.00508906	0.00516796	0.01578947	0
graspKERNEL	0	0	0	0.0617284	0.04580153	0.05167959	0.07105263	0
graspNUT	0.02941176	0	0	0.07407407	0.10941476	0.16795866	0.13157895	0
graspSHELL	0	0	0	0	0	0	0	0
graspSTONE	0	0	0	0.04938272	0.06615776	0.03617571	0.03947368	0
kickNUT	0	0	0	0	0	0	0	0
kickSTONE	0	0	0	0	0	0	0	0
kissKERNEL	0	0	0	0.00411523	0.00254453	0	0.00263158	0
kissNUT	0.02941176	0	0	0	0.00254453	0.00516796	0.00263158	0
kissSHELL	0	0	0	0	0	0	0	0
kissSTONE	0.00980392	0	0	0.00823045	0.01017812	0	0	0
passKERNEL	0	0	0	0.00411523	0	0	0	0
passNUT	0.03921569	0	0	0	0	0	0	0
passSHELL	0	0	0	0	0	0	0	0
passSTONE	0	0	0	0.00411523	0.00254453	0	0.00526316	0
peelhandKERNEL	0	0	0	0	0	0	0	0

peelhandSHELL	0	0	0	0.00823045	0.00254453	0	0	0
peelteethKERNEL	0	0	0	0	0	0	0	0
peelteethNUT	0	0	0	0	0	0	0	0
peelteethSHELL	0	0	0	0.01646091	0.03562341	0.01033592	0.00526316	0
placeKERNEL	0	0	0	0.02057613	0.00763359	0	0	0
placeNUT	0	0	0	0.07407407	0.10687023	0.14728682	0.11052632	0
placeSHELL	0	0	0	0	0	0	0	0
placeSTONE	0	0	0	0	0	0	0	0
provideKERNEL	0	0	0	0	0	0	0	0
provideNUT	0	0	0	0	0	0	0	0
pullfootSTONE	0	0	0	0	0	0	0	0
pullhandNUT	0	0	0	0	0	0	0	0
pullhandSTONE	0.00980392	0	0	0	0.00508906	0.00775194	0.00526316	0
pushfootSTONE	0	0	0	0	0.00254453	0.00516796	0	0
pushhandNUT	0.01960784	0	0	0.00411523	0	0	0	0
pushhandSTONE	0.00980392	0	0	0	0.00254453	0	0.00526316	0
rakefootNUT	0	0	0	0	0	0	0	0
rakehandHAND	0	0	0	0	0	0	0	0
rakehandKERNEL	0	0	0	0	0	0	0	0
rakehandNUT	0.02941176	0	0	0	0	0	0	0
rakehandSTONE	0	0	0	0	0	0	0	0
reorientHAND	0	0	0	0	0	0	0	0
reorientNUT	0	0	0	0	0	0	0	0
reorientSTONE	0.05882353	0	0	0.02057613	0.02035623	0.02842377	0.00789474	0
rollfootSTONE	0	0	0	0	0	0	0	0
rollhandNUT	0.00980392	0	0	0	0	0	0	0
rollhandSTONE	0.03921569	0	0	0.02880658	0.01272265	0.00516796	0.01842105	0
spitKERNEL	0	0	0	0.01646091	0	0	0	0
spitNUT	0	0	0	0	0.00508906	0	0	0
spitSHELL	0	0	0	0	0.01017812	0	0.00526316	0
stompNUT	0	0	0	0	0	0	0	0
stompSTONE	0	0	0	0	0	0	0	0
storeNUT	0	0	0	0	0	0	0	0
strikeonehandHAND	0.01960784	0	0	0.00411523	0	0	0	0
strikeonehandKERNEL	0	0	0	0	0	0	0	0
strikeonehandNUT	0	0	0	0	0	0	0	0
strikeonehandSTONE	0	0	0	0.20164609	0.24173028	0.29715762	0.23947368	0
striketwohandHAND	0	0	0	0	0	0	0	0
striketwohandNUT	0	0	0	0	0	0	0	0
striketwohandSTONE	0.01960784	0	0	0	0	0	0	0
supportfootNUT	0	0	0	0	0	0	0	0
supportfootSTONE	0	0	0	0.00823045	0.01272265	0.00258398	0.00263158	0
supporthandNUT	0	0	0	0	0	0	0	0
supporthandSTONE	0	0	0	0	0	0.01550388	0	0
takeKERNEL	0	0	0	0	0	0	0	0
takeNUT	0	0	0	0	0	0	0	0
takeSHELL	0	0	0	0	0	0	0	0
takeSTONE	0	0	0	0	0	0	0	0
throwNUT	0	0	0	0	0	0	0	0
throwSTONE	0	0	0	0	0	0.00258398	0.00526316	0
touchfootKERNEL	0	0	0	0	0	0	0	0
touchfootNUT	0	0	0	0	0	0	0	0
touchfootSTONE	0.16666667	0	0	0.03703704	0.02798982	0.0129199	0.00789474	0
touchhandKERNEL	0	0	0	0	0	0.00258398	0.00526316	0
touchhandNUT	0.02941176	0	0	0.06995885	0.0178117	0.0129199	0.05526316	0
touchhandSHELL	0	0	0	0.00823045	0	0	0	0
touchhandSTONE	0.35294118	0	0	0.12345679	0.13231552	0.09043928	0.06578947	0

Table S17. Proportion of action-object combinations performed by individuals of each standardised age category. Data describes all sampled action-object combinations from all individuals.

Action-Object Combination	Relative Age (Years)											
	-6	-5	-4	-3	-2	-1	0	1	2	3	4	5
biteKERNEL	0.1417004	0	0.0725	0.0230417	0.0051387 5	0	0.0004458 3	0.0072765 1	0.000757	0.0035017 5	0	0
biteNUT	0.0040485 8	0.0025	0.0075	0.0253456 2	0.0657759 5	0.0250521 9	0.0169416	0.0155925 2	0.0098410 3	0.008004	0.01	0
biteSHELL	0	0	0	0	0	0	0.0013374 9	0	0	0	0	0
biteSTONE	0	0	0	0	0	0	0.0031208 2	0.0005197 5	0	0	0	0
brushKERNEL	0	0	0	0	0	0	0.0004458 3	0	0	0	0	0
brushNUT	0	0	0.0025	0.0007680 5	0.0005138 7	0.0020876 8	0.0013374 9	0	0	0	0	0
brushSHELL	0.0040485 8	0	0	0	0	0	0.0008916 6	0.0005197 5	0.000757	0	0	0

brushSTONE	0	0	0	0	0	0.0041753	0.0004458	0.0005197	0	0.002001	0	0
dropKERNEL	0.0202429	0	0.01	0.0046082	0.0030832	0.0125261	0.0017833	0.0015592	0.001514	0.0015007	0.002	0.002
dropNUT	0.0161943	0.017	0.012	0.0115207	0.0334018	0.0313152	0.0075791	0.0114345	0.0068130	0.004002	0.012	0.01
dropSHELL	0	0.005	0.01	0.0076804	0.0097636	0.0459290	0.0089166	0.0083160	0.0060560	0.006003	0.017	0.027
dropSTONE	0.0080971	0.01	0	0.0215053	0.0308324	0.0104384	0.0641997	0.0556133	0.0310370	0.0350175	0.03	0.057
eatKERNEL	0	0.012	0.012	0.0184331	0.0513874	0.1356993	0.0534997	0.0649688	0.0439061	0.0520260	0.055	0.1
eatSHELL	0	0	0	0	0	0	0	0	0	0	0	0
flipSTONE	0.0040485	0.07	0.015	0.0230414	0.0262076	0.0020876	0.0102541	0.0083160	0.0136260	0.0155077	0.002	0.017
graspKERNEL	0.0971659	0.012	0.062	0.0376344	0.0385406	0.1858037	0.0508247	0.0660083	0.0439061	0.0505252	0.055	0.077
graspNUT	0.0242915	0.04	0.022	0.0437788	0.1032888	0.0730688	0.1341952	0.1340956	0.1582134	0.1310655	0.162	0.09
graspSHELL	0.0040485	0	0	0.0015361	0.0010277	0.0020876	0.0013374	0.0005197	0	0	0	0.002
graspSTONE	0.0161943	0.01	0	0.0337941	0.0395683	0.0125261	0.0766830	0.0670478	0.0446631	0.0465232	0.022	0.065
kickNUT	0	0	0	0	0	0	0	0	0	0	0	0
kickSTONE	0	0	0	0.0007680	0	0	0.0004458	0	0	0	0.002	0
kissKERNEL	0.1093117	0	0.02	0.0061443	0.0015416	0	0.0022291	0.0005197	0	0.0015007	0	0
kissNUT	0.0242915	0.002	0.005	0.0084485	0.0113052	0	0.0062416	0.0046777	0.0075700	0.0035017	0.002	0
kissSHELL	0	0	0	0	0	0	0.0004458	0	0	0	0	0
kissSTONE	0.0040485	0	0.012	0.0138248	0.004111	0	0.0017833	0.0025987	0	0.0015007	0	0.007
passKERNEL	0.0161943	0.002	0	0.0007680	0.0010277	0	0.0013374	0.0031185	0	0	0	0
passNUT	0	0.025	0.01	0.0076804	0.0082219	0	0.0022291	0.002079	0.000757	0.002001	0	0
passSHELL	0	0	0	0.0007680	0	0	0.0008916	0	0	0	0	0
passSTONE	0.0080971	0	0	0.0030722	0.0025693	0	0.0102541	0.0103950	0.0030280	0.0035017	0	0.002
peelhandKERNEL	0	0	0	0	0	0	0	0	0	0	0	0
peelhandSHELL	0	0.015	0	0.0038402	0.0051387	0.0104384	0.0075791	0.004158	0.0045420	0.0010005	0	0.015
peelteethKERNEL	0	0	0	0	0.0010277	0	0	0.0010395	0	0.0010005	0	0
peelteethNUT	0	0	0	0	0	0	0	0	0	0	0	0
peelteethSHELL	0	0.007	0.005	0.0153609	0.0220966	0.0918580	0.0200624	0.0176715	0.0181680	0.010005	0.015	0.06
placeKERNEL	0	0	0.002	0.0007680	0.0005138	0	0.0026749	0.0015592	0.000757	0.0005002	0	0.002
placeNUT	0	0	0	0.0069124	0.0231243	0.0271398	0.0998662	0.1044698	0.1233913	0.1140570	0.132	0.082
placeSHELL	0	0	0	0	0	0	0	0	0	0	0	0
placeSTONE	0	0	0	0.0038402	0.0005138	0	0.0035666	0.0005197	0.001514	0.0005002	0	0
provideKERNEL	0	0	0	0	0	0	0	0	0	0	0	0
provideNUT	0	0	0	0	0	0	0.0004458	0	0	0	0	0
pullfootSTONE	0	0	0	0.0015361	0.0005138	0	0.0008916	0.0005197	0	0	0	0
pullhandNUT	0	0	0	0	0.0061665	0	0	0	0	0	0	0
pullhandSTONE	0.0080971	0.035	0.015	0.0291858	0.0354573	0.0083507	0.0053499	0.004158	0.0075700	0.0050025	0	0
pushfootSTONE	0	0.007	0	0.0069124	0.0015416	0	0.0080249	0.0015592	0.0030280	0.0015007	0.007	0
pushhandNUT	0	0	0	0.0015361	0.0010277	0	0.0004458	0	0	0	0.007	0
pushhandSTONE	0	0	0	0.0084485	0.0035971	0.0020876	0.0124832	0.0025987	0.000757	0.0015007	0.01	0
rakefootNUT	0	0	0	0	0	0	0.0004458	0	0	0	0	0
rakehandHAND	0	0	0	0	0	0	0	0	0	0	0	0
rakehandKERNEL	0	0	0	0	0	0	0	0	0	0	0	0
rakehandNUT	0	0.015	0	0.0099846	0.0277492	0.0396659	0.0026749	0.0103950	0.0121120	0.0085042	0	0.005
rakehandSTONE	0	0	0	0	0	0	0	0	0	0	0	0
reorientHAND	0	0	0	0	0	0	0.0004458	0	0	0	0	0
reorientNUT	0	0	0	0	0	0	0	0	0	0	0	0
reorientSTONE	0.0040485	0.087	0.007	0.0345622	0.0071942	0.0020876	0.0120374	0.0062370	0.0105980	0.0065032	0.012	0.042
rollfootSTONE	0	0	0	0.0007680	0.0005138	0	0.0008916	0	0	0.0005002	0	0
rollhandNUT	0	0	0	0.0007680	0	0	0.0004458	0	0.000757	0	0	0
rollhandSTONE	0	0.055	0.017	0.0599078	0.0159301	0	0.0200624	0.0088357	0.0030280	0.0090045	0.005	0.007
spitKERNEL	0.0728744	0	0.02	0.0061443	0	0	0.0022291	0	0.001514	0	0	0
spitNUT	0	0	0	0	0.0020555	0	0.0017833	0.0010395	0.001514	0	0	0
spitSHELL	0.0080971	0	0	0.0015361	0.0056526	0.0104384	0.0017833	0.0077962	0.0052990	0.0025012	0.01	0.005
stompNUT	0.0040485	0	0	0	0	0	0.0008916	0	0	0	0	0
stompSTONE	0	0.09	0.015	0.0138248	0.0010277	0	0.0004458	0.0015592	0	0	0	0
storeNUT	0	0	0	0	0.0035971	0	0.0026749	0	0.0022710	0	0	0
strikeonehandHAND	0.0080971	0.022	0.02	0.046851	0.0560123	0.1064718	0.0147124	0.0072765	0	0.0015007	0	0
strikeonehandKERNEL	0.0080971	0	0	0	0	0	0	0	0	0	0	0
strikeonehandNUT	0	0	0	0.0015361	0	0	0.0013374	0	0	0.0050025	0	0
strikeonehandSTONE	0	0.005	0	0.0737327	0.0647482	0.0167014	0.1462327	0.2084199	0.3050719	0.3381690	0.327	0.242
striketwohandHAND	0.0080971	0	0.022	0.0069124	0	0	0.0004458	0.0010395	0	0	0	0
striketwohandNUT	0	0	0	0	0	0	0	0.0005197	0	0	0	0
striketwohandSTONE	0	0	0	0.0030722	0	0	0	0.0062370	0.001514	0	0	0.017

supportfootNUT	0	0	0	0	0	0	0	0	0	0	0	0
supportfootSTONE	0	0	0	0.0038402 5	0.0025693 7	0.0020876 8	0.0164957 6	0.0083160 1	0.0166540 5	0.0135067 5	0.002 5	0.01
supporthandNUT	0	0	0	0	0	0	0	0	0	0	0	0
supporthandSTONE	0	0	0	0	0.0005138 7	0	0.0004458 3	0.0005197 5	0.0060560 2	0.0015007 5	0	0
takeKERNEL	0	0	0	0.0030722	0.0046248 7	0.0020876 8	0.0008916 6	0.0010395	0	0	0	0
takeNUT	0	0	0	0	0	0	0	0.0005197 5	0	0	0	0
takeSHELL	0	0	0	0	0	0	0	0.0005197 5	0	0	0	0
takeSTONE	0	0	0	0	0.0005138 7	0	0.0004458 3	0	0	0	0	0
throwNUT	0	0	0	0	0	0	0.0004458 3	0.0010395	0.000757	0	0	0
throwSTONE	0	0	0	0.0007680 5	0.0015416 2	0	0.0008916 6	0.0005197 5	0.0037850 1	0.0035017 5	0	0
touchfootKERNEL	0	0	0.002 5	0.0007680 5	0	0	0	0	0	0	0	0
touchfootNUT	0	0	0.002 5	0.0023041 5	0	0	0.0013374 9	0	0.001514	0	0	0
touchfootSTONE	0.1133603 2	0.14	0.182 5	0.1075268 8	0.0683453 2	0.0020876 8	0.0325457	0.0140332 6	0.0098410 3	0.0065032 5	0.007 5	0.005
touchhandKERNEL	0.1012145 7	0	0.027 5	0.0099846 4	0.0030832 5	0.0125261	0.0004458 3	0.0057172 6	0.001514	0.0015007 5	0.005	0
touchhandNUT	0.0080971 7	0.015	0.02	0.0207373 3	0.0416238 4	0.0647181 6	0.0445831 5	0.0348232 8	0.0287660 9	0.0545272 6	0.04	0.035
touchhandSHELL	0	0	0	0	0.0025693 7	0.0334029 2	0.0035666 5	0	0	0.0005002 5	0	0
touchhandSTONE	0.1538461 5	0.295	0.365	0.2188940 1	0.1521068 9	0.0250521 9	0.0668747 2	0.0696465 7	0.0552611 7	0.0440220 1	0.042 5	0.01

56

Chapter 5

The Impact of Old Age on Tool Using Abilities Varies in Wild Chimpanzees

5.1 Abstract

With increasing old-age, most organisms experience a reduction in the efficacy of biological systems (senescence). However, due to a number of methodological challenges, scientific understanding of how animals senesce in the wild is still in its naissance. This is particularly true for long-living, nonhuman apes (henceforth apes), whose extended lifespans make longitudinal research into the dynamics of ageing difficult. Yet, research into the senescence of apes is exceptionally informative for understanding how animals are able to evolve extended lifespans, and also as translatable models for research into human ageing. There is therefore a need to characterize the ageing process of great-apes in the wild, preferable with data that tracks the ageing process at the level of the individual. We present a longitudinal analysis of how nut cracking, a tool-use behaviour of wild chimpanzees at Bossou, Guinea, changes as individuals experience progressive old-age. We report that chimpanzees show detectable changes in nut cracking with increasing old age, including a reduction in engagement with nuts and stone tools; and increase in the time taken to select stone tools; and a reduction in the efficiency with which they crack and process individual nuts. We also report that the effects of senescence are highly variable between individuals; each individual exhibited a unique constellation of behavioural changes, and some individuals showed few changes over the years, whereas others showed many. These findings indicate that chimpanzee tool-use behaviours are subject to senescence in the wild; however, the extent and nature of this senescence is unique to individuals.

5.2 Introduction

Senescence is typically understood as the progressive reduction in an individual's reproductive fitness with increasing age (Nussey et al., 2013). Across animals, senescence produces deleterious outcomes for an exceptional number of physiological, cognitive and behavioural processes (Medawar, 1951; Nussey et al., 2013). Under the disposable soma theory, senescence can be predicted through the need for organisms to allocate limited energetic resources to either cellular maintenance, or reproduction (Kirkwood, 1977); as natural selection favours reproduction earlier in an individual's lifespan, it therefore does this at the expense of mechanisms for cellular maintenance later in life, and so, biological systems senesce (Kirkwood, 1977). Therefore, in species with long lifespans – including humans – living to extreme old age requires an individual to possess a genotype which favours allocation of cellular resources towards the long-term maintenance of biological systems (Kirkwood, 1977).

Primates show extensive variation in the length of their lifespans (Muntané et al., 2018); and within their lifespans, species across the primate order show considerable differences in both the time of onset of aging, as well as the rate of senescence (Colchero et al., 2021). Our understanding of ageing in nonhuman animals has been greatly aided through the study of captive primates, especially small, short-living species (e.g. marmosets, grey mouse lemurs, tamarins; Colman, 2018; Hozer et al., 2019; Languille et al., 2012; Lemere et al., 2008; Rothwell et al., 2021; Sadoun et al., 2019; Salmon, 2016; Tardif et al., 2011) and slightly larger, longer-living macaques (Colman and Binkley, 2002; Comrie et al., 2018; Didier et al., 2016; Gray and Barnes, 2019; Herndon and Lacreuse, 2002; Roberts et al., 1997; Upright and Baxter, 2021; Zhdanova et al., 2011). This, in turn, allows for the effects of aging to be observed over comparatively shorter timescales to long-living primates, including humans. The study of long-living apes also has attracted considerable attention, given their close phylogenetic proximity to humans [6](Bizon and Woods, 2009; Colman and Binkley, 2002; Corr et al., 2002; Lacreuse et al., 2020, 2018, 2014; Lane, 2000; Lowenstine et al., 2016; Mattison and Vaughan, 2017; Messaoudi and Ingram, 2012). Nonhuman primates – especially apes – provide excellent translational models for the study of human ageing, given their high genetic, physiological and behavioural similarities (Bizon and Woods, 2009; Colman, 2018; Frye et al., 2022; Lane, 2000). Accordingly, studies of nonhuman primates have unveiled a myriad of degenerative processes with progressive aging similar to those seen in humans, including in social behaviours

(Machanda and Rosati, 2020; Neal Webb et al., 2019; Siracusa et al., 2022), cognitive functions (Comrie et al., 2018; Didier et al., 2016; Gray and Barnes, 2019; Herndon and Lacreuse, 2002; Lacreuse et al., 2020, 2018, 2014), physiology (Colman and Binkley, 2002; Colman, 2018; Didier et al., 2016; Lowenstine et al., 2016), behaviours in captivity (Hozer et al., 2019; Tarou et al., 2002; Zhdanova et al., 2011), and neurological aging, including the pathological hallmarks of various neurodegenerative diseases, such as Alzheimer's disease and Parkinson's disease (Arnsten et al., 2019; Blesa et al., 2018; Cramer et al., 2018; Edler et al., 2021, 2020, 2017; Emborg, 2017; Kimura et al., 2001; Li et al., 2022; Munger et al., 2019; Ndung'u et al., 2012; Perez et al., 2016; Rodriguez-Callejas et al., 2016).

In contrast with studies in captivity, understanding how ageing influences the biology of animals in the wild presents many methodological challenges (Corr et al., 2002; Hosaka and Huffman, 2015; Nussey et al., 2013), which has consequently skewed research on ageing towards a focus on captive individuals. Accurately estimating the ages of wild animals is challenging. Furthermore, the reduced number of wild animals that live to extreme old-age, as well as the difficulty tracking and collecting longitudinal data on old-aged individuals, present barriers to collecting sufficiently large sample sizes for rigorous statistical analyses (Corr et al., 2002; Nussey et al., 2013). These difficulties are compounded in the case of longitudinal analyses of the effects of aging, where logistical and financial barriers may constrain long-term data collection. Despite these challenges, a number of studies have aimed to characterize the effects of aging in wild primates (Anderson et al., 2021; Bronikowski et al., 2011, 2002; Colchero et al., 2021; Fujisawa et al., 2010; Hämäläinen et al., 2014; Hosaka and Huffman, 2015; Jurmain, 1989; Morbeck et al., 2002; Paul et al., 1993; Siracusa et al., 2022; Thompson et al., 2020), with some drawing on longitudinal datasets collected over extended periods of time (Anderson et al., 2021; Bronikowski et al., 2011, 2002; Colchero et al., 2021; Hosaka and Huffman, 2015; Paul et al., 1993; Siracusa et al., 2022; Thompson et al., 2020). These studies are exceptionally informative to the study of ageing in primates, given their high ecological relevance. In contrast with captive studies – which often focus on individual aspects of cognitive and physiological ageing – studies on wild primates permit the specific facets of ageing identified in captive studies to be understood within the context of higher-level behaviours (e.g. navigation and ranging, foraging, social behaviours, etc.) and the demographic consequences of such changes estimated, including survivability in-situ (Anderson et al., 2021; Bronikowski et al., 2011; Colchero et al., 2021; Hosaka and

Huffman, 2015; Siracusa et al., 2022). As such, studies in the wild are irreplaceably valuable for understanding how aging affects complex aspects of nonhuman primate biology, in ecologically relevant settings, and their consequences for individual survival.

The questions surrounding ageing research are manifold. Within the present study, we investigate the effects of progressive old-age on the senescence of a highly complex aspect of the behaviours of many non-human primates: tool use. Tool-use behaviours are highly challenging, requiring tool-users to draw upon a wide array of high-level cognitive abilities, including planning and the flexible assembly of actions into goal-directed behaviours (Bril, 2015; Byrne et al., 2013; Carvalho et al., 2008; Greenfield, 1991; Hayashi, 2015); an understanding of causal relationships between objects (Hayashi, 2015; Matsuzawa, 1996; Sanz and Morgan, 2010); as well as knowledge of physical properties of objects (Carvalho et al., 2008; Falótico et al., 2022; Fragaszy et al., 2023; Sirianni et al., 2015). Many of the cognitive abilities underlying these high-level processes, such as planning and the sequential organization of actions, have been observed to decrease with progressive old age in captive primates, including motor coordination (Lacreuse et al., 2014; Languille et al., 2012), working memory (Frye et al., 2022; Languille et al., 2012; Sadoun et al., 2019; Samson and Barnes, 2013), and executive functioning (Frye et al., 2022; Lacreuse et al., 2020; Languille et al., 2012; Sadoun et al., 2019; Upright and Baxter, 2021). Additionally, successful tool-users must rely on a number of physical traits including strength, dexterity, and visual acuity (Troscianko et al., 2012; Van Schaik et al., 1999). Physical condition is observed to decline in both captive and wild primates, such as through reduced bone mass (Colman and Binkley, 2002; Lowenstine et al., 2016; Nichols and Zihlman, 2002); muscle wasting (sarcopenia) (Cann, 2015; Lowenstine et al., 2016; Morbeck et al., 2002); the development of arthritis (Lowenstine et al., 2016), and reduced visual acuity (Fujisawa et al., 2010; Lowenstine et al., 2016) with likely deleterious consequences for individual strength and dexterity with old age. Therefore, tool use likely represents a behaviour that is at specific risk of old-age degradation in wild primates. Tool-use behaviours also represent ideal model behaviours for studying primate ageing in the wild, given their immediate ecological relevance in the environments of wild primates (Boesch, 2013; Falótico et al., 2022), and due to many different species of primate readily using tools throughout their lifetimes, including several species of monkey and all species of great ape (Shumaker et al., 2011).

The present study is a longitudinal investigation into the tool-use behaviours of wild West-African chimpanzees (*Pan troglodytes verus*) at Bossou, Guinea, as individuals experience progressive old-age. The chimpanzees of Bossou have been studied since 1976 (Matsuzawa et al., 2011; Sugiyama, 1981), offering an exceptional body of data on their tool-use behaviours in the form of a longitudinal video archive (the Bossou Archive; Biro et al., 2006, 2003; Carvalho et al., 2008; Hayashi, 2015; Humle and Matsuzawa, 2002; Inoue-Nakamura and Matsuzawa, 1997; Matsuzawa et al., 2011; Schofield et al., 2019, 2023). Notably, an outdoor laboratory has been used continuously since 1988 to study one of the most complex tool-use behaviours of the Bossou chimpanzees: the cracking of hard-shelled nuts with hammer and anvil stones ('nut cracking'; Matsuzawa, 1994). Nut cracking represents a challenging technological behaviour for nonhuman primates, and is habitually performed in the wild by several communities of chimpanzees (Carvalho and McGrew, 2012), capuchin monkeys (*Sapajus* spp.; Fragaszy et al., 2023; Resende et al., 2008) and long-tailed macaques (Haslam et al., 2013; Luncz et al., 2019). For chimpanzees at Bossou, nut cracking reflects their most complex tool-use behaviour as it involves the simultaneous combination of multiple tool objects in a hierarchical fashion: a nut is placed on an anvil stone [level one], and a hammer stone is directed at this composite object [level two] (Matsuzawa, 1996). Individuals will strike the nut on the anvil with the hammer stone until the nut is cracked open, and the edible kernel inside extracted and consumed. On rare occasions, the use of a third 'wedge' stone may be placed under the anvil for stability, further elevating tool complexity up to 'level 3' tool use (Matsuzawa, 1996, 1991); however the extent to which this is intentionally performed is unclear (Hayashi and Inoue-Nakamura, 2011). Such hierarchical complexity in the tool use behaviours of wild chimpanzees is believed to be unique to nut cracking using separate, detached hammer and anvil stones (Hayashi and Takeshita, 2022), and is therefore regarded as a challenging natural task for chimpanzees. Alongside the nested associations between objects, the task of cracking a nut with stone tools presents many other challenges, including the need to understand the physical properties of both nuts and stone tools (Carvalho et al., 2008; Falótico et al., 2022; Sirianni et al., 2015), as well as how to draw upon these physical properties to efficiently crack open nuts and consume the edible kernels inside (Carvalho et al., 2008; Fragaszy et al., 2023). Like many other tool behaviours, the process of cracking nuts and consuming kernels also exists within a wider operation chain, where chimpanzees must organize sequences of actions to address multiple different sub-goals during a

continuous bout of behaviour (i.e. *acquire resources, combine nuts and tool objects, process kernels, dispose of waste*; Carvalho et al., 2008), and therefore, requires clear planning (Byrne et al., 2013). Therefore, among all tool behaviours, nut cracking is an excellent candidate behaviour for the study of senescence, as it involves numerous cognitive and physical aspects which are at risk of degradation with age (Byrne et al., 2013; Haidle, 2010)

We present data on the nut-cracking behaviours of five chimpanzees at the outdoor laboratory at Bossou between the years of 1999 to 2016, as they progressively age from approximately 39-44 years-old to 56-61 years-old. We report on a number of metrics describing the nut-cracking behaviours of old-aged chimpanzees, including attendance at the nut-cracking site, frequency of engagement in nut cracking (a metric of motivation to perform the task, which may decrease with age); the time taken to select stone tools (a decision which, if cognition deteriorates, may take longer, or need to be performed on more occasions), and the efficiency of cracking and processing individual nuts. Our findings highlight that wild chimpanzees undergo notable, but highly variable changes in tool-use behaviours with progressive old-age, a finding which spans across all measured aspects of stone-tool use. We discuss the possible underpinnings of such changes (i.e. possible cognitive, physiological, and motivational causes), and outline future avenues of research at the intersection of wild primate ageing and tool use.

5.3 Methods

5.3.1 Study site and video archive

Established in 1976, Bossou-Nimba (07° 390' N; 008° 300' W) is one of a small number of sites for long-term research on wild West-African chimpanzees (Matsuzawa et al., 2011). Chimpanzees at Bossou possess an extensive repertoire of tool-use behaviours (Humle, 2011), including nut cracking (Biro et al., 2006; Matsuzawa, 1994). The chimpanzees at Bossou were previously at a stable population size of around 20 individuals, however, following a flu-like epidemic in 2002, this population was greatly reduced down to approx. 15 individuals (Matsuzawa et al., 2004). In subsequent years, the population continued to reduce in size, and in 2023 the population now consists of four individuals.

Nut cracking by Bossou chimpanzees has been studied for several decades through the use of an 'outdoor laboratory' (established in 1988; henceforth 'outdoor lab'). Open during the dry season of each

year (approx. November-February), the outdoor lab is a maintained natural clearing in the forest (approx. 7 x 20 m) where piles of nuts are provided for chimpanzees (frequently oil-palm nuts, *Elaeis guineensis,* which occur naturally in the home range of chimpanzees at Bossou; however, in some years, coula nuts, *Coula edulis,* are also provided, which are not habitually cracked by these chimpanzees), as well as a central matrix of stone tools, and a raceme of edible oil-palm fruits (see Figure S1 for a visualization of the outdoor lab). The outdoor lab also features a water point (a hollowed section of the trunk of a Richinodendron tree, *Richinodendron heudelotii*) from which chimpanzees may extract water for drinking using leaf tools. Chimpanzees visit the outdoor lab spontaneously as part of their daily ranging behaviours. Upon arrival, their behaviours are recorded by observers using video cameras located behind a screen of palm fronds. In 2011 a second clearing was made available to chimpanzees (the Salon). Data collection at the Salon ran concurrently with that at the original outdoor lab location, with an identical experimental set-up.

Video data collected at the outdoor lab has recently been collated into a longitudinal archive spanning almost three decades (Schofield et al., 2019), spanning from 1990 to the present day. The Bossou archive also contains data on the composition of all recorded encounters with groups of chimpanzees at the outdoor lab across this timeframe, as well as a family lineage data for all individuals (including birth data for individuals born after the establishment of research at Bossou). The Bossou archive therefore presents a novel opportunity for longitudinal analysis of whether and how the tool-use behaviours of wild chimpanzees change over the lifetimes of individuals.

In the present analysis, we collect and analyse data on the behaviours of chimpanzees at the outdoor lab at Bossou, spanning a seventeen-year period and sampled at five timepoints separated by intervals of 3-5 years (field seasons 1999-2000, 2004-2005, 2008-2009, 2011-2012, and 2016-2017; henceforth, each field season is referred to by its initial year). For the present analysis of data collected between 1999 and 2011, we exclusively used data collected at the original outdoor lab (except when estimating rate of attendance for 2011, see *Attendance and Behaviours at the outdoor lab*). The original outdoor lab was not in use during the 2016 field season; we therefore sampled data collected at the Salon only.

5.3.2 Subjects

The exact age at which chimpanzees may be considered 'old' is a point of continued debate. However, chimpanzees are generally considered to have reached old-age at approximately 35-40 years old, with female chimpanzees living to 46 being in the top 95 percentile for lifespan in the wild (Campos et al., 2022; Finch and Austad, 2015; Morbeck et al., 2002). We therefore confined our analysis to individuals who were above at least 30 years of age in at least three of the five sampled field seasons (allowing for the longitudinal analysis of behaviours, and also the detection of behavioural changes compared to what can be expected for each individual during the prime of their adulthood). Under these criteria, we were able to include four old-age females (Fana, Jire, Velu and Yo) and one old-age male (Tua) in our analyses. All five of these individuals were present at Bossou when the long-term research project was established in 1976; as a consequence, their birth years are estimates based on physical growth characteristics at the time of first observation. Given that these estimated birth years range from 1956 to 1961, all five individuals are included within our definition for 'old age' as their ages ranged from between 39-44 years in 1999 to 56-61 years in 2016. All four females were present at Bossou throughout the entire sampled time-frame for our analysis; however, Tua, the only adult male, disappeared in September 2013 (presumed dead). Therefore, data for Tua spans a shorter timeframe between the 1999 and 2011 field seasons. As all five focal individuals' ages are within 5 years of each other, we use the progression through field seasons as a proxy for increasing age, and treat all individuals as similarly 'old' at each field season.

5.3.3 Attendance at the outdoor lab

We compared the rate at which old-age individuals attend the outdoor lab compared to adult individuals below the age of 30 years. Adult individuals were defined as those over the age of eight years (based on age at first parturition at Bossou; Matsuzawa et al., 2011); this category actually encompasses individuals in the adolescent and subadult stages; however, we use the term 'adult' here to indicate individuals who regularly migrate around the home range independently of their mothers. We excluded two adult females (Pama and Nina) who never learnt to successfully crack nuts using stone tools. We counted the number of encounters (times an individual attended the outdoor lab) for each individual within each field season, using individual presence/absence data for each time a group of chimpanzees visited the outdoor lab. In the 2011

field season, where both the Salon and Bureau were open to chimpanzees, attendance was pooled across both sites. The field seasons of each year differed in length, and therefore the number of encounters was converted into a 'rate of attendance' at the outdoor lab. The rate of attendance was calculated by dividing the overall number of encounters with a particular chimpanzee by the total length of each field season in days. The length of each field season was estimated by calculating the total number of days between the first and last encounter of a field season. Thus, the rate of attendance provides an estimate of how frequently individuals attended the outdoor lab per day.

5.3.4 Behaviours at the outdoor lab

To estimate whether progressive old-age influenced the likelihood that individuals would engage in nut cracking behaviours, we sampled the first 10 encounters for each individual during each field season, and for each encounter, timed how long individuals engaged in one of four different behavioural categories using continuous behaviour coding:

[1] **Engaging with Nuts and Stone Tools** – This included any interaction with nuts, nut fragments (including shells and kernels), and stones. Coding began when an individual first touched a nut, nut fragment, or stone tool.

[2] **Drinking Water** – Coding began when an individual stripped leaves from branches to begin manufacturing a leaf tool to aid in drinking water, or, if reusing a tool that had previously been made and discarded, when they collected the tool, and began to approach the water point to drink.

[3] **Eating Fruits** – Coding began whenever an individual began picking oil-palm fruits from the raceme, or collecting and consuming oil-palm fruits off of the ground.

[4] **Other** – Any other behaviour (e.g. grooming, playing, resting). If an individual dropped all items relevant to specified behaviours 1-3 (e.g. leaf tools, stones, fruits) and was idle for at least one minute, they were considered to be resting, and behaviour was marked as 'Other'.

For field seasons where individuals did not visit the outdoor lab on at least 10 occasions, all available encounters were used. When comparing the amount of time invested in each behaviour, we exclusively used data collected at the Bureau. The Bureau is situated at the top of a steep climb, whereas the Salon is at a lower altitude, and is easier to access. This difference in accessibility may influence the

behaviours performed by chimpanzees at either site, e.g. more time resting at the Bureau. We therefore largely restrict our comparison of time invested in each type of behaviour to data collected between 1999 and 2011.

Behaviour coding was conducted using BORIS (Friard and Gamba, 2016), and videos were viewed on a 59cm monitor. The timepoint at which a focal chimpanzee entered and left the encounter was also coded using as a discrete time codon ('INPAB', where PAB stands for 'Party at Bureau'). For each encounter, we summed the total time a focal chimpanzee engaged in all behaviours across categories 1 – 4, and compared this value with the total time elapsed between the 'INPAB' codons marking the entrance and exit of a focal chimpanzee. Any remaining time that was not accounted for by the behaviour categories 1 – 4 was attributed to the category 'OTHER', as it reflected 'dead' time, such as between an individual entering the outdoor lab, and selecting a behaviour to engage in. For each individual, we summed the total amount of time they were present across all sampled encounters of a field season, as well as the total time they were identified to be engaging in each category of behaviour across each field season. We divided the total time an individual spent in each behaviour category with the total time that individual was observed across the sampled encounters of a particular field season. The resulting proportion allowed us to compare investment in behaviours across both individuals and field seasons, as it controls for the amount of time each individual was observed.

5.3.5 Stone-tool selection

Chimpanzees select stone tools based on their physical characteristics such as raw material, size and weight (Carvalho et al., 2008; Sirianni et al., 2015). Therefore, stone-tool selection at the central stone matrix represents a complex decision-making task where chimpanzees must evaluate an extensive set of options (57 total stones). We measured the time taken for the old-aged chimpanzees to select stone tools at the central matrix during each of the sampled field seasons. We sampled the first 10 encounters with each individual for each field season. We began timing when chimpanzees approached the matrix and we considered their gaze to be fixed on at least one stone-tool. We stopped timing when chimpanzees turned away from the matrix holding all acquired stone-tools. We recorded the number of stone tools taken by the focal chimpanzee during each instance of stone-tool selection (typically one or two stones). We also

recorded the number of stone tools that had been removed from the stone-tool matrix prior to each stone selection event (including those removed by other individuals, as well as the focal chimpanzee during previous instances of stone-tool selection). We could therefore incorporate into our analysis a metric of how many options were available to chimpanzees during each stone-tool selection event (where higher numbers of previously selected tools indicated a smaller pool of possible choices; see section 5.3.7 for how this was factored into our model).

5.3.6 Coding sequences of discrete actions during nut cracking

Efficient tool use requires individuals to organize actions into goal-directed sequences (Byrne et al., 2013). Adult chimpanzees who are proficient in nut cracking perform the behaviour using five to six highly frequent actions, including those which are imperative to the success of cracking open nuts with hammer stones (e.g. grasp nut, place nut, strike hammer, grasp kernel, eat kernel). However, chimpanzees also supplement these common actions with an extended repertoire of less frequent, but functionally useful actions (e.g. supporting the anvil with the foot; peeling shells from the kernel with their hands, etc; Howard-Spink et al. In Review).

To characterize how the efficiency of nut cracking behaviours changes for chimpanzees experiencing progressive old-age, we characterized the fine-grained sequences of actions used by chimpanzees during nut cracking in each sampled field season. To code sequences of actions, we used an ethogram of 34 action types and 6 objects (see Table S1 for full ethogram; Howard-Spink et al, In Review). The six possible objects included: Hammer, Anvil, Nut, Kernel (the edible interior of a nut), Shell (the inedible exterior of a nut), and Bare Hand (for use when individuals performed an action in the absence of an object, e.g, striking the anvil with bare hand). Stone tools were categorized as ‘Hammer’ or ‘Anvil’ based on how they were used by the individual. If an individual swapped over their hammer and anvil stones, the stones were reassigned accordingly. Thus, stone tools were coded by their function at any specific point in a sequence.

Coding of action sequences commenced when an individual began interacting with a nut, nut fragment, or stone, and ceased when an individual dropped all relevant objects and either began engaging in an alternative behaviour (e.g. grooming, feeding on oil-palm fruits, etc.) or rested for longer than one

minute. Actions and objects were coded in tandem (e.g. 'Reorient Anvil', 'Grasp Kernel', 'Drop Shell') producing action sequences which describe the functional movements of objects. For our analysis, we consider each descriptive bigram (e.g. 'Grasp Hammer') a single sequence element, and henceforth we use the term 'action' to refer to these composite descriptions of object manipulation. Actions were coded as discrete time-points during behavioural observation, and the time of each action automatically recorded in BORIS. At each point where a chimpanzee began processing a new nut (defined as when an individual touches or grasps a nut which is then placed on the Anvil), a 'NEW NUT' codon was added to the sequence. Additionally, we coded a 'TOOL CHANGE' codon for each point an individual changed tools. Tool changes included each instance an individual swapped over their hammer and anvil stones, swapped out at least one stone tool for a new stone, or moved across the outdoor lab to use a hammer-anvil set previously abandoned by another user. 'NEW NUT' and 'TOOL CHANGE' codons were not included in estimations of the size of the total action repertoire for each individual. Fine-grained action coding was conducted for each individual in each field season until at least 1000 actions had been collected, and included sequences of actions which described the cracking of at least 20 nuts in their entirety.

Action sequence data was exported from BORIS, and 'NEW NUT' codons were used to guide visual inspection and annotation of where action sequences were directed at individual nuts. Action sequences were then parsed into shorter sequences which were directed at the cracking of individual nuts and consumption of their kernels. Only sequences which described the entire processing of a nut, from acquisition of the nut to complete consumption of the kernel, were included. A number of metrics of efficiency were extracted from action sequences directed at individual nuts:

[1] Time to process nuts and consume all kernel. We calculated total time by finding the difference in the timepoint for the first and last actions in a sequence directed at an individual nut.

[2] Number of actions used to process nuts and consume all kernel. This was estimated by counting the total number of coded actions within an action sequence for a particular nut.

[3] N**umber of unique types of action used to process nuts and consume all kernel**. This is different to [2] as it describes the variety of actions employed, rather than the number (e.g. for the action sequence *A,A,B,C,B,C*, where letters denote hypothetical actions, the number of actions is six, and the number of action types is three {*A*, *B*, *C*}).

[4] N**umber of times the nut was placed on the anvil**. During nut cracking, the nut can roll off of the anvil, and requires repositioning to continue with nut cracking. The number of times the nut was placed on the anvil was estimated by counting the number of 'place NUT' codons in the action sequences for each nut.

[5] N**umber of strikes of the hammer stone.** Estimated by counting the number of 'strikeonehand HAMMER' and 'striketwohand HAMMER' codons in a sequence. The former corresponds to striking down on an object using a hammer stone that is held in one hand; the latter describes the same behaviour, but where the hammer stone is held in two hands (a far rarer occurrence for adult chimpanzees).

[6] The number of tool reorientations for each nut. Chimpanzees occasionally reorient tools during tool use, with these adjustments likely reflecting attempts to achieve greater efficiency. Tool adjustments were estimated by counting all of the reorient (horizontal rotation) or flip (vertical rotation) actions associated with hammer and anvil stones.

[7] **Tool changes.** We counted the number of times individuals changed tools during an action sequence directed at a particular nut by counting the number of 'TOOL CHANGE' codons within that sequence.

5.3.7 Statistical analyses

For attendance data, we refrained from using statistical models to describe changes in the data, as attendance between individuals is non-independent, and would therefore violate model assumptions. We also did not use statistical models for the analysis of the proportions of time chimpanzees engaged in different categories of behaviours at the outdoor lab; different chimpanzees may have different behaviours which they prefer both when young and at old-age, and therefore descriptions of changes at the level of the individual are more informative.

For tool-selection times, and the metrics of efficiency for nut cracking, we used linear and generalized linear mixed-effect models to assess for the effects of age. Linear mixed effect models were used in any instance where time was a response variable (and time was logged to confer normality); whereas, if a response variable was measured in counts (e.g. number of actions used to crack open a nut), generalized linear mixed-effect models were used, assuming a Poisson distribution. In both instances, year (scaled about the mean) was used as a fixed effect. We included individual as a random intercept in the model, as well as a random slope for the effect of increasing year for each individual. Our decision to include

a random slope is supported by previous research on captive and wild primates, which suggests that the effects of senescence are highly variable across individuals for a number of physiological and cognitive systems (Freire-Cobo et al., 2021; Hämäläinen et al., 2014; Morbeck et al., 2002; Rothwell et al., 2021; Tarou et al., 2002). We also included the specific encounter as an additional random intercept (fixed slope) to avoid pseudoreplication from multiple tool-selection events for the same encounter.

When analysing tool-selection times, the number of stones chosen by an individual during tool selection (two levels: 'One Stone' or 'Two Stones'); and the number of stones removed from the matrix prior to this stone selection event, were also included as fixed effects.

We restricted the use of models to describe changes in the metrics of nut cracking efficiency based on whether, for at least one individual, the median value for a particular efficiency metric in one year fell outside the interquartile range of any previous year.

We compared these models with models that did not include year as a fixed effect (and therefore assumed no effect of age). We also compared models with those that assume an effect of year, but assume this effect is the same across all individuals (and therefore, do not include year as a random slope). In the case of tool-selection times, which included extra fixed effects, we also compared our model fit to this model (a complete null) to evaluate the explanatory power of our model in comparison to data which is only grouped by the encounter, and the individual. All model comparisons were performed using AIC (lower is better).

5.4 Results

We sampled a range of longitudinal behavioural data from five old-aged chimpanzees as they engaged in behaviours at the outdoor lab at Bossou in the 1999, 2004, 2008, 2011, and 2016 field seasons (see Table 1 for summary of the number of encounters, as well as the total duration of observation for each individual in each field season). From the first 10 encounters for each individual in each field season, we sampled the duration of all tool-selection events (see Table S2) as well as the duration for which each individual engaged in different behaviours at the outdoor lab (see Fig 1c). We also sampled the first 1000 sequential actions used during nut cracking (and where required, we increased this sample to include action sequences used to crack and process 20 nuts in their entirety; see Table 1).

5.4.1 Attendance at the outdoor lab

Across the sampled field seasons, the number of adult chimpanzees who were proficient in nut-cracking varied from 11 (1999) to seven individuals (2004 and 2016), and the number of individuals over the age of 30 years remained fairly stable between six (1999, 2011) and five (2004, 2008, 2016) individuals. In 1999, the rate of attendance for old-aged individuals (39-44 years old) at the outdoor lab was similar to that of adult chimpanzees below the age of 30. Over subsequent years, the proportion of old-aged individuals which showed lower rates of attendance than younger adults increased; in 2004, four of the five old-aged individuals (now aged 44-49 years) showed lower rates of attendance compared to the two adult individuals below the age of 30. This ratio remained relatively constant across subsequent years, despite variation in the average attendance rate for each year (mean encounters day^{-1}: 1999 = 0.71; 2004 = 0.784; 2008 = 0.394; 2011 = 0.606; 2016 = 0.381). In 2016, all old-aged individuals (now 56-61 years old) showed lower attendance rates than the two adults below the age of 30 (see Fig 1a & b).

5.4.2 Behaviours at the outdoor lab

We compared the proportion of time individuals engaged in various categories of behaviours ('Engaging with nuts and stone tools', 'Drinking water', 'Eating oil-palm fruits', and 'Other') across the first 10 encounters with each individual during each sampled field season (see Fig. 1c). Between the years of 1999 and 2011, Yo, Tua, and Jire showed a relatively small change in the proportion of time invested in engagement with nuts and stone tools (change in % time engaging with nuts and stone tools between earliest and latest year sampled for each individual; Jire = -5.5%; Tua = +6.9%; Yo = +8.89%). However, two old-aged individuals (Fana and Velu) showed a notable decrease in the proportion of time they spent engaging with nuts and stone tools in 2011 (% time engaging with nuts and stone tools in each season; Fana: 1999 = 62.3%; 2011 = 15.6%; Velu: 1999 = 51.6%; 2011 = 4.96%). In 2011, Velu spent a much larger proportion of time eating fruits compared with 1999 (+35.5% of total time) as well as an increase in the amount of time drinking water from the water point (+25.9%); however, for Velu, data for 2011 were estimated from a single encounter, reducing our certainty that this reflects a repeatable and progressive change in Velu's behaviour.

For Fana, the decrease in total time engaging with nuts and stone tools was accompanied by a corresponding increase in time engaging in 'Other' behaviours (+38.8%), including resting and grooming. Fana also showed a decrease in the proportion of total encounters in which she interacted with nuts and stone tools between 2008 and 2011 (2008 = 80%, n = 10; 2011 = 28.6%, n = 7; see Table 1), and when extending this comparison to 2016, the proportion of encounters Fana engaged with nuts and stone tools remained considerably lower than in 2008 (2016 = 40%, n = 10). A similar reduction was observed for Yo (2008 = 90%, n = 10 ; 2011 = 33%, n = 3, 2016 = 40%, n = 5; see Table 1); however, across these fewer encounters, the proportion of time Yo engaged with nuts and stone tools remained relatively constant throughout the years, with a small increase in 2016 (see Fig. 1c).

5.4.3 Tool selection time

Between 1999 and 2016, we recorded the duration of 108 stone-tool selection events across 49 encounters for the five focal old-aged individuals (see Fig. 2a, and Table S2). The mixed-effect model with the year of the field season as a fixed effect, and a random slope for each individual, offered a better explanation for the total variation in the time taken to select tools, compared to the model which assumes no effect of increasing year, as well as the null model ($AIC_{Year\text{-}RandomSlope}$: 225.8; $AIC_{Without\text{-}Year}$: 234.0; AIC_{null}: 234.3 see Fig. 2b for a visualization of the random slope model; Table S3 for all AIC; and Table S4 for a summary of the mixed effect model with random slope). To verify that a random-slope model offers a better explanation for the data than a model which assumes the same effect of year across individuals (fixed slope), we refit the random-slope model using restricted maximum likelihood, and compared this model with a mixed effect model with a random intercept for each individual, but a fixed slope (i.e. an identical effect of increasing year across all individuals). The random-slope model performed significantly better than the fixed slope model ($AIC_{Year\text{-}Random}$: 238.2; $AIC_{Year\text{-}Fixed}$: 246.4). This confirms that the best model for our data is one which assumes that individuals vary in the extent to which the increasing year of the field season (a proxy for age) influences the duration of stone-tool selection. The random-slope model identifies that Yo underwent the greatest increase in stone-tool selection time across sampled field seasons (intercept: 2.39; slope: +0.52; coefficients taken from the model fit by maximum likelihood; slope relates to the scaled metric of year), and the second highest increase was for Fana (intercept: 1.96; slope = +0.227). The only individual to show a

negative relationship between duration of stone tool selection and increasing years was Tua (intercept: 1.26; slope: -0.249).

5.4.4 Efficiency of nut processing

Across the five focal old-aged chimpanzees, we recorded sequences of actions used to crack 1602 individual nuts (1538 oil-palm nuts and 64 coula nuts). Among the sampled field seasons, coula nuts were only provided to chimpanzees in 2011. We coded action sequences for cracking coula nuts from three old-aged individuals: Yo (n = 21), Tua (n = 26), and Jire (n = 17). We did not observe Fana or Velu cracking any nuts at the Bureau during the 2011 field season. Jire was the only individual for whom we coded actions directed at the cracking of both oil-palm and coula nuts in 2011. As coula nuts only appear in one sampled field season, for the present analysis we filtered data to include solely the 1538 oil-palm nuts when modelling the influence of progressive old-age on the efficiency of nut cracking. We chose to filter the data in this way to avoid correlation between year and nut type within generated models, and also to ensure a fair comparison of behaviour across years and across individuals.

We modelled five metrics of efficiency for the cracking and processing of oil-palm nuts which may be influenced by progressive old-age (where 'processing' includes placement on the anvil, peeling of shells, consuming of kernel, and disposal of waste items, e.g. shell). These metrics include: the total time taken to crack and process nuts; the number of actions used; the number of unique types of actions used; the number of strikes of the hammer stone; and the number of stone-tool reorientations.

For metrics of total time; the number of actions, and the number of strikes, models which included year as a fixed effect explained variation in the data better than corresponding null models (total time: AIC_{Year} = 3085, AIC_{Null} = 3092; number of actions: AIC_{Year} = 9452, AIC_{Null} = 9485; number of strikes: AIC_{Year} = 6582, AIC_{Null} = 6617). For the number of unique action types and the number of tool reorientations, models which include the effect of changing year did not explain significantly more variation in the data than corresponding null models (action types: AIC_{Year} = 6216, AIC_{Null} = 6214; tool reorientations: AIC_{Year} = 747, AIC_{Null} = 746). For the models of total time duration and number of actions, Yo was identified as having the strongest increase across progressive field seasons (time: intercept = 3.19, scaled year = 0.128; actions: intercept = 2.81, scaled year = 0.098; see Table S10 for coefficients for all individuals). This relationship

reflects both the increase in mean time taken for Yo to crack and process nuts between 1999 and 2016 ($\underline{t}_{1999}$ = 27.4s, n = 66; $\underline{t}_{2016}$ = 55.9s, n = 33) as well as the increase in the median number of actions used within that time ($median_{1999}$ = 13 actions, n = 66; $median_{2016}$ = 27 actions, n = 33).

A similar increase in the total amount of time taken to crack and process nuts was identified for Velu (time: intercept = 2.63, scaled year = 0.0677) reflecting a mean increase between 1999 and 2016 ($\underline{t}_{1999}$ = 16.8s, n = 85; $\underline{t}_{2016}$ = 43.3, n = 5); however, for Velu, a similar relationship was not identified for the number of actions (actions: intercept = 2.40, scaled year = -0.0495), despite a median increase in number of actions used to crack and process nuts in 2016 ($median_{1999}$ = 10 actions, n = 85; $median_{2016}$ = 17 actions, n = 5). This may have in part been due to the low sample size for nut cracking data collected for Velu in 2016, where we only observed the entire cracking and processing of five nuts. However, our model does not support the conclusion that the number of actions Velu was using to crack nuts and consume kernels was increasing over sampled field seasons. An alternative hypothesis may be that Velu was simply moving between actions more slowly, leading to a longer duration of time over which nuts were cracked and processed.

The model describing changes in the number of strikes of the hammer stone across field seasons identified the strongest relationships for Tua (scaled year = 0.195) and Yo (scaled year = 0.186). For Tua, this relationship is based on a shallow but identifiable change in striking behaviours between 1999-2008 (Tua cracked coula nuts in 2011, and was no longer present in 2016). Alternatively, Yo showed a large increase in the number of strikes of the hammer stone between 1999 and 2016 ($median_{1999}$ = 4, n_{1999} = 66; $median_{2016}$ = 12, n = 33).

For the three individuals observed to crack coula nuts in 2011, Yo showed the largest change in efficiency in cracking and processing in 2011, compared to oil-palm nuts in 2011 (see Fig. 4 and Table 2). Between 2008 and 2011, Yo demonstrated an increase in mean total time to crack and process nuts (increase = +191.9 s; % change = +683%), as well as the median number of actions (+85, +71.4%) and different action types (+5, +71.4%) employed, and the median number of times each nut was placed on the anvil (+11, +1100%). In 2011, Yo also exhibited a greater variability in the number of tool adjustments (IQR_{2008} = 0; IQR_{2011} = 5), and the number of tool changes (IQR_{2008} = 0; IQR_{2011} = 8) performed when cracking and processing each nut. Tua showed a slight increase in the total time taken to crack open nuts,

the number of strikes of the hammer stone, and both the number of actions used to crack and process coula nuts in 2011 (n = 26) compared to oil-palm nuts in 2008 (n = 81) (see Table 2); however, all other metrics of efficiency showed little to no change between 2008 and 2011. Jire, the only individual observed cracking both oil-palm and coula nuts, showed highly similar mean and median values of efficiency for both nut types in 2011 (see Fig. 4 and Table 2), with notable increases in the median number of actions, unique types of actions, strikes of the hammer stone, and reorientations of stone tools, and mean time taken when cracking and processing coula nuts.

5.4.5 Action repertoire

When cracking oil-palm nuts, mixed effect models identified an increase in the number of actions used by Yo in cracking and processing, but did not indicate an increase in the number of different types of actions employed. To understand which actions were becoming more frequent, we took the first 1000 actions recorded for Yo in 1999 and 2016, and calculated the proportion of actions which belonged to each unique action type (see Table S12). We identified which actions showed at least a 5% change in the proportion of sampled action sequence data between these two years (see Table 3). The number of strikes of the hammer stone (strikeonehand HAMMER) increased by 9.1%, corroborating our model which identified an increase in the number of strikes of the hammer stone used by Yo to crack oil-palm nuts between 1999 and 2016. The proportion of actions used to process kernels following the cracking of oil-palm nuts also increased (peelteeth SHELL: +6.82%; eat KERNEL: +5.12%), reflecting longer periods in which Yo would peel fragments of kernel off of shell using her teeth, and divide the consumption of kernel across a larger number of bites. The proportion of actions associated with acquiring nuts (grasp NUT) and placing nuts on the anvil stone (place NUT) decreased (grasp NUT: -5.61%; place NUT: -5.51%); this may reflect the fewer nuts Yo was observed cracking in 2016 compared to 1999, leading to fewer instances of a nut being placed on the anvil (n_{1999} = 141; n_{2016} = 33).

5.5 Discussion

The aim of our study was to characterize whether wild chimpanzees experiencing progressive old-age exhibit behavioural changes in a natural tool-use task, and if so, the extent to which these behavioural

changes represent the senescence of tool-use behaviours. We measured how five old-aged individuals engaged with nut cracking tool-use behaviours at Bossou, Guinea, at semi-regular intervals between 1999 and 2016. We collected data from 96 encounters with the five focal old-aged chimpanzees during this sampling window, including 108 stone-tool selection events, and the cracking and processing of 1606 individual nuts. We identified that old-age individuals attended nut cracking sites less frequently than younger adults who also crack nuts using stone tools – a trend which became more prominent as older individuals continued to age – and for two of the five old-age individuals, the proportion of time spent engaging with nuts and stone tools at the outdoor lab also decreased. The effects of progressive old-age on time taken to select stone tools was variable between individuals, as was the effect of progressive old-age on the efficiency with which chimpanzees cracked and processed nuts (see Table 4 for a summary across all individuals). Our analysis therefore identified a number of changes in the tool-use behaviours of old-aged chimpanzees as they aged between 39-44 to 56-61 years old, including the likelihood that old-aged chimpanzees engage in a tool-use task, the time taken to acquire relevant tool objects, and the efficiency with tools are used to achieve behavioural goals.

Between 1999 and 2016, the rate at which old-aged individuals attended the outdoor laboratory decreased. By 2016, all old-aged adults demonstrated a rate of attendance lower than younger adults in the community ($n_{old\text{-}age}$= 5; $n_{younger\text{-}adult}$= 2). This trend is compatible with the hypothesis that individuals may be increasingly less likely to visit the outdoor lab with progressive old-age. The possible underlying causes of such a reduction are manifold, including but not limited to a lesser interest in food-types available at the outdoor lab compared to younger individuals; an increased difficulty in nut cracking leading to a reduction in motivation to attend the outdoor lab; or due to reduced mobility inhibiting frequent visitation of the outdoor lab during active field seasons. Physiological changes (Lowenstine et al., 2016); changes in physical and cognitive attributes relevant to tool use (Colman and Binkley, 2002; Didier et al., 2016; Erwin et al., 2002; Lacreuse et al., 2018; Mattison and Vaughan, 2017; Sadoun et al., 2019; Upright and Baxter, 2021); and changes in locomotion (Neal Webb et al., 2019) have previously been described as senescent features in captive and wild primates, and therefore may influence the decisions made by wild chimpanzees during navigation and feeding behaviours.

An explanation of reduced motivation to engage in nut cracking (including altered dietary preferences, or reduced physical and cognitive attributes with age), may be particularly relevant to individuals which showed a decrease in nut cracking behaviours when present at the outdoor lab (Fana and Velu). For Velu, the mean time taken to crack and process nuts increased, as did the proportion of time invested in the consumption of oil-palm fruits, which may reflect both a reduction in the ease with which Velu was able to successfully crack and process oil-palm nuts, as well as an increase in the time Velu invested in feeding from alternative food sources. For Fana - who showed a relatively constant efficiency during nut cracking between 1999 and 2016 - reduced efficiency of nut cracking is less likely to explain her reduction in engagement with nuts and stone tools across years; thus, the reduction in engagement with nuts and stone tools for Fana may come from alternative changes in motivation, e.g. dietary preferences. Notably, in 2011, chimpanzees at the Bureau were presented with additional piles of coula nuts alongside oil-palm nuts. Whilst coula nuts were provided to chimpanzees on semi-regular occurrences throughout the period of 1993 to 2005, Fana was the only adult individual who showed no interest in manipulating or cracking Coula nuts by the end of this period (Biro et al., 2006). This could suggest that the change in the proportion of nuts of different species that were provided in 2011 may have elicited a reduced desire to engage with nuts and stone tools for Fana. We cannot therefore be certain whether the observed change in engagement with nuts and stone tools for Fana is related to solely ageing, as it may be influenced by a lifelong bias towards the cracking of a particular species of nut. However, in the 2016 field season, where only oil-palm nuts were provided, Fana spent approximately 31.1% of her time in the outdoor lab engaging with nuts and stone tools (measured across 10 encounters), which is a reduction of 17% from the 2008 field season (encounters = 10). The reduction in engagement with nuts and stone tools for Fana between 2008 and 2016 is also reflected in the proportion of encounters where Fana demonstrated any interaction with nuts or stone tools (2008 = 80%; 2016 = 40%). Thus, nut preference alone cannot explain the reduction of interactions with nuts and stone tools by Fana across the latter years of her life. Conversely, the effects of ageing, and nut preference, may represent two non-mutually exclusive explanations for the behavioural changes observed for Fana across field seasons.

An additional factor which may have influenced attendance at the outdoor lab across field seasons is a possible change in the social behaviours of old-aged individuals, a behavioural change which may have

been compounded by demographic changes at Bossou between 1999 and 2016. When attending the outdoor lab, it is common for individuals to arrive in small groups (frequently 2-3 individuals), with further individuals joining the encounter over time. The decision for an individual to attend the outdoor lab is therefore not independent of the behaviour of others within the community, particularly when considering the subgroup with whom an individual is moving during daily ranging. A number of species of nonhuman primates, including chimpanzees, have been observed exercising greater social selectivity with increasing age (Bons et al., 2006; Corr et al., 2002; Machanda and Rosati, 2020; Neal Webb et al., 2019; Siracusa et al., 2022), and at Bossou, social network analyses have revealed that Yo and Velu became increasingly peripheral to the community with increasing age (Schofield et al., 2023). Greater social selectivity by old-aged chimpanzees may lead to a reduction in their likelihood of attending the outdoor lab during daily ranging; this reduction may be borne from a decreased likelihood of travelling with conspecifics, and thus a lesser likelihood that old-aged individuals are brought to the outdoor lab through moving collectively with other community members. Furthermore, old-aged individuals may be less likely to choose to visit the outdoor lab when identifying that other members of the community are present (e.g. such as through attending to long-distance vocalizations from conspecifics). Increased individual isolation through social selectivity could be further exacerbated by the reduction in adult individuals present in the Bossou community between 1999 and 2016 (n_{1999} = 13; n_{2016}=7), where a reduced number of adult conspecifics leads to infrequent formation of subgroups.

Exactly how increased social selectivity may combine with changes in the demographic structure of wild primate communities is currently an open question, particularly concerning its influence on how frequently old-age individuals are guided towards cognitively and physically challenging behaviours by conspecifics, including tool use. It is possible that such social changes may explain the changes in the attendance of old-aged individuals at the outdoor lab who, when present, regularly engage with nuts and stone tools (Jire, Tua, Yo). Exactly which factors contributed to the decline in attendance rates at the outdoor lab across field seasons cannot be determined by data within the present study. However, we recommend that future research investigates how ageing in wild primates - including social changes, as well as changes in physical condition and dietary needs - may influence whether individuals choose to engage in complex foraging tasks, particularly those involving the procurement and use of tools.

When selecting stone tools for nut cracking, chimpanzees attend to a number of physical characteristics of available stones (Carvalho et al., 2008; Sirianni et al., 2015). The best model for the effects of progressive field-season on stone tool selection was one which describes individual variation in the effects of increasing year (a proxy for more extreme old-age). Yo showed the greatest increase in stone-tool selection time, followed by Fana, whereas Tua was the only individual to show a decrease in stone tool selection with increasing years. Similarly to our previous discussion of attendance data, elucidating the exact mechanistic underpinnings of this increase for Yo and Fana, and the decrease for Tua, are not within the scope of the present study; however, possible influences of reduced motivation, reduced cognitive abilities, or the need for an individual to account for reduced physical condition (e.g. strength, dexterity), may all have increased the challenge of stone tool selection for Yo and Fana. Within captivity, great apes experiencing old-age have been reported to exhibit lower rates of object manipulation (Tarou et al., 2002); however, why this is the case remains to be explained. We recommend that further research interrogates how progressive ageing influences the behaviours of wild primates during object manipulation. In particular, whether old-age primates are able to accurately predict the physical properties of objects with a level of precision which is equivalent to younger adults, including for objects which are pertinent to tool-use tasks. Additionally, future research should investigate whether old-aged primates need to account for reduced physical condition when selecting suitable materials for tool-use tasks, and if so, whether they are able to do so in a manner which permits efficient manipulation of tool objects. Understanding how the senescence of cognitive and physical systems may interface during the manipulation of objects, including during tool-use, may provide mechanistic insight into our observation of reduced efficiency in stone-tool selection with increasingly extreme old-age.

The efficiency with which nuts were cracked and processed by individuals changed across field seasons, with considerable inter-individual variation in the extent of change. Velu showed an increase in the total amount of time taken to successfully crack open oil-palm nuts and consume all kernel, whereas Fana, Jire and Tua showed relatively little change in the efficiency of nut cracking and processing across years. The greatest reduction in efficiency was seen in Yo, who showed an increase in the total time taken, number of actions employed, and number of strikes of the hammer stone when cracking and processing individual nuts. The increase in the number of actions employed by Yo reflected a greater proportion of

actions dedicated to both striking nuts with the hammer stone, and the processing of kernels and shells following the point at which a nut was successfully cracked, including peeling shell from kernels using her mouth, and consuming kernels in a greater number of bites. This increase in the number of kernel processing actions may either be a product of low-quality striking, where more peeling of the shell is required, or may signal alternative physical changes for Yo. For example, periodontal disease, and the associated loss and breakage of teeth are common in captive and wild great apes (Lowenstine et al., 2016), which may reduce the efficacy with which some old-aged chimpanzees are able to peel shells away from kernels using their teeth, and bite into and chew segments of kernel.

As well as a reduced efficiency processing oil-palm nuts, Yo also exhibited the greatest difficulty when cracking and processing coula nuts in 2011 compared to Jire and Tua (the only other two individuals observed cracking coula nuts); e.g., for the total time taken to crack and consume nuts – an overarching efficiency metric that is contingent on number of actions, strikes, tool rotations, etc. – Yo showed a mean increase of approximately 192 seconds (3.2 minutes) between 2008 and 2011. Tua and Jire also demonstrated an increase in time, reflecting that overall, coula nuts required more time and effort to be cracked and fully processed; however, the difference between behaviours targeting each nut type for Tua and Jire was much lower than for Yo (Tua = 44.1 seconds; Jire = 22.8 seconds).

The following section of this chapter focuses on the behaviours of Yo, as of all five individuals, she exhibited the greatest changes in behaviours with old-age. We present this discussion as a case study of how tool-use can be affected by old-age, and speculate why.

The dramatic decrease for the processing of coula nuts by Yo may reflect a difficulty in generalizing nut-cracking behaviours across nuts of different species. Oil-palm trees occur within the home range of the Bossou community; however, naturally occurring Coula nuts are not found at Bossou (Biro et al., 2003). Coula nuts are larger and rounder than oil-palm nuts (and thus can be more liable to roll off of anvil stones), and have more fibrous outer shells, which may require more elaborate sequences of striking and peeling actions to separate from kernels (Boesch and Boesch, 1983). Thus, the cracking of Coula nuts reflects a distinctive and infrequent task where individuals must generalize a tool-use behaviour across to a new nut species with unique physical properties. Data for the cracking of coula nuts by Yo came from a single, three-hour long encounter in 2011, where Yo spent one hour and 17 minutes cracking the first 20 coula

nuts (for comparison, in 2008, the first 20 oil-palm nuts that we observed Yo crack had a combined duration of approximately 14 minutes). During this encounter, Yo performed 115 tool changes (a comparatively rare behaviour when cracking and processing oil-palm nuts; see table 2 and figure 4) and 108 tool reorientations (three observed in 2008 across the cracking of 108 oil-palm nuts) during her entire bout of nut-cracking. During the longest behavioural sequence aimed at a single coula nut (the twelfth nut Yo cracked during this encounter, taking 15 minutes and 9 seconds to crack and process, using 440 individual actions), Yo performed 76 instances of positioning and repositioning the nut on the anvil, 118 strikes of the hammer stone, 42 tool changes, and 19 tool adjustments. By 2016, these metrics had returned to a similar scale as to what was observed for Yo in 2008; however, with a notable, but smaller increase in duration, number of actions, and number of strikes of the hammer stone used to crack and process oil-palm nuts.

Why Yo found the cracking of coula nuts so difficult in 2011 presents an interesting question, particularly as in previous years, Yo showed exceptional readiness to engage in the cracking of coula nuts. Coula nuts were first introduced to chimpanzees at the outdoor lab in 1993, when Yo was the only adult individual to begin cracking coula nuts without engaging in a phase of exploratory behaviour (which was demonstrated by all other adults present in the community; Biro et al., 2006). This behaviour suggested that Yo was in fact an emigrant to the population, possibly having migrated to Bossou from the neighbouring Yealé population, where both oil-palm and coula nuts are readily available (Biro et al., 2006). With repetitive presentation of coula nuts throughout intermittent field seasons (1996, 2000, 2002, 2005), more individuals engaged in the cracking and consumption of coula nuts, producing an infrequent, yet solvable tool-use task for the chimpanzees at Bossou (Biro et al., 2003).

There are numerous hypotheses for why Yo showed a dramatic reduction in the efficiency of cracking coula nuts in 2011; we consider some likely hypotheses in turn. First, it is possible that a short-term effect (such as dehydration, hunger, physical injury) may have inhibited cognitive or physical systems required for streamlined tool action. We reject these hypotheses on the basis that the Bureau (where data was collected at 2011) featured a water point, as well as a raceme of oil-palm fruits (which offers a simpler feeding task for chimpanzees); yet, Yo chose to spend the majority of this three-hour encounter engaged in nut cracking (87.8% of total time), thus excluding hypotheses of extreme dehydration and hunger. We also noticed no aspects of Yo's behaviour or condition which suggested physical injury.

Alternatively, the changes in nut processing efficiency for Yo may be grounded in physical ageing, where the significant decrease in efficiency in nut processing compared to Tua and Jire reflect the variable rates of behavioural senescence between individuals. The exceptional difficulty Yo experienced cracking coula nuts may be a product of physical deterioration. With progressive old-age, muscle wasting, bone degradation, and consequential reductions in strength and motor abilities have been documented in many species of nonhuman primates (Cann, 2015; Colman and Binkley, 2002; Didier et al., 2016; Erwin et al., 2002; Mattison and Vaughan, 2017), particularly for ageing female primates (Didier et al., 2016; Erwin et al., 2002; Mattison and Vaughan, 2017); and specifically in chimpanzees, progressive reductions in visual acuity (Fujisawa et al., 2010) and motor coordination for fine-grained dexterity (Lacreuse et al., 2014), have also been observed. Such deterioration of physical characteristics may impede the efficacy of tool-use behaviours, including during nut cracking, and particularly for species of nuts which are especially challenging to crack.

An alternative hypothesis is that, with progressive old-age, Yo struggled to generalize nut cracking behaviours to species of nuts which she encounters infrequently. When engaging in nut cracking, individuals are required to possess specific knowledge of how to use tool objects, including the organization of sequential actions (Byrne et al., 2013); the knowledge of the physical properties of objects (Carvalho et al., 2008), and the knowledge of how to precisely manipulate, orient and combine objects to successfully crack nuts (Biro et al., 2006; Bril et al., 2009; Matsuzawa, 1996). Increasing age is noted to influence a number of cognitive facets pertinent to the tool-use behaviours of both humans and nonhuman primates, including behavioural flexibility (Lacreuse et al., 2018; Languille et al., 2012), executive function (Lacreuse et al., 2020; Sadoun et al., 2019; Upright and Baxter, 2021), and various memory systems, including working, recognition, and spatial memory (Languille et al., 2012; Mattison and Vaughan, 2017; Rothwell et al., 2021; Sadoun et al., 2019; Upright and Baxter, 2021). It is possible that when faced with an infrequent tool-use task, where an individual has a reduced capacity to remember previous solutions to a task, the diminished cognition supporting behavioural flexibility may inhibit the generation of effective solutions. We recommend that further research into the behaviours of ageing nonhuman primates examines the interplay of task frequency, memory, and behavioural flexibility when evaluating the likelihood that individuals successfully perform complex behaviours with increasing old-age. Additionally, further research on how

reductions in the physical condition of nonhuman apes with progressive ageing – including strength and dexterity – influences the efficiency with which apes are able to complete complex feeding tasks would be informative for the results of this study.

Understanding how primates age in-situ and how their natural daily lives are affected by ageing is a field of research with many open questions. We have herein reported on a longitudinal investigation of how progressive old-age influences the behaviours of five wild chimpanzees during one of their most complex tool-use tasks: the cracking of hard-shelled nuts with hammer and anvil stones. We report that the rate at which chimpanzees engaged in nut cracking behaviours, the rate at which they select tool objects, and the efficiency with which they successfully crack open nuts and consumed kernels, all exhibited changes with increasing age. Most notably, we outline how these changes are highly variable between individuals, with some individuals showing extremely few behavioural changes with progressive old-age, and other individuals demonstrating reductions in efficiency across multiple aspects of nut cracking behaviours, including when transitioning between the cracking of nuts of different species. Tool-use therefore represents a complex aspect of the behavioural repertoire of wild chimpanzees where individuals exhibit variation in their susceptibility to senescence with extreme old-age. The extent to which similar patterns of senescence are observed within other complex foraging tasks of wild chimpanzees, including those which involve the use of tools, would be highly informative to understanding how progressive old age may influence the foraging niche of wild chimpanzees. Additionally, we have outlined further avenues of research which we believe would be informative to the results of this study, including those which examine the intersection of ageing, cognition, physical condition, and the generation of flexible, successful solutions to complex feeding tasks. Research at the intersection of primate ageing, behaviour, and niche exploitation in the wild is invaluable to the construction of suitable artificial environments which support the welfare of primates experiencing progressive ageing, and also for predicting the community dynamics of ageing populations in the wild. Understanding the process of ageing in wild animals is challenging; however, through data collected at long-term field sites, important questions of ageing in wild nonhumans may be answered, with translatable outcomes for animal welfare, the management of communities of wild animals, and our understanding of the evolution of the human ageing process.

5.6 Figures

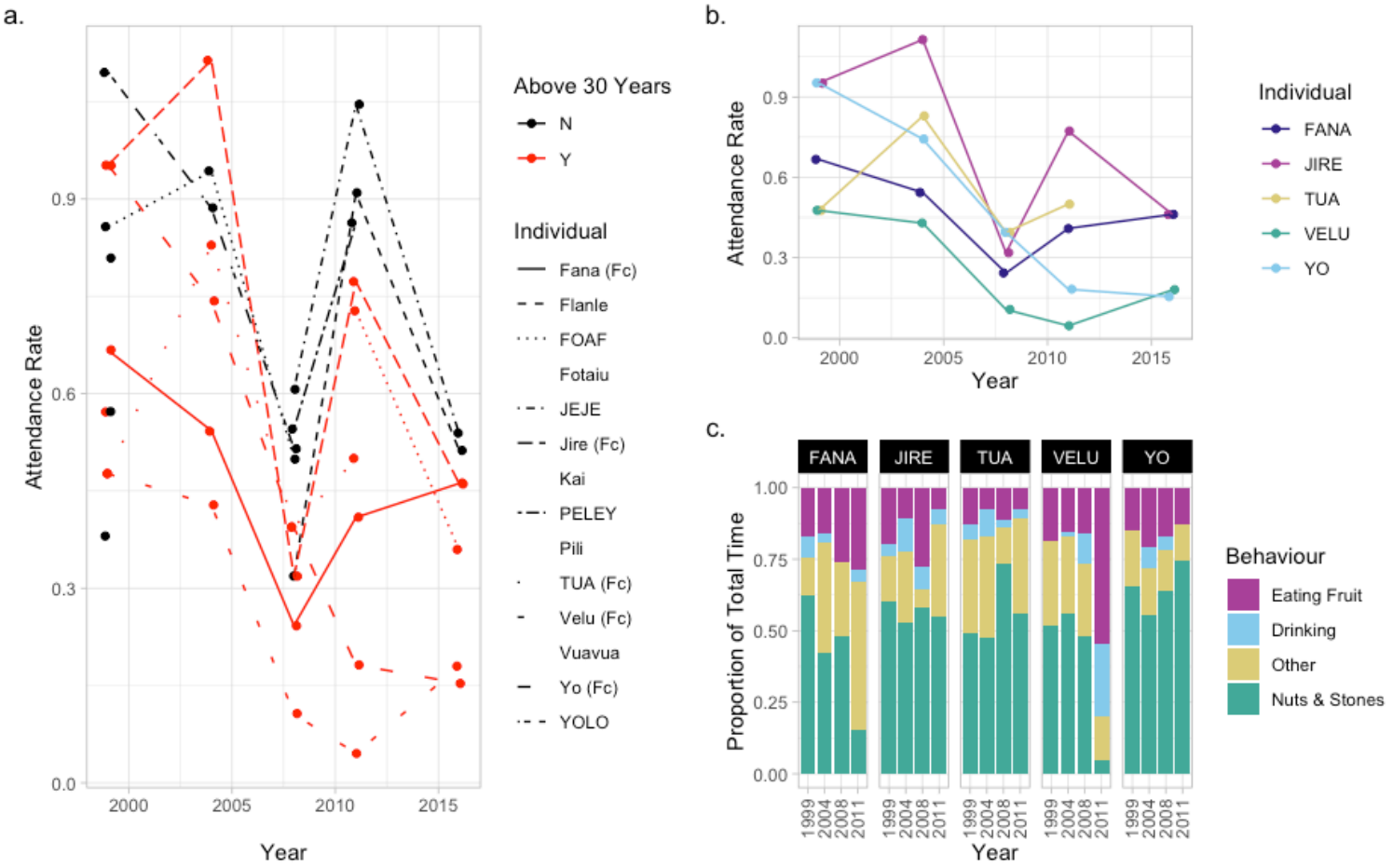


Figure 1. Attendance and behaviour of old-aged chimpanzees at the Outdoor Lab. (a) Attendance rate for individuals at the outdoor lab between the field seasons commencing in 1999 and 2016. Red points and lines indicate individuals are over 30 years old (thus defined as having reached old age); black points and lines indicate adult individuals younger than 30 years. Lines are drawn for all individuals who attended the outdoor lab in two or more field seasons. The names of males are provided in all capitals, and females are provided with capital and lower-case letters. Focal old-aged individuals are indicated with Fc in brackets. **(b)** Attendance data for the five focal old-aged individuals who attended the outdoor lab in at least three field seasons. **(c)** The proportion of total time individuals spent engaging in four different categories of behaviour at the outdoor lab between 1999 and 2011. Proportions were estimated across the first 10 encounters with each individual during each field season (data collected at the Bureau only).

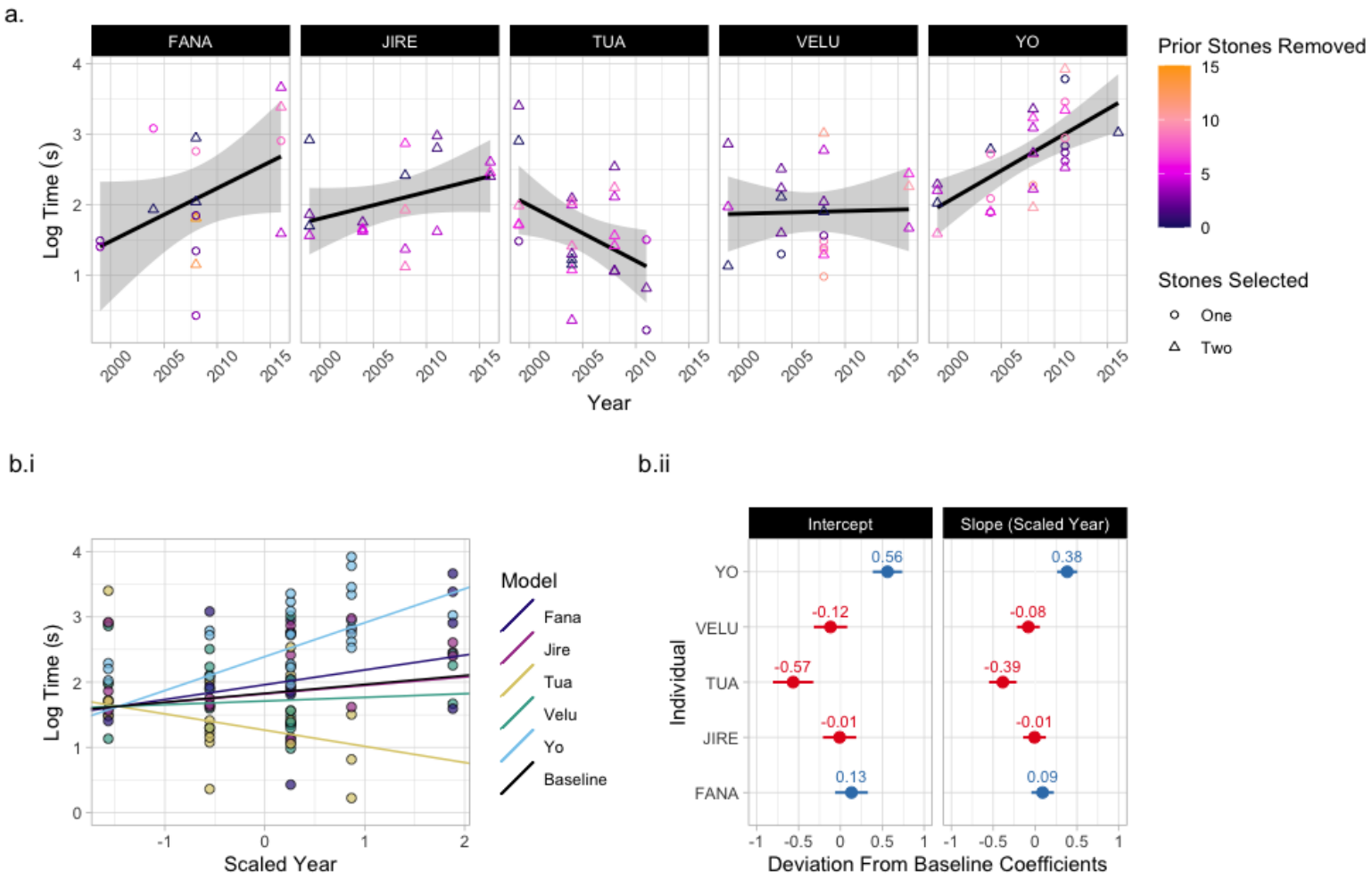


Figure 2. Duration of stone-tool selection events. (a) Tool-selection duration times for each old-aged individual. Colour correlates with the number of stone tools removed from the matrix prior to that particular tool selection event. Shape indicates the number of tools selected by an individual in a given tool selection event. The lines and shaded areas represent a smoothed linear relationship describing the data for each individual. **(b)** A mixed effect model describing the duration of stone tool selection events across a scaled parameter of the year for each field season. Individual is included in the model as both a random intercept and slope. Plot shows the model's prediction of the relationship between the duration of stone-tool selection and year for each individual, compared with the baseline fixed effect of year. **(c)** The difference between the coefficients for intercept and slope between the baseline fixed effect of year, compared to the intercept and slope for each individual. Values are taken from the model plotted in panel b.

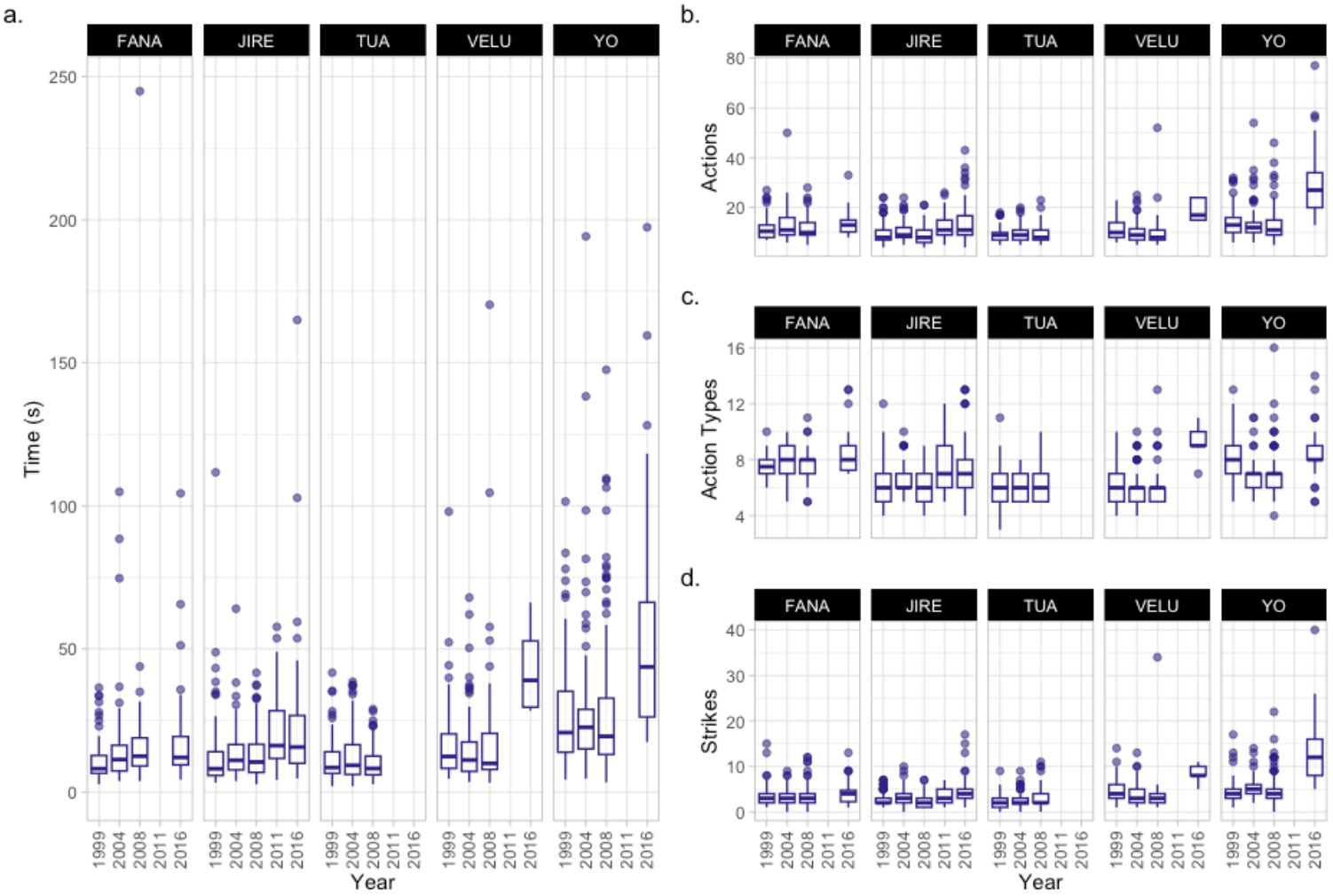


Figure 3. Metrics of efficiency for the cracking and processing of oil-palm nuts. This plot only includes metrics for which corresponding models were produced. All data relate to the cracking and processing of individual oil-palm nuts. These metrics include (a) the total amount of time taken for each nut, (b) the number of discrete actions, (c) the number of unique action types, (d) the number of hammer strikes.

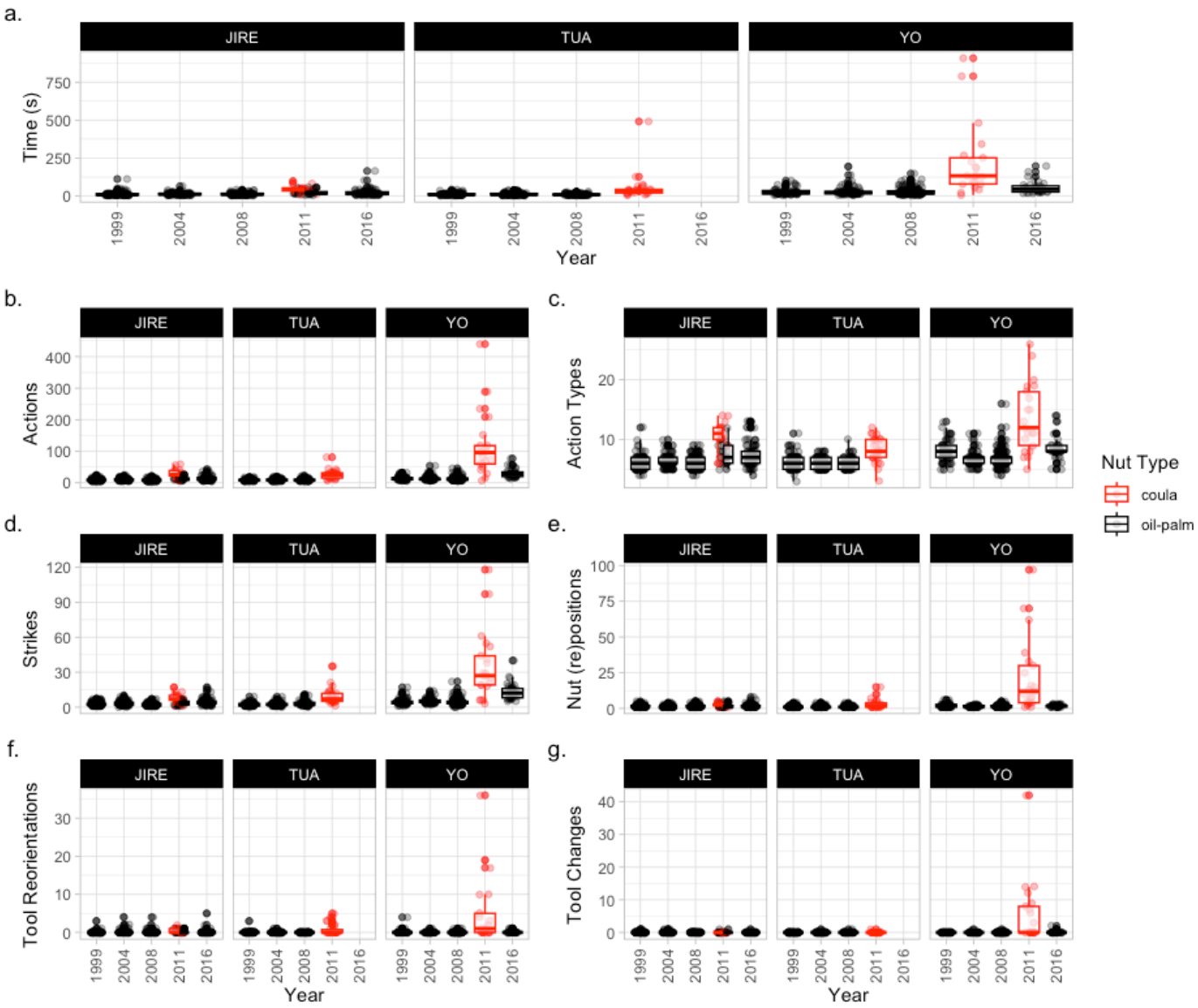


Figure 4. Metrics for the cracking and processing of both oil-palm and coula nuts. Data is confined to individuals who cracked both types of nuts. Data for coula nuts is in red, and oil-palm is in black. Coula nuts were only provided experimentally in 2011, and Jire is the only individual to be observed cracking both types of nuts during this field season. Data describes the cracking and processing of individual nuts, including (a) the total time taken; (b) the total number of actions used; (c) the number of unique types of actions; (d) the number of hammer strikes; (e) the number of times the nut had to be placed and replaced on the anvil; (f) the number of reorientations of stone tools, and (g) the number of times stone tools were switched over, or switched out for new tools.

5.7 Tables

Table 1. Summary of sampled observations for each focal old-age individual. Total time observed includes all time individuals were present in the first 10 encounters of each field season (Observed Encounters). Dashed lines represent where no data was collected for an individual in a given year.

ID	DOB*	Age (Years)					Observed Encounters (% including interaction with nuts or stone tools)					Total Time Observed (minutes)					Action Sequences Coded (for Individual Nuts)				
		1999	2004	2008	2011	2016	1999	2004	2008	2011	2016	1999	2004	2008	2011	2016	1999	2004	2008	2011	2016
Fana	1956	44	49	53	56	61	10 (70%)	10 (70%)	10 (80%)	7 (28.6%)	10 (40%)	280.6	275.2	184.2	105.7	283.5	80	77	80	-	70
Jire	1958	42	47	51	54	59	10 (80%)	10 (80%)	10 (90%)	10 (60%)	10 (80%)	339.4	349.9	275.0	282.1	308.6	100	91	104	42	82
Tua	1957	43	48	52	55	-	10 (70%)	10 (80%)	10 (80%)	5 (60%)	-	174.4	212.1	204.3	116.0	-	103	96	81	26	-
Velu	1959	41	46	50	53	58	10 (60%)	10 (80%)	7 (85.7%)	1 (100%)	7 (42.9%)	189.4	281.8	158	23.1	202.4	85	99	50	-	5
Yo	1961	39	44	48	51	56	10 (80%)	10 (70%)	10 (90%)	3 (33%)	5 (40%)	200.7	304.5	363.7	211.3	282.7	66	70	141	21	33

*Date of birth (DOB) was estimated for these individuals at the start of longitudinal data collection at Bossou (1976). Thus, ages for individuals are an estimate. Ages are approximated from January of the estimated year of birth, and the end of November of each field season (the approximate start of each field season).

Table 2. Summary of nut cracking and processing metrics for Tua, Jire and Yo between 2008 and 2016. Total time duration is summarised by mean and standard deviation. All other metrics are summarized by medians and interquartile ranges. Horizontal lines indicate where no data is available for a given year. Information on how each metric is defined and estimated can be found in the Methods.

Individual	Metric	Year and Nut Type			
		2008	2011		2016
Tua		**oil-palm (n = 81)**	**coula (n = 26)**		**-**
	Means (sd)				
	Total Time (s)	10.6 (6.34)	54.7 (92.6)		-
	Medians (IQR)				
	Actions	8 (4)	25.5 (16)		-
	Action Types	6 (2)	8 (3)		-
	Strikes	2 (2)	7 (6.75)		-
	Nut Positioning	1 (0)	2 (2.75)		-
	Tool Reorientations	0 (0)	0 (0.75)		-
	Tool Changes	0 (0)	0 (0)		-
Jire		**oil-palm (n = 104)**	**oil-palm (n = 25)**	**coula (n = 17)**	**oil-palm (n = 82)**
	Means (sd)				
	Total Time (s)	12.8 (8.37)	21.8 (14.9)	44.6 (21.6)	21.9 (22.3)
	Medians (IQR)				
	Actions	8 (5)	11 (6)	26 (17)	11 (7.75)
	Action Types	6 (2)	7 (3)	11 (2)	7 (2)
	Strikes	2 (2)	3 (3)	7 (4)	4 (2)
	Nut Positioning	1 (1)	1 (1)	3 (1)	1 (1)
	Tool Reorientations	0 (0)	0 (0)	0 (1)	0 (0)
	Tool Changes	0 (0)	0 (0)	0 (0)	0 (0)
Yo		**oil-palm (n = 104)**	**coula (n = 21)**		**oil-palm (n = 33)**
	Means (sd)				
	Total Time (s)	28.1 (24.6)	220 (238)		55.9 (42.3)
	Medians (IQR)				
	Actions	11 (6)	96 (58)		27 (14)
	Action Types	7 (1)	12 (9)		8 (1)
	Strikes	4 (2)	27 (25)		12 (8)
	Nut Positioning	1 (1)	12 (26)		2 (1)
	Tool Reorientations	0 (0)	1 (5)		0 (0)
	Tool Changes	0 (0)	0 (8)		0 (0)

Table 3. Actions which showed a proportional change (>0.05) in the first 1000 sampled actions for Yo. Data confined to the first and last sampled field seasons. Difference indicates the change in proportion for each action type between 1999 and 2016.

Action	Proportion of total sampled actions		
	1999	2016	Difference
strikeonehand HAMMER	0.354	0.445	+0.091
eat KERNEL	0.087	0.138	+0.051
peelteeth SHELL	0.056	0.124	+0.068
grasp NUT	0.113	0.057	-0.056
place NUT	0.096	0.045	-0.051

Table 4. Summary of changes observed in each individual with progressive old age. Data includes the changes in attendance, engagement with nuts and stone tools, total tool-selection time, and the efficiency metrics for the cracking and processing of oil-palm nuts. Horizontal lines reflect no change.

Individual	Sex	Attendance	Engagement	Tool Selection Time	Efficiency Metrics for oil-palm cracking			
					Total Time	Actions	Action Types	Strikes
Fana	F	Decreased	Decreased	Increase	-	-	-	
Jire	F	Decreased	-	-	-	-	-	
Tua	M	-	-	Strong Decrease	-	-	-	**Mild Increase**
Velu	F	Decreased	Decreased	-	**Increase**	-	-	
Yo*	F	Decreased	Mild Increase	Strong Increase	**Increase**	**Increase**	-	**Increase**

***This table does not include information describing the cracking and processing of Coula nuts – see discussion.**

5.8 References

Anderson, J.A., Johnston, R.A., Lea, A.J., Campos, F.A., Voyles, T.N., Akinyi, M.Y., Alberts, S.C., Archie, E.A., Tung, J., 2021. High social status males experience accelerated epigenetic aging in wild baboons. eLife 10, e66128. https://doi.org/10.7554/eLife.66128

Arnsten, A.F.T., Datta, D., Leslie, S., Yang, S.-T., Wang, M., Nairn, A.C., 2019. Alzheimer's-like pathology in aging rhesus macaques: Unique opportunity to study the etiology and treatment of Alzheimer's disease. Proc. Natl. Acad. Sci. 116, 26230–26238. https://doi.org/10.1073/pnas.1903671116

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. Anim. Cogn. 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. Cogn. Dev. Chimpanzees 476–508. https://doi.org/10.1007/4-431-30248-4_28

Bizon, J.L., Woods, A. (Eds.), 2009. Animal Models of Human Cognitive Aging. Humana Press, Totowa, NJ. https://doi.org/10.1007/978-1-59745-422-3

Blesa, J., Trigo-Damas, I., del Rey, N.L.-G., Obeso, J.A., 2018. The use of nonhuman primate models to understand processes in Parkinson's disease. J. Neural Transm. 125, 325–335. https://doi.org/10.1007/s00702-017-1715-x

Boesch, C., 2013. Ecology and cognition of tool use in chimpanzees, in: Sanz, C.M., Call, J., Boesch, C. (Eds.), Tool Use in Animals. Cambridge University Press, pp. 21–47. https://doi.org/10.1017/CBO9780511894800.003

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

Bons, N., Rieger, F., Prudhomme, D., Fisher, A., Krause, K.-H., 2006. Microcebus murinus: a useful primate model for human cerebral aging and Alzheimer's disease? Genes Brain Behav. 5, 120–130. https://doi.org/10.1111/j.1601-183X.2005.00149.x

Bril, B., 2015. Learning to Use Tools: A Functional Approach to Action, in: Francophone Perspectives of Learning Through Work. pp. 95–118. https://doi.org/10.1007/978-3-319-18669-6_5

Bril, B., Dietrich, G., Foucart, J., Fuwa, K., 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? Anim. Cogn. 12, 217–235. https://doi.org/10.1007/s10071-008-0184-x

Bronikowski, A.M., Alberts, S.C., Altmann, J., Packer, C., Carey, K.D., Tatar, M., 2002. The aging baboon: Comparative demography in a non-human primate. Proc. Natl. Acad. Sci. 99, 9591–9595. https://doi.org/10.1073/pnas.142675599

Bronikowski, A.M., Altmann, J., Brockman, D.K., Cords, M., Fedigan, L.M., Pusey, A., Stoinski, T., Morris, W.F., Strier, K.B., Alberts, S.C., 2011. Aging in the Natural World: Comparative Data Reveal Similar Mortality Patterns Across Primates. Science 331, 1325–1328. https://doi.org/10.1126/science.1201571

Byrne, R.W., Sanz, C.M., Morgan, D.B., 2013. Chimpanzees plan their tool use, in: Sanz, C.M., Call, J., Boesch, C. (Eds.), Tool Use in Animals. Cambridge University Press, pp. 48–64. https://doi.org/10.1017/CBO9780511894800.004

Campos, F.A., Altmann, J., Cords, M., Fedigan, L.M., Lawler, R., Lonsdorf, E.V., Stoinski, T.S., Strier, K.B., Bronikowski, A.M., Pusey, A.E., Alberts, S.C., 2022. Female reproductive aging in seven primate species: Patterns and consequences. Proc. Natl. Acad. Sci. 119, e2117669119. https://doi.org/10.1073/pnas.2117669119

Cann, J.A., 2015. Nonhuman Primate Models of Human Disease, in: The Nonhuman Primate in Nonclinical Drug Development and Safety Assessment. Elsevier, pp. 257–277. https://doi.org/10.1016/B978-0-12-417144-2.00013-5

Carvalho, S., Cunha, E., Sousa, C., Matsuzawa, T., 2008. Chaînes opératoires and resource-exploitation strategies in chimpanzee (Pan troglodytes) nut cracking. J. Hum. Evol. 55, 148–163. https://doi.org/10.1016/j.jhevol.2008.02.005

Carvalho, S., McGrew, W., 2012. The origins of the Oldowan: Why chimpanzees (Pan troglodytes) still are good models for technological evolution in Africa, in: Domínguez-Rodrigo, M. (Ed.), Stone Tools and Fossil Bones. Cambridge University Press, pp. 201–221. https://doi.org/10.1017/CBO9781139149327.010

Colchero, F., Aburto, J.M., Archie, E.A., Boesch, C., Breuer, T., Campos, F.A., Collins, A., Conde, D.A., Cords, M., Crockford, C., Thompson, M.E., Fedigan, L.M., Fichtel, C., Groenenberg, M., Hobaiter, C., Kappeler, P.M., Lawler, R.R., Lewis, R.J., Machanda, Z.P., Manguette, M.L., Muller, M.N., Packer, C., Parnell, R.J., Perry, S., Pusey, A.E., Robbins, M.M., Seyfarth, R.M., Silk, J.B., Staerk, J., Stoinski, T.S., Stokes, E.J., Strier, K.B., Strum, S.C., Tung, J., Villavicencio, F., Wittig, R.M., Wrangham, R.W., Zuberbühler, K., Vaupel, J.W., Alberts, S.C., 2021. The long lives of primates and the 'invariant rate of ageing' hypothesis. Nat. Commun. 12, 3666. https://doi.org/10.1038/s41467-021-23894-3

Colman, R., Binkley, N., 2002. Skeletal Aging in Macaque Monkeys, in: Aging in Nonhuman Primates, Interdisciplinary Topics in Gerontology. Karger, pp. 32–37.

Colman, R.J., 2018. Non-human primates as a model for aging. Biochim. Biophys. Acta BBA - Mol. Basis Dis. 1864, 2733–2741. https://doi.org/10.1016/j.bbadis.2017.07.008

Comrie, A.E., Gray, D.T., Smith, A.C., Barnes, C.A., 2018. Different macaque models of cognitive aging exhibit task-dependent behavioral disparities. Behav. Brain Res. 344, 110–119. https://doi.org/10.1016/j.bbr.2018.02.008

Corr, J.A., Martin, L.J., Boysen, S., 2002. Comparative Models of Cognitive Decline in Aging Great Apes, in: Aging in Nonhuman Primates, Interdisciplinary Topics in Gerontology. Karger, pp. 196–208.

Cramer, P.E., Gentzel, R.C., Tanis, K.Q., Vardigan, J., Wang, Y., Connolly, B., Manfre, P., Lodge, K., Renger, J.J., Zerbinatti, C., Uslaner, J.M., 2018. Aging African green monkeys manifest transcriptional, pathological, and cognitive hallmarks of human Alzheimer's disease. Neurobiol. Aging 64, 92–106. https://doi.org/10.1016/j.neurobiolaging.2017.12.011

Didier, E.S., MacLean, A.G., Mohan, M., Didier, P.J., Lackner, A.A., Kuroda, M.J., 2016. Contributions of Nonhuman Primates to Research on Aging. Vet. Pathol. 53, 277–290. https://doi.org/10.1177/0300985815622974

Edler, M.K., Munger, E.L., Groetz, H., Raghanti, M.A., 2021. Nonhuman primates as models for aging and Alzheimer's disease, in: Assessments, Treatments and Modeling in Aging and Neurological Disease. Elsevier, pp. 527–537. https://doi.org/10.1016/B978-0-12-818000-6.00047-0

Edler, M.K., Munger, E.L., Meindl, R.S., Hopkins, W.D., Ely, J.J., Erwin, J.M., Mufson, E.J., Hof, P.R., Sherwood, C.C., Raghanti, M.A., 2020. Neuron loss associated with age but not Alzheimer's disease pathology in the chimpanzee brain. Philos. Trans. R. Soc. B Biol. Sci. 375, 20190619. https://doi.org/10.1098/rstb.2019.0619

Edler, M.K., Sherwood, C.C., Meindl, R.S., Hopkins, W.D., Ely, J.J., Erwin, J.M., Mufson, E.J., Hof, P.R., Raghanti, M.A., 2017. Aged chimpanzees exhibit pathologic hallmarks of Alzheimer's disease. Neurobiol. Aging 59, 107–120. https://doi.org/10.1016/j.neurobiolaging.2017.07.006

Emborg, M.E., 2017. Nonhuman Primate Models of Neurodegenerative Disorders. ILAR J. 58, 190–201. https://doi.org/10.1093/ilar/ilx021

Erwin, J., Hoff, P., Ely, J., Perl, D., 2002. One Gerontology: Advancing Understanding of Aging through Studies of Great Apes and Other Primates, in: Aging in Nonhuman Primates, Interdisciplinary Topics in Gerontology. Karger, pp. 1–21.

Falótico, T., Valença, T., Verderane, M.P., Fogaça, M.D., 2022. Stone tools differences across three capuchin monkey populations: food's physical properties, ecology, and culture. Sci. Rep. 12, 14365. https://doi.org/10.1038/s41598-022-18661-3

Finch, C.E., Austad, S.N., 2015. Commentary: is Alzheimer's disease uniquely human? Neurobiol. Aging 36, 553–555. https://doi.org/10.1016/j.neurobiolaging.2014.10.025

Fragaszy, D.M., Aiempichitkijkarn, N., Eshchar, Y., Mangalam, M., Izar, P., Resende, B., Visalberghi, E., 2023. The development of expertise at cracking palm nuts by wild bearded capuchin monkeys, Sapajus libidinosus. Anim. Behav. 197, 1–14. https://doi.org/10.1016/j.anbehav.2022.12.008

Freire-Cobo, C., Edler, M.K., Varghese, M., Munger, E., Laffey, J., Raia, S., In, S.S., Wicinski, B., Medalla, M., Perez, S.E., Mufson, E.J., Erwin, J.M., Guevara, E.E., Sherwood, C.C., Luebke, J.I., Lacreuse, A., Raghanti, M.A., Hof, P.R., 2021. Comparative neuropathology in aging primates: A perspective. Am. J. Primatol. 83. https://doi.org/10.1002/ajp.23299

Friard, O., Gamba, M., 2016. BORIS: a free, versatile open-source event-logging software for video/audio coding and live observations. Methods Ecol. Evol. 7, 1325–1330. https://doi.org/10.1111/2041-210X.12584

Frye, B.M., Craft, S., Register, T.C., Kim, J., Whitlow, C.T., Barcus, R.A., Lockhart, S.N., Sai, K.K.S., Shively, C.A., 2022. Early Alzheimer's disease-like reductions in gray matter and cognitive

function with aging in nonhuman primates. Alzheimers Dement. Transl. Res. Clin. Interv. 8. https://doi.org/10.1002/trc2.12284
Fujisawa, M., Matsubayashi, K., Soumah, A.G., Kasahara, Y., Nakatsuka, M., Matsuzawa, T., 2010. Farsightedness (presbyopia) in a wild elderly chimpanzee: The first report. Geriatr. Gerontol. Int. 10, 113–114. https://doi.org/10.1111/j.1447-0594.2009.00575.x
Gray, D.T., Barnes, C.A., 2019. Experiments in macaque monkeys provide critical insights into age-associated changes in cognitive and sensory function. Proc. Natl. Acad. Sci. 116, 26247–26254. https://doi.org/10.1073/pnas.1902279116
Greenfield, P.M., 1991. Language, tools and brain: The ontogeny and phylogeny of hierarchically organized sequential behavior. Behav. Brain Sci. 531–595.
Haidle, M.N., 2010. Working-Memory Capacity and the Evolution of Modern Cognitive Potential: Implications from Animal and Early Human Tool Use. Curr. Anthropol. 51, S149–S166. https://doi.org/10.1086/650295
Hämäläinen, A., Dammhahn, M., Aujard, F., Eberle, M., Hardy, I., Kappeler, P.M., Perret, M., Schliehe-Diecks, S., Kraus, C., 2014. Senescence or selective disappearance? Age trajectories of body mass in wild and captive populations of a small-bodied primate. Proc. R. Soc. B Biol. Sci. 281, 20140830. https://doi.org/10.1098/rspb.2014.0830
Haslam, M., Gumert, M.D., Biro, D., Carvalho, S., Malaivijitnond, S., 2013. Use-Wear Patterns on Wild Macaque Stone Tools Reveal Their Behavioural History. PLoS ONE 8, e72872. https://doi.org/10.1371/journal.pone.0072872
Hayashi, M., 2015. Perspectives on object manipulation and action grammar for percussive actions in primates. Philos. Trans. R. Soc. B Biol. Sci. 370. https://doi.org/10.1098/rstb.2014.0350
Hayashi, M., Inoue-Nakamura, N., 2011. From Handling Stones and Nuts to Tool-Use, in: From Handling Stones and Nuts to Tool-Use. Springer Japan, Tokyo, Japan, pp. 175–182.
Hayashi, M., Takeshita, H., 2022. Hierarchical object combination and tool use in the great apes and human children. Primates. https://doi.org/10.1007/s10329-022-01003-2
Herndon, J.G., Lacreuse, A., 2002. The Rhesus Monkey Model as a Heuristic Resource in Cognitive Aging Research, in: Aging in Nonhuman Primates, Interdisciplinary Topics in Gerontology. Karger, pp. 178–195.
Hosaka, K., Huffman, M., 2015. Life History and Health, in: Nakamura, M., Hosaka, K., Itoh, N., Zamma, K. (Eds.), Mahale Chimpanzees: 50 Years of Research. Cambridge University Press, Cambridge, UK, pp. 311–384.
Hozer, C., Pifferi, F., Aujard, F., Perret, M., 2019. The Biological Clock in Gray Mouse Lemur: Adaptive, Evolutionary and Aging Considerations in an Emerging Non-human Primate Model. Front. Physiol. 10, 1033. https://doi.org/10.3389/fphys.2019.01033
Humle, T., 2011. The Tool Repertoire of Bossou Chimpanzees, in: The Chimpanzees of Bossou and Nimba. Springer Japan, Tokyo, Japan, pp. 61–72.
Humle, T., Matsuzawa, T., 2002. Ant-dipping among the chimpanzees of Bossou, Guinea, and some comparisons with other sites. Am. J. Primatol. 58, 133–148. https://doi.org/10.1002/ajp.10055
Inoue-Nakamura, N., Matsuzawa, T., 1997. Development of Stone Tool Use by Wild Chimpanzees (Pan troglodytes). J. Comp. Psychol. 111, 159–173. https://doi.org/10.1037/0735-7036.111.2.159
Jurmain, R., 1989. Trauma, degenerative disease, and other pathologies among the gombe chimpanzees. Am. J. Phys. Anthropol. 80, 229–237. https://doi.org/10.1002/ajpa.1330800211
Kimura, N., Nakamura, S., Goto, N., Narushima, E., Hara, I., Shichiri, S., Saitou, K., Nose, M., Hayashi, T., Kawamura, S., Yoshikawa, Y., 2001. Senile Plaques in an Aged Western Lowland Gorilla. Exp. Anim. 50, 77–81. https://doi.org/10.1538/expanim.50.77
Kirkwood, T.B.L., 1977. Evolution of ageing. Nature 270, 301–304. https://doi.org/10.1038/270301a0
Lacreuse, A., Parr, L., Chennareddi, L., Herndon, J.G., 2018. Age-related decline in cognitive flexibility in female chimpanzees. Neurobiol. Aging 72, 83–88. https://doi.org/10.1016/j.neurobiolaging.2018.08.018
Lacreuse, A., Raz, N., Schmidtke, D., Hopkins, W.D., Herndon, J.G., 2020. Age-related decline in executive function as a hallmark of cognitive ageing in primates: an overview of cognitive and neurobiological studies. Philos. Trans. R. Soc. B Biol. Sci. 375, 20190618. https://doi.org/10.1098/rstb.2019.0618

189 Lacreuse, A., Russell, J.L., Hopkins, W.D., Herndon, J.G., 2014. Cognitive and motor aging in female
190 chimpanzees. Neurobiol. Aging 35, 623–632.
191 https://doi.org/10.1016/j.neurobiolaging.2013.08.036
192 Lane, M., 2000. Nonhuman primate models in biogerontology. Exp. Gerontol. 35, 533–541.
193 https://doi.org/10.1016/S0531-5565(00)00102-9
194 Languille, S., Blanc, S., Blin, O., Canale, C.I., Dal-Pan, A., Devau, G., Dhenain, M., Dorieux, O.,
195 Epelbaum, J., Gomez, D., Hardy, I., Henry, P.-Y., Irving, E.A., Marchal, J., Mestre-Francés, N.,
196 Perret, M., Picq, J.-L., Pifferi, F., Rahman, A., Schenker, E., Terrien, J., Théry, M., Verdier, J.-M.,
197 Aujard, F., 2012. The grey mouse lemur: A non-human primate model for ageing studies. Ageing
198 Res. Rev. 11, 150–162. https://doi.org/10.1016/j.arr.2011.07.001
199 Lemere, C.A., Oh, J., Stanish, H.A., Peng, Y., Pepivani, I., Fagan, A.M., Yamaguchi, H., Westmoreland,
200 S.V., Mansfield, K.G., 2008. Cerebral Amyloid-Beta Protein Accumulation with Aging in Cotton-
201 Top Tamarins: A Model of Early Alzheimer's Disease? Rejuvenation Res. 11, 321–332.
202 https://doi.org/10.1089/rej.2008.0677
203 Li, Z., He, X., Wu, S., Huang, R., Li, H., Wang, Z., Wang, L., Qin, D., Kong, Y., Guo, Y., Ma, X., Turck,
204 C.W., Xiong, Z., Wang, W., Hu, X., 2022. Naturally occurring Alzheimer's disease in rhesus
205 monkeys (preprint). Neuroscience. https://doi.org/10.1101/2022.10.20.513120
206 Lowenstine, L.J., McManamon, R., Terio, K.A., 2016. Comparative Pathology of Aging Great Apes:
207 Bonobos, Chimpanzees, Gorillas, and Orangutans. Vet. Pathol. 53, 250–276.
208 https://doi.org/10.1177/0300985815612154
209 Luncz, L.V., Gill, M., Proffitt, T., Svensson, M.S., Kulik, L., Malaivijitnond, S., 2019. Group-specific
210 archaeological signatures of stone tool use in wild macaques. eLife 8, e46961.
211 https://doi.org/10.7554/eLife.46961
212 Machanda, Z.P., Rosati, A.G., 2020. Shifting sociality during primate ageing. Philos. Trans. R. Soc. B
213 Biol. Sci. 375, 20190620. https://doi.org/10.1098/rstb.2019.0620
214 Matsuzawa, T., 1996. Chimpanzee intelligence in nature and in captivity: Isomorphism of symbol use and
215 tool use, in: Great Ape Societies. pp. 196–212.
216 Matsuzawa, T., 1994. Field Experiments on use of Stone Tools in the wild, in: Chimpanzee Cultures. pp.
217 351–370.
218 Matsuzawa, T., 1991. Nesting cups and metatools in chimpanzees. Behav. Brain Sci. 14, 570–571.
219 https://doi.org/10.1017/S0140525X00071417
220 Matsuzawa, T., Hulme, T., Sugiyama, Y., 2011. The Chimpanzees of Bossou and Nimba.
221 Matsuzawa, T., Humle, T., Koops, K., Biro, D., Hayashi, M., Sousa, C., Mizuno, Y., Kato, A., Yamakoshi,
222 G., Ohashi, G., Sugiyama, Y., Kourouma, M., 2004. Wild chimpanzees at Bossou-Nimba: Deaths
223 through a flu-like epidemic in 2003 and the green corridor project. Primate Res 20, 45–55.
224 Mattison, J.A., Vaughan, K.L., 2017. An overview of nonhuman primates in aging research. Exp.
225 Gerontol. 94, 41–45. https://doi.org/10.1016/j.exger.2016.12.005
226 Medawar, P., 1951. An Unsolved Problem of Biology: An Inaugural Lecture Delivered at University
227 College, London, 6 December, 1951., Inaugural Lecture (University College, London); 1951. H.K.
228 Lewis and Co., London.
229 Messaoudi, I., Ingram, D.K., 2012. Overview of aging research using nonhuman primate models. AGE 34,
230 1047–1049. https://doi.org/10.1007/s11357-011-9370-x
231 Morbeck, M., Galloway, A., Sumner, D., 2002. Getting Old at Gombe: Skeletal Aging in Wild-Ranging
232 Chimpanzees, in: Aging in Nonhuman Primates, Interdisciplinary Topics in Gerontology. Karger,
233 pp. 48–62.
234 Munger, E.L., Edler, M.K., Hopkins, W.D., Ely, J.J., Erwin, J.M., Perl, D.P., Mufson, E.J., Hof, P.R.,
235 Sherwood, C.C., Raghanti, M.A., 2019. Astrocytic changes with aging and Alzheimer's disease-
236 type pathology in chimpanzees. J. Comp. Neurol. 527, 1179–1195.
237 https://doi.org/10.1002/cne.24610
238 Muntané, G., Farré, X., Rodríguez, J.A., Pegueroles, C., Hughes, D.A., De Magalhães, J.P., Gabaldón,
239 T., Navarro, A., 2018. Biological Processes Modulating Longevity across Primates: A
240 Phylogenetic Genome-Phenome Analysis. Mol. Biol. Evol. 35, 1990–2004.
241 https://doi.org/10.1093/molbev/msy105
242 Ndung'u, M., Härtig, W., Wegner, F., Mwenda, J.M., Low, R.W.C., Akinyemi, R.O., Kalaria, R.N., 2012.
243 Cerebral amyloid β(42) deposits and microvascular pathology in ageing baboons: Brain amyloid

244 and microvascular pathology in baboons. Neuropathol. Appl. Neurobiol. 38, 487–499.
245 https://doi.org/10.1111/j.1365-2990.2011.01246.x
246 Neal Webb, S.J., Hau, J., Lambeth, S.P., Schapiro, S.J., 2019. Differences in Behavior Between Elderly
247 and Nonelderly Captive Chimpanzees and the Effects of the Social Environment. J. Am. Assoc.
248 Lab. Anim. Sci. 58, 783–789. https://doi.org/10.30802/AALAS-JAALAS-19-000019
249 Nichols, K., Zihlman, A., 2002. Skeletal and Dental Evidence of Aging in Captive Western Lowland
250 Gorillas: A Preliminary Report, in: Aging in Nonhuman Primates, Interdisciplinary Topics in
251 Gerontology. Karger, pp. 22–31.
252 Nussey, D.H., Froy, H., Lemaitre, J.-F., Gaillard, J.-M., Austad, S.N., 2013. Senescence in natural
253 populations of animals: Widespread evidence and its implications for bio-gerontology. Ageing
254 Res. Rev. 12, 214–225. https://doi.org/10.1016/j.arr.2012.07.004
255 Paul, A., Kuester, J., Podzuweit, D., 1993. Reproductive senescence and terminal investment in female
256 Barbary macaques (Macaca sylvanus) at Salem. Int. J. Primatol. 14, 105–124.
257 https://doi.org/10.1007/BF02196506
258 Perez, S.E., Sherwood, C.C., Cranfield, M.R., Erwin, J.M., Mudakikwa, A., Hof, P.R., Mufson, E.J., 2016.
259 Early Alzheimer's disease–type pathology in the frontal cortex of wild mountain gorillas (Gorilla
260 beringei beringei). Neurobiol. Aging 39, 195–201.
261 https://doi.org/10.1016/j.neurobiolaging.2015.12.017
262 Resende, B.D. de, Ottoni, E.B., Fragaszy, D.M., 2008. Ontogeny of manipulative behavior and nut-
263 cracking in young tufted capuchin monkeys (*Cebus apella*): a Perception-action perspective.
264 Dev. Sci. 11, 828–840. https://doi.org/10.1111/j.1467-7687.2008.00731.x
265 Roberts, J., Gilardi, K., Lasley, B., Rapp, P., 1997. Reproductive senescence predicts cognitive decline in
266 aged female monkeys. NeuroReport 8, 2047–2051. https://doi.org/10.1097/00001756-
267 199705260-00048
268 Rodriguez-Callejas, J.D., Fuchs, E., Perez-Cruz, C., 2016. Evidence of Tau Hyperphosphorylation and
269 Dystrophic Microglia in the Common Marmoset. Front. Aging Neurosci. 8.
270 https://doi.org/10.3389/fnagi.2016.00315
271 Rothwell, E.S., Freire-Cobo, C., Varghese, M., Edwards, M., Janssen, W.G.M., Hof, P.R., Lacreuse, A.,
272 2021. The marmoset as an important primate model for longitudinal studies of neurocognitive
273 aging. Am. J. Primatol. 83. https://doi.org/10.1002/ajp.23271
274 Sadoun, A., Rosito, M., Fonta, C., Girard, P., 2019. Key periods of cognitive decline in a nonhuman
275 primate model of cognitive aging, the common marmoset (Callithrix jacchus). Neurobiol. Aging
276 74, 1–14. https://doi.org/10.1016/j.neurobiolaging.2018.10.003
277 Salmon, A.B., 2016. Moving toward 'common' use of the marmoset as a non-human primate aging model.
278 Pathobiol. Aging Age-Relat. Dis. 6, 32758. https://doi.org/10.3402/pba.v6.32758
279 Samson, R.D., Barnes, C.A., 2013. Impact of aging brain circuits on cognition. Eur. J. Neurosci. 37,
280 1903–1915. https://doi.org/10.1111/ejn.12183
281 Sanz, C.M., Morgan, D.B., 2010. The Complexity of Chimpanzee Tool-Use Behaviors, in: The Mind of the
282 Chimpanzee: Ecological and Experimental Perspectives. The University of Chicago Press, pp.
283 127–140.
284 Schofield, D., Nagrani, A., Zisserman, A., Hayashi, M., Matsuzawa, T., Biro, D., Carvalho, S., 2019.
285 Chimpanzee face recognition from videos in the wild using deep learning. Sci. Adv. 5, 1–10.
286 https://doi.org/10.1126/sciadv.aaw0736
287 Schofield, D.P., Albery, G.F., Firth, J.A., Mielke, A., Hayashi, M., Matsuzawa, T., Biro, D., Carvalho, S.,
288 2023. Automated face recognition using deep neural networks produces robust primate social
289 networks and sociality measures. Methods Ecol. Evol. 14, 1937–1951.
290 https://doi.org/10.1111/2041-210X.14181
291 Shumaker, R., Walkup, K., Beck, B., 2011. Animal Tool Behavior: The Use and Manufacture of Tools by
292 Animals. The John Hopkins University Press, Baltimore, Maryland, USA.
293 Siracusa, E.R., Negron-Del Valle, J.E., Phillips, D., Platt, M.L., Higham, J.P., Snyder-Mackler, N., Brent,
294 L.J.N., 2022. Within-individual changes reveal increasing social selectivity with age in rhesus
295 macaques. Proc. Natl. Acad. Sci. 119, e2209180119. https://doi.org/10.1073/pnas.2209180119
296 Sirianni, G., Mundry, R., Boesch, C., 2015. When to choose which tool: multidimensional and conditional
297 selection of nut-cracking hammers in wild chimpanzees. Anim. Behav. 100, 152–165.
298 https://doi.org/10.1016/j.anbehav.2014.11.022

Sugiyama, Y., 1981. Observations on the population dynamics and behavior of wild chimpanzees at Bossou, Guinea, in 1979-1980. Primates 22, 435–444. https://doi.org/10.1007/BF02381236

Tardif, S.D., Mansfield, K.G., Ratnam, R., Ross, C.N., Ziegler, T.E., 2011. The Marmoset as a Model of Aging and Age-Related Diseases. ILAR J. 52, 54–65. https://doi.org/10.1093/ilar.52.1.54

Tarou, L.R., Bloomsmith, M., Hoff, M., Erwin, J., Maple, T., 2002. The Behavior of Aged Great Apes, in: Aging in Nonhuman Primates, Interdisciplinary Topics in Gerontology. Karger, pp. 209–231.

Thompson, M.E., Machanda, Z.P., Fox, S.A., Sabbi, K.H., Otali, E., Thompson González, N., Muller, M.N., Wrangham, R.W., 2020. Evaluating the impact of physical frailty during ageing in wild chimpanzees (*Pan troglodytes schweinfurthii*). Philos. Trans. R. Soc. B Biol. Sci. 375, 20190607. https://doi.org/10.1098/rstb.2019.0607

Troscianko, J., Von Bayern, A.M.P., Chappell, J., Rutz, C., Martin, G.R., 2012. Extreme binocular vision and a straight bill facilitate tool use in New Caledonian crows. Nat. Commun. 3, 1110. https://doi.org/10.1038/ncomms2111

Upright, N.A., Baxter, M.G., 2021. Prefrontal cortex and cognitive aging in macaque monkeys. Am. J. Primatol. 83. https://doi.org/10.1002/ajp.23250

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. J. Hum. Evol. 36, 719–741. https://doi.org/10.1006/jhev.1999.0304

Zhdanova, I.V., Masuda, K., Quasarano-Kourkoulis, C., Rosene, D.L., Killiany, R.J., Wang, S., 2011. Aging of Intrinsic Circadian Rhythms and Sleep in a Diurnal Nonhuman Primate, *Macaca mulatta*. J. Biol. Rhythms 26, 149–159. https://doi.org/10.1177/0748730410395849

5.9 Supplementary materials

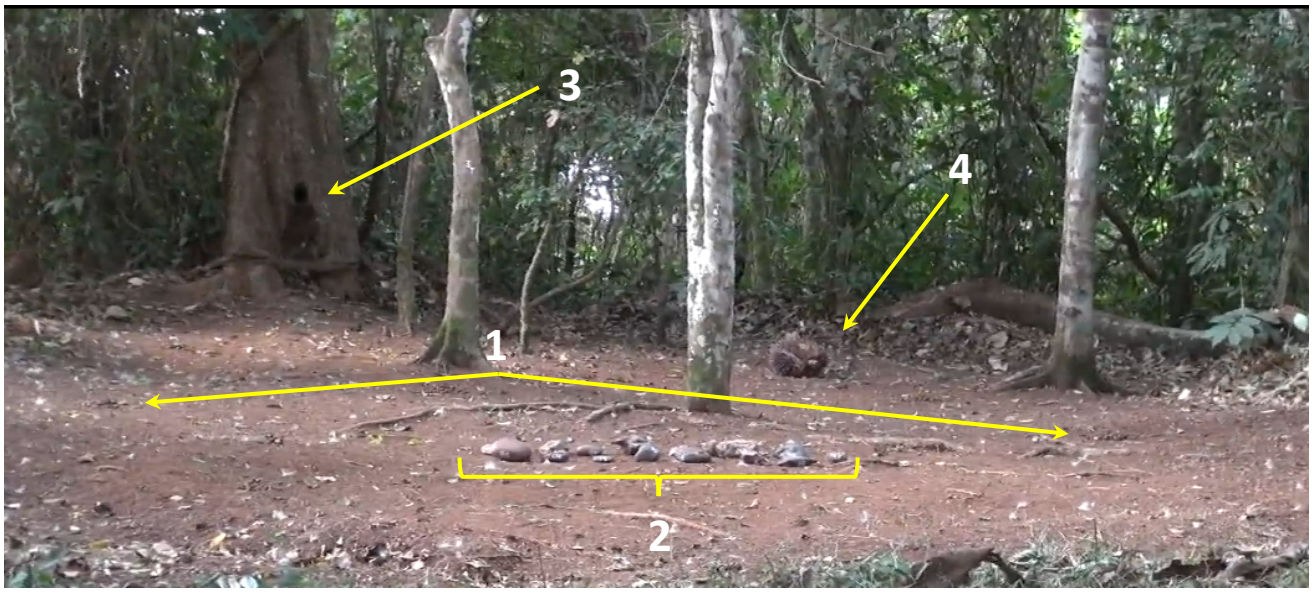


***Figure S1. The outdoor laboratory, Bossou (The Bureau)**. Key features of the Bureau are: 1. Provided piles of oil-palm nuts (two piles are indicated; typically, a total of 6-12 piles of 40-50 nuts each were provided), 2. Central matrix of available stone tools, 3. Water point, 4. Raceme of oil-palm fruits.

* This figure and parts of this legend are identical to figure S1 and corresponding legend in the supplementary materials for Chapter 2

Table S1. Ethogram of codable actions for observations of nut-cracking behaviours*. Actions in bold are coded alongside a corresponding object. There are 6 possible corresponding objects: 1. Nut, 2. Hammer, 3. Anvil, 4. Kernel, 5. Shell, 6. Bare Hand. Event codes in italics are used to denote the start and end of observable sequences. Coding commenced when individuals began interacting with stones, nuts, or nut-fragments. Coding ceased when individuals began engaging in a new behaviour e.g. play, grooming, eating oil-palm fruits. On the occasions where an individual moved out of clear sight of the video recording, or actions became obscured by an individual's body position, sequences were terminated with a 'Not Visible' codon, and marked as incomplete.

Action	Description
Bite	Place object in mouth and bite with teeth. Differs from 'Eat' as there is no consumption. Differs from 'Store' as object moves in and out of mouth whilst chimp is stationary. Differs from 'Peel Teeth' as bite applies general force, whereas peel with mouth is to remove shell fragments from kernel dexterously. Differs from 'Kiss' as object enters inside the mouth.
Brush	Brush objects off the anvil.
Drop	Place object(s) on ground.
Eat	Consume object. Differs from bite and store as it requires successful ingestion.
Flip	Flip object over.
Grasp	Grasp an object and move off the ground.
Kick	Apply rapid, hard force on object with the foot, so that the object is displaced.
Kiss	Place object to lips or nose, but not inside of the mouth.
Pass	Pass object between hands.
Peel Hand	Peel shell off of kernel with hands.
Peel Teeth	Peel shell off of kernel with teeth.
Place	Place an object on an anvil.
Provide	Directly hand an object to another individual.
Pull Foot	Pull an object across the ground with foot.
Pull Hand	Pull an object across the ground with hand.
Push Foot	Push an object across the ground with foot.
Push Hand	Push an object across the ground with hand.
Rake Foot	Pull many objects towards oneself using foot/leg.
Rake Hand	Pull many objects towards oneself using hand/arm.
Reorient	Rotate object horizontally.
Roll Foot	Roll object along the floor with foot.
Roll Hand	Roll object along the floor with hand.
Spit	Let object fall from mouth or lips.
Stomp	Whilst standing, apply strong force to object with foot.
Store	Place object(s) in mouth for transportation. Separated from bite, eat, peel teeth as it is followed by transportation across the outdoor laboratory, before then being removed from the mouth intact.
Strike One Hand	Strike with one hand, (and associated object).
Strike Two Hand	Strike with two hands, (and associated object).
Support Foot	Support object with foot.
Support Hand	Support object with hand.
Take	Receive an object directly from another individual.
Throw	Throw object away from self, horizontally or vertically.
Touch Foot	Touch or grasp object without moving it using foot.
Touch Hand	Touch or grasp object without moving it using hand.
Relocate	Stand up and move to a new area; is immediately followed by another coding action.
Start	Start of a sequence.
End Bout	End of a sequence.
Not Visible	Individual moves out of view, and coding cannot continue. Differs from 'End Bout', as there is no evidence the individual has stopped engaging with stones, nuts or nut-fragments.

* This table and legend are identical to table S2 and corresponding legend in the supplementary materials for chapter

Table S2. The number of stone tool selection events sampled for each individual in each field season.

	Year					
Individual	1999	2004	2008	2011	2016	Total
Fana	2	2	8	0	4	16
Jire	4	4	5	3	3	19
Tua	6	9	7	3	0	25
Velu	3	5	10	0	3	21
Yo	4	5	8	9	1	27

Table S3. Models of stone-tool selection duration across years, with AIC. AIC values reported for models fitted by Maximum Likelihood. PAB is the encounter in which stone tool selection events occurred.

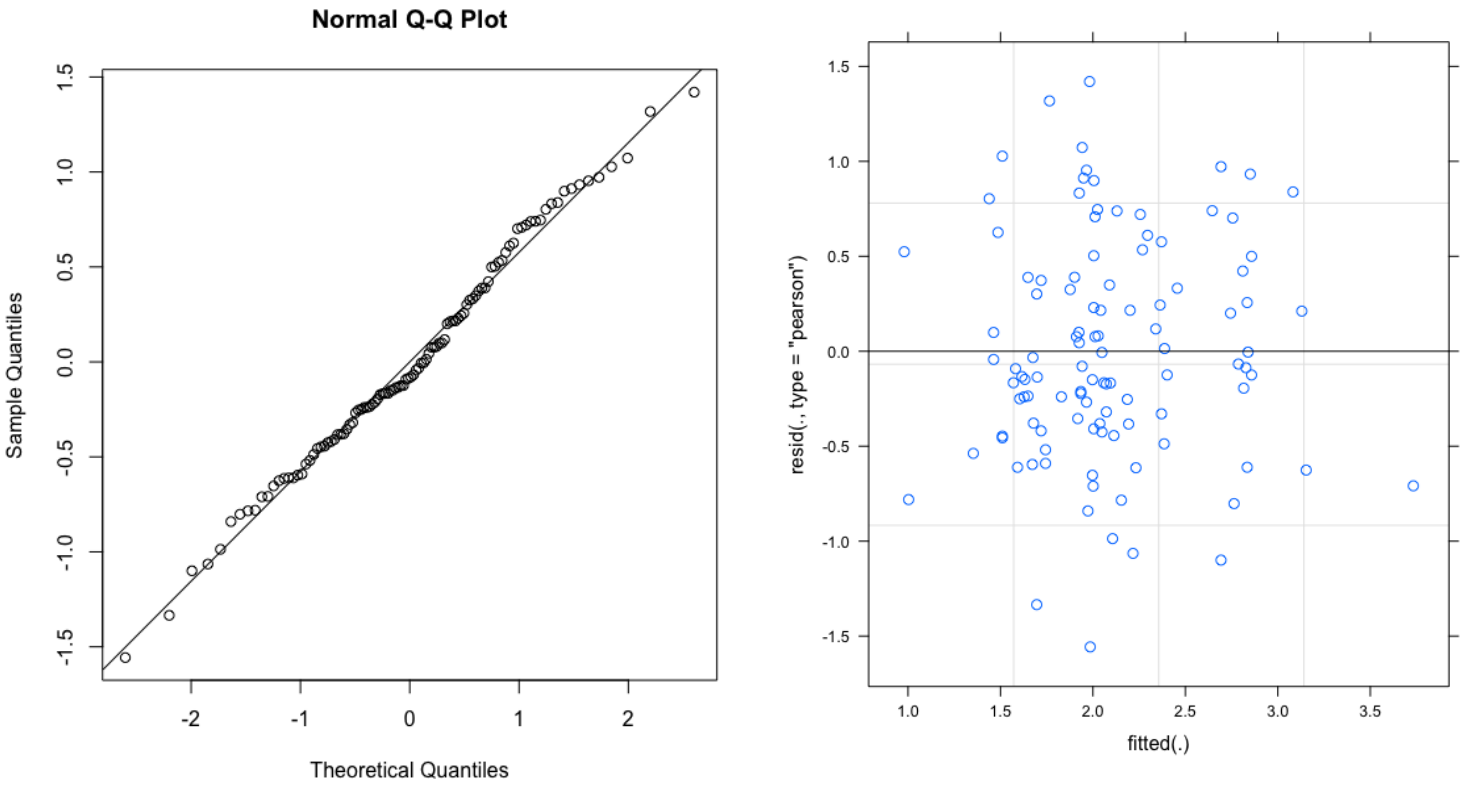
Model	Formula	df	AIC
Individual Random Slope and Intercept for Scaled Year.	Log(Time) ~ Year-Scaled + Stones Selected + Stones Previously Taken + (1 + Year-Scaled|ID) + (1|PAB)	9	225
Dropped Year	Log(Time) ~ Stones Selected + Stones Previously Taken + (1|ID) + (1|PAB)	6	234
Null for All Fixed Effects	Log(Time) ~ 1 + (1|ID)+ (1|PAB)	4	234
Individual Random Intercept Fixed Slope	Log(Time) ~ Year-Scaled + Stones Selected + Previously Taken + (1|ID) + (1|PAB)	7	233

Table S4. Summary output for mixed-effect model with individual as a random slope, and encounter and individual as random intercepts. 108 observations, 49 encounters, 5 individuals.

Log(Time) ~ Year-Scaled + Stones Selected + Stones Previously Taken + (1 + Year-Scaled|ID) + (1|PAB)

Random Effect	Variance	SD	
Encounter	1.429e-10	1.196e-05	
ID (Intercept)	1.441e-01	3.796e-01	
ID (Slope – Scaled Year)	6.699e-02	5.934e-01	
(Residual)	3.521e-01	5.934e-01	
Fixed Effect	**Estimate**	**SE**	**t value**
(Intercept)	1.829	0.223	8.201
Scaled Year	0.137	0.130	1.049
Two Stones Selected	0.347	0.136	2.554
Stones Previously Taken	-0.012	0.018	-0.668

26



27
28 **Figure S2. Plots to assess fit for the effect of increasing year on the duration of stone-tool selection, with Individual and**
29 **encounter as random effects, and a random slope for individuals.** The left illustrates a quantile-quantile plot (points closer to the
30 represent a better fit to the models assumption of normality); the right is a fitted vs residual plot (more evenly dispersed points about
31 the line is better).

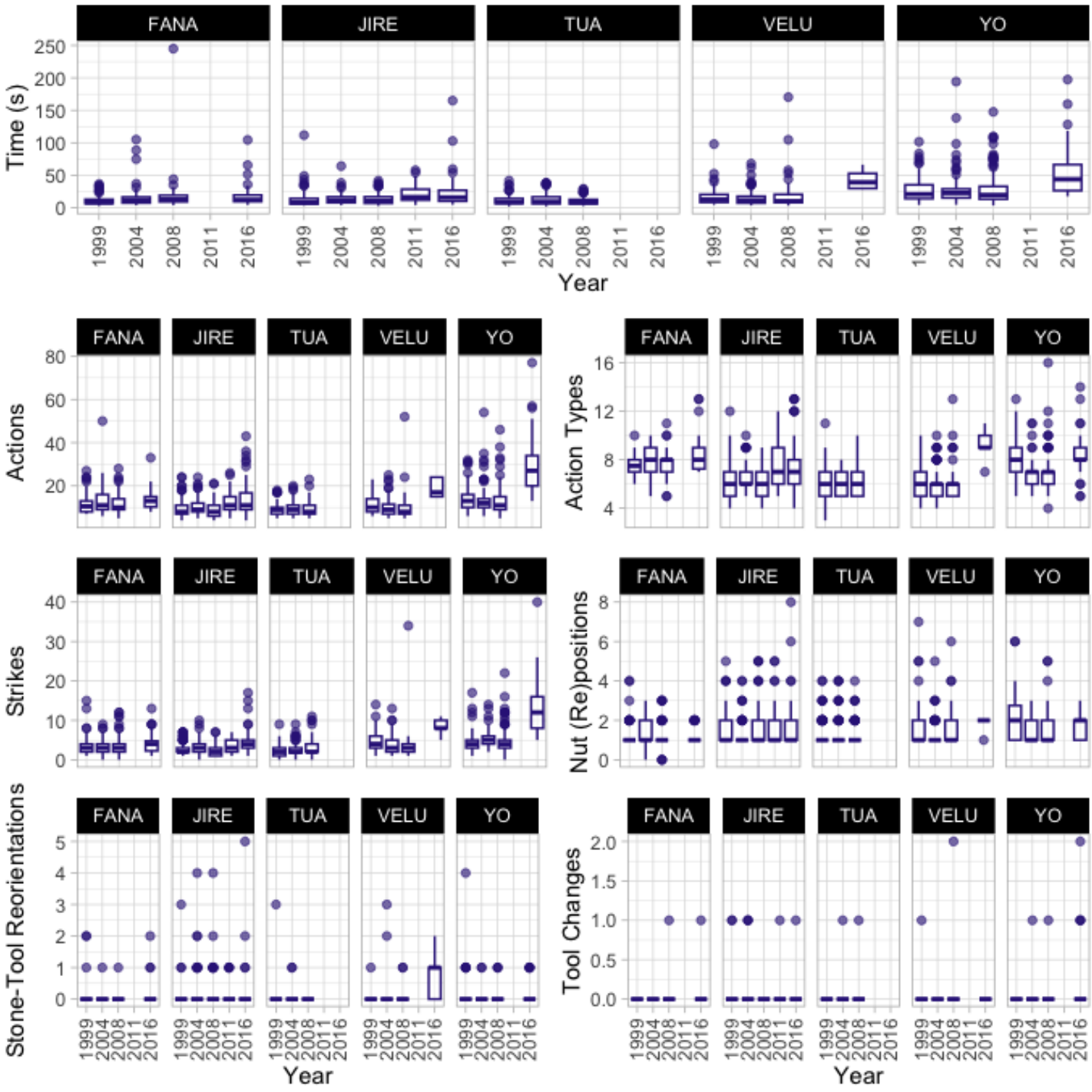


Figure S3. Boxplots describing metrics of efficiency for oil-palm nut cracking and processing, for each individual in each field season.

Table S5. Summary output for the random slope mixed-effect model for the total time taken to crack and process oil-palm nuts over sampled field seasons. 1538 observations, 20 encounters, 5 individuals.

lmer(Log_Time ~ Scaled Year + (Scaled Year|ID) + (1|Encounter) , REML = F)

Random Effect	Variance	SD	
Encounter	0.0286	0.169	
ID (Intercept)	0.0890	0.298	
ID (Slope – Scaled Year)	0.00151	0.0388	
(Residual)	0.418	0.647	
Fixed Effect	**Estimate**	**SE**	**t value**
(Intercept)	2.66	0.142	18.8
Scaled Year	0.077	0.030	2.60

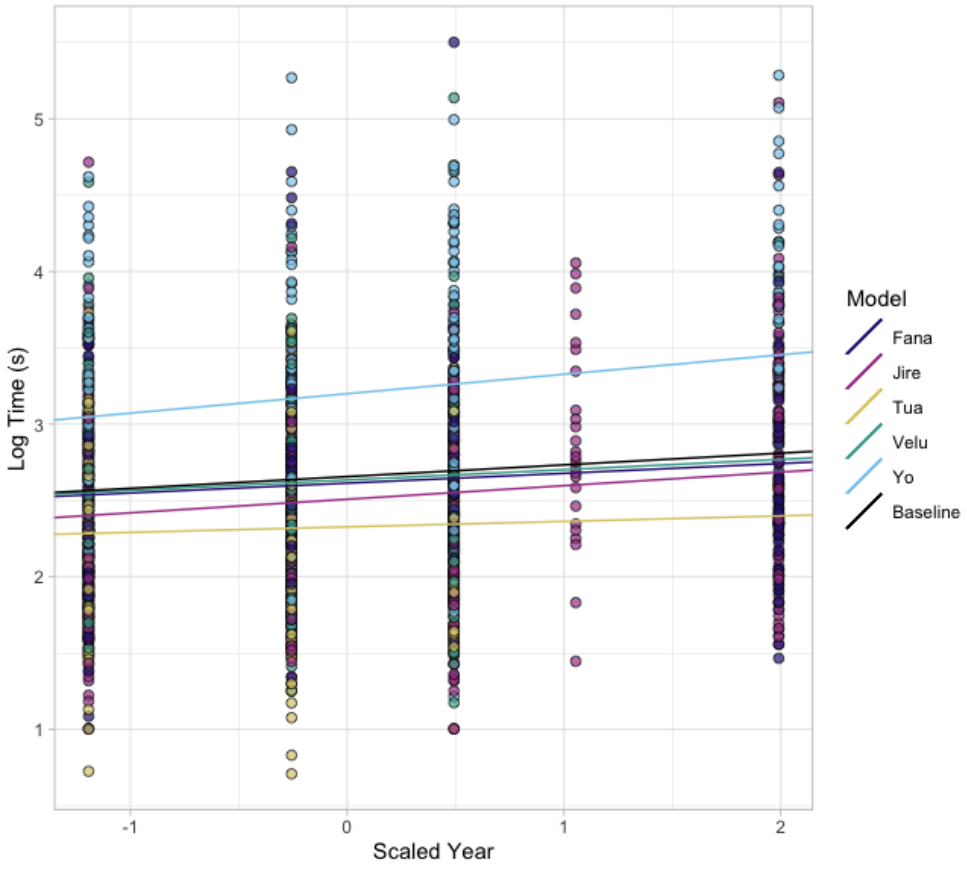


Figure S4. Random-slope mixed-effect model for the total time taken to process individual oil-palm nuts across sampled field seasons. Data points for each individual are colour coded. Lines correspond to how the model fit data relating to each individual. The black 'baseline' describes the baseline coefficients for model intercept and slope.

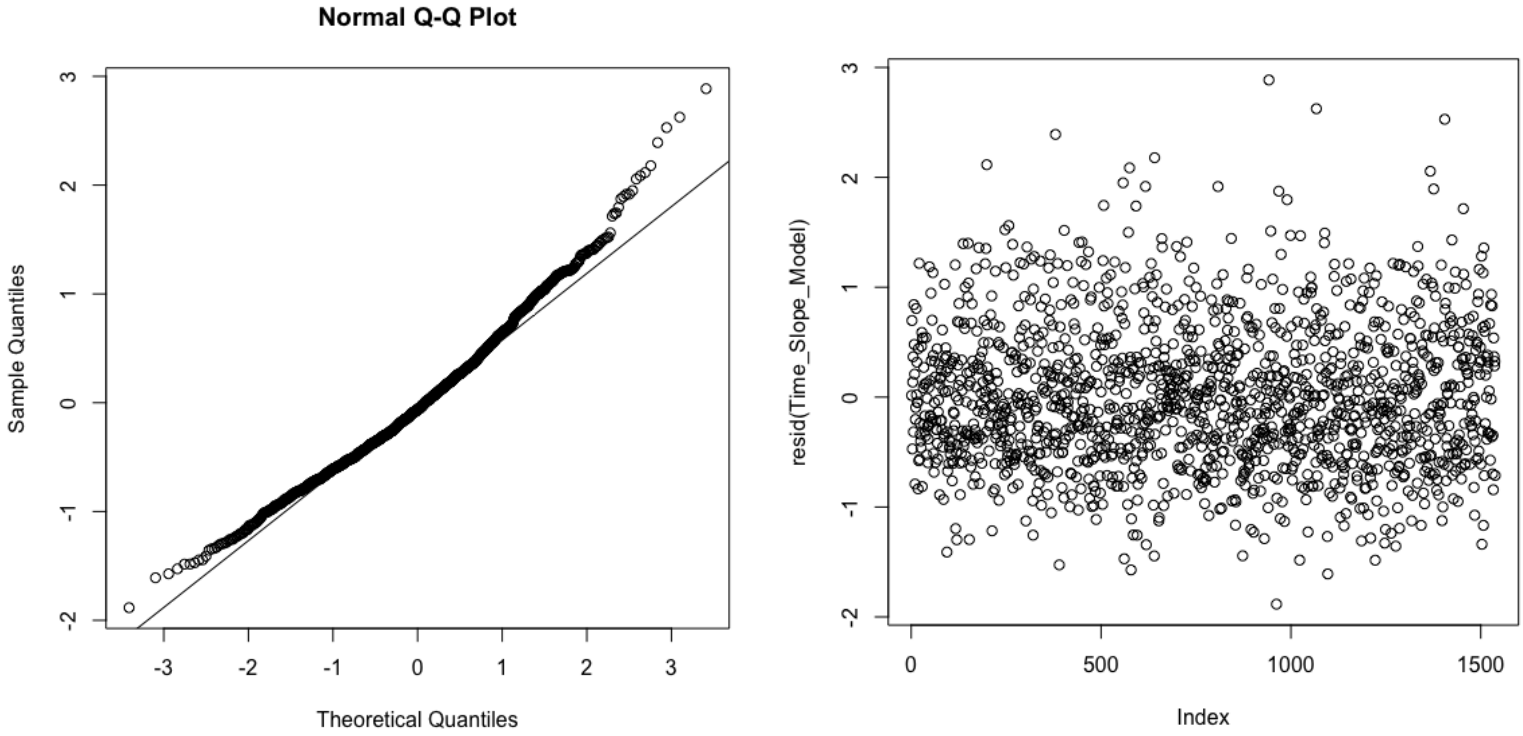


Figure S5. Plots to assess fit for the effect of increasing year on the time taken to crack and process oil-palm nuts, with Individual and encounter as random effects, and a random slope for individuals. The left illustrates a quantile-quantile plot (points closer to the represent a better fit to the models assumption of normality); the right is a fitted vs residual plot (more evenly dispersed points about the line is better).

Table S6. Summary output for the random slope mixed-effect model for the number of discrete actions used to crack and process oil-palm nuts over sampled field seasons. 1538 observations, 20 encounters, 5 individuals.

glmer(Action Events ~ Scaled Year + (Scaled Year|ID) + (1|Encounter), family = poisson)

Random Effect	Variance	SD	
Encounter	0.0836	0.289	
ID (Intercept)	0.0287	0.170	
ID (Slope – Scaled Year)	0.00344	0.0587	
Fixed Effect	Estimate	SE	z value
(Intercept)	2.56	0.102	25.2
Scaled Year	0.022	0.0292	0.769

Table S7. Summary output for the random slope mixed-effect model for the number of unique types of action used to crack and process oil-palm nuts over sampled field seasons. 1538 observations, 20 encounters, 5 individuals.

glmer(Unique Action Types~ Scaled Year + (Scaled Year|ID) + (1|Encounter), family = poisson)

Random Effect	Variance	SD	
Encounter	0.00197	0.0445	
ID (Intercept)	0.00744	0.0863	
ID (Slope – Scaled Year)	0.000138	0.0118	
Fixed Effect	Estimate	SE	z value
(Intercept)	1.926	0.0434	44.4
Scaled Year	0.026	0.0148	1.73

Table S8. Summary output for the random slope mixed-effect model for the number strikes of the hammer stone used to crack and process oil-palm nuts over sampled field seasons. 1538 observations, 20 encounters, 5 individuals.

glmer(Strikes ~ Scaled Year + (Scaled Year|ID) + (1|Encounter), family = poisson)

Random Effect	Variance	SD	
Encounter	0.157	0.397	
ID (Intercept)	0.0415	0.204	
ID (Slope – Scaled Year)	0.0108	0.104	
Fixed Effect	Estimate	SE	z value
(Intercept)	1.46	0.131	11.1
Scaled Year	0.0794	0.0514	1.55

Table S9. Summary output for the random slope mixed-effect model for the number stone-tool reorientations performed during the cracking and processing of oil-palm nuts over sampled field seasons. 1538 observations, 20 encounters, 5 individuals.

glmer(Strikes ~ Scaled Year + (Scaled Year|ID) + (1|Encounter), family = poisson)

Random Effect	Variance	SD	
Encounter	0.07941	0.2818	
ID (Intercept)	0.329	0.574	
ID (Slope – Scaled Year)	0.202	0.450	
Fixed Effect	Estimate	SE	z value
(Intercept)	-3.0978	0.3092	-10.019
Scaled Year	0.1489	0.2546	0.585

Table S10. Intercept and slope for individual random effects for nut metrics of total time, total number of actions, and total number of strikes.

Metric	Individual	Intercept	Scaled Year (Slope)
Total Time	**Fana**	2.61	0.0644
	Jire	2.51	0.0890
	Tua	2.33	0.0363
	Velu	2.63	0.0677
	Yo	3.20	0.128
Actions	**Fana**	2.68	-0.0283
	Jire	2.51	0.0487
	Tua	2.42	0.0431
	Velu	2.40	-0.0495
	Yo	2.81	0.0985
Strikes	**Fana**	1.41	0.00784
	Jire	1.32	0.0507
	Tua	1.29	0.195
	Velu	1.48	-0.043
	Yo	1.82	0.186

Table S12. Each unique action type employed by Yo in 1999 and 2016, described as a proportion of the first 1000 actions observed for Yo in each year. The difference between years is found, and whether this difference is greater than 0.05 (5%) is determined. A direction of change between years is also indicated for each action.

Action	1999	2016	2016 - 1999	Difference > 0.05?	direction
brush SHELL	0.01632302	0.00981354	0.00650948	FALSE	decrease
drop ANVIL	0.00429553	0.00392542	0.00037012	FALSE	decrease
drop HAMMER	0.03006873	0.00785083	0.02221789	FALSE	decrease
drop KERNEL	0.00085911	0.00294406	0.00208496	FALSE	increase
drop NUT	0.00429553	0.00392542	0.00037012	FALSE	decrease
drop SHELL	0.01546392	0.02551521	0.01005129	FALSE	increase
eat KERNEL	0.08676976	0.13837095	0.05160119	TRUE	increase
flip ANVIL	0.00257732	0	0.00257732	FALSE	decrease
flip HAMMER	0.00085911	0	0.00085911	FALSE	decrease
flip KERNEL	0.00085911	0	0.00085911	FALSE	decrease
grasp ANVIL	0.00429553	0.00392542	0.00037012	FALSE	decrease
grasp HAMMER	0.04553265	0.00588813	0.03964452	FALSE	decrease
grasp KERNEL	0.07044674	0.05888126	0.01156548	FALSE	decrease
grasp NUT	0.11340206	0.05691855	0.05648351	TRUE	decrease
kiss KERNEL	0.00257732	0	0.00257732	FALSE	decrease
kiss NUT	0.00085911	0	0.00085911	FALSE	decrease
pass HAMMER	0.00085911	0	0.00085911	FALSE	decrease
pass KERNEL	0.00171821	0	0.00171821	FALSE	decrease
pass NUT	0.01718213	0.00196271	0.01521942	FALSE	decrease
peelhand SHELL	0.00257732	0.00392542	0.0013481	FALSE	increase
peelteeth SHELL	0.05584192	0.12365064	0.06780871	TRUE	increase
place HAMMER	0.01202749	0.00196271	0.01006478	FALSE	decrease
place KERNEL	0.00601375	0.00098135	0.00503239	FALSE	decrease
place NUT	0.09621993	0.0451423	0.05107763	TRUE	decrease
relocate	0.00687285	0.00294406	0.00392879	FALSE	decrease
reorient ANVIL	0.00945017	0.00392542	0.00552475	FALSE	decrease
rollhand HAMMER	0.00085911	0	0.00085911	FALSE	decrease
spit SHELL	0.00085911	0.00098135	0.00012225	FALSE	increase
strikeonehand HAMMER	0.35395189	0.44455348	0.09060159	TRUE	increase
strikeonehand NUT	0.00085911	0	0.00085911	FALSE	decrease
supportfoot ANVIL	0.00343643	0.00294406	0.00049236	FALSE	decrease
touchfoot ANVIL	0.00085911	0	0.00085911	FALSE	decrease
touchhand ANVIL	0.00429553	0.00392542	0.00037012	FALSE	decrease
touchhand HAMMER	0.00515464	0	0.00515464	FALSE	decrease
touchhand KERNEL	0.00601375	0.00294406	0.00306968	FALSE	decrease
touchhand NUT	0.01460481	0.03140334	0.01679853	FALSE	increase
touchhand SHELL	0.00085911	0.00392542	0.00306631	FALSE	increase
bite SHELL	0	0.00098135	0.00098135	FALSE	increase
brush HAMMER	0	0.00098135	0.00098135	FALSE	increase
grasp SHELL	0	0.00294406	0.00294406	FALSE	increase
reorient HAMMER	0	0.00098135	0.00098135	FALSE	increase
supporthand ANVIL	0	0.00098135	0.00098135	FALSE	increase

Chapter 6

General Discussion

6.1.1 Summary of results

This thesis examines the sequential organization of actions performed by wild chimpanzees as they engage in one of their most complex technological behaviours: the cracking of hard-shelled nuts using hammer and anvil stones (nut cracking). Specifically, this thesis considers how chimpanzees organize sequential actions to successfully perform nut cracking behaviours; how the repertoire of actions used by chimpanzees for nut cracking develops during infancy and the juvenile phase; and thirdly, how the nut cracking behaviours of chimpanzees senesce as individuals experience progressive old-age in the wild. To answer these questions, I examined the tool-use behaviours of the chimpanzees of the Bossou Forest, Guinea, using an archive of several decades of video footage collected at an 'outdoor laboratory' located in the centre of the community's home range.

In **Chapter 2**, I developed an ethogram to code the behaviours used by chimpanzees during nut cracking at the outdoor laboratory at Bossou, and collected over 8000 actions used by eight chimpanzees during the 2012 field season. Using estimations of mutual information (MI), I was able to demonstrate that long-distance dependencies exist within the sequences of actions produced by chimpanzees during nut cracking, and that for half of sampled adults, these dependencies persisted once the repetition of actions was controlled for. Chapter 2 also revealed that the decay of information between elements separated by increasing sequential distances was best characterized by models which involved a power-law term, which is a key signature of hierarchical organization. A transition-point analysis revealed that, for individuals whose MI-decay was best approximated by a composite decay model (including exponential and power-law terms), exponential decay of MI occurred between the first 2-8 elements. This supports the idea that chimpanzees may organize actions into predictable subroutines of 2-8 elements long (or in some cases, organize actions exclusively by hierarchical organization, as suggested by two individuals whose MI decay was fully characterized by a power-law).

In **Chapter 3**, I developed a dictionary-based compression algorithm, which I applied to the same dataset used in Chapter 2. The action sequences produced by chimpanzees compressed to a similar extent to Markov sequences, except for the individual for whom we collected the largest corpus of actions. The action sequences of adults compressed to a greater extent than those of infants and juveniles, suggesting that the use of regularly reoccurring subroutines by chimpanzees during action organization is something

which becomes increasingly common as individuals develop through adolescence and subadulthood. Through analysing the dictionaries produced by five individuals, I identified variation in the rules used for compression between individuals. This variation included rules which represented particularly frequent use of particular subroutines for individuals, as well as rules whose differences between individuals were likely artefacts of the compression process. We also identified a number of pairs of rules which varied within the dictionaries of individuals, and may have indicated behavioural flexibility in action organization, including possible centre-embedding.

In **Chapter 4,** I longitudinally sampled over 13,000 actions performed by chimpanzees as they engaged with nuts and stone tools between the ages of one and eight years old, and analysed the size and composition of action repertoires both before and after individuals acquired the skill of nut cracking. I also sampled over 11,000 actions used by adults during nut cracking, at four time points between 1999 and 2012. This repertoire analysis revealed that the repertoires of actions used by chimpanzees during nut cracking grow as individuals explore the performance of different possible actions with nuts and stone tools (e.g. touching, stomping, and biting objects), and at the age at which nut cracking is first observed, this repertoire begins to slowly decrease in size, and likely continues to be 'pruned' during adolescence and adulthood. This analysis also revealed that striking downwards with one hand – a particularly salient behaviour in nut cracking – is often acquired at ages which precede the successful performance of the behaviour; however, other key actions, such as placing a nut on the anvil, are not.

In **Chapter 5,** I longitudinally sampled the nut cracking behaviours of five individuals as they experienced progressive old-age. Through sampling at five timepoints across the period of 1999 to 2016, I identified inter-individual variability in how old-age influenced the nut cracking behaviours of wild chimpanzees. Whilst some individuals were highly robust to the process of ageing, and demonstrated minimal changes in their tool-use behaviours with old-age, some individuals exhibited profound changes in their nut cracking behaviours over the years. This included a reduction in the rate of engagement with stone tools; an increase in the amount of time taken to select tools; and a reduction in the efficiency with which nuts were cracked using stone tools. Importantly, the specific constellation of changes was unique to each individual.

This thesis provides new insight into the organization, development, and senescence of wild chimpanzee stone-tool use, using an extensive corpus of behavioural data, and captures the behaviours of chimpanzees during tool use at an exceptional level of granularity. This thesis reports on a number of computationally intensive methodologies for understanding the sequential behaviours of a non-human animal – the chimpanzee – and presents a number of methodological considerations for future research on the sequential behaviours of animals. The results of Chapters 2-5 also present interesting points of discussion for models of human behavioural evolution, including the evolution of highly hierarchical behaviours, complex cultural practices, and the senescent processes which occur towards the end of the human lifetime.

6.1.2 Nut cracking as a sequential behaviour

Chapters 2 and 3 provide key insights into the sequential organization used by wild chimpanzees during nut cracking. MI decay suggests that sequences of actions used during nut cracking are organized, at least in part, hierarchically. For the individuals who were identified as organizing their actions in a hierarchical fashion, MI decay also identifies that actions are organized into subroutines of 2-8 actions, which are themselves combined into extended sequences of behaviours. Dictionary-based compression describes how subroutines are organized over a maximum of three hierarchical levels; and that of these subroutines of actions, several reflect core processes to nut cracking and are universal across individuals (e.g. the grasping and consuming of fragments of kernel). Chimpanzees support these universals with less frequently employed subroutines of actions, and the frequency with which these optional subroutines are performed varies highly between individuals (e.g. storing nuts in the mouth for transportation was commonly performed by one individual, but rarely by others, despite some individuals demonstrating that it was a behaviour which they know how to perform). Subroutines may themselves not be fixed in the minds of chimpanzees, as, within the dictionaries of particular individuals, dictionary-based compression identified a number of candidate subroutines which were similar in their organization of actions, but differed by the presence of a single central action, indicating flexibility in the morphology of subroutines. Overall, the majority of actions performed by proficient chimpanzees during nut cracking belonged to a small number of different action types (as indicated in both Chapter 2 and Chapter 4), and therefore, the subroutines of

actions used for nut cracking are predominantly comprised of around six manual operations ('grasp', 'place', 'strike', 'peel', 'eat' and 'drop'), for which grasping and dropping are the only actions which are generalized to many different objects. These actions are then supplemented through the use of a number of rarer actions, through the use of infrequent subroutines of actions.

Overall, the results of this thesis support previous claims that the manual actions of great apes represent a hierarchical domain of behaviour (Byrne and Russon, 1998). The hierarchical organization of manual actions in great apes was first proposed using two qualitative descriptions: the actions used by wild gorillas during nettle processing tasks, and the novel behaviours acquired by sanctuary-living orangutans (Byrne and Russon, 1998). Whilst these models were used to propose a specific mode of social learning for great-apes (the copying of subgoals through program-level imitation), the actions of primates became more frequently described using hierarchical models (Terrace, 2005), including during tool-use. Many of the current descriptions of primate tool-use implicitly assume hierarchical organizations of actions used by primates, where the *chaîne operatoire* is organized using subgoals of a behaviour (Carvalho et al., 2008; Corat et al., 2016; Sanz and Morgan, 2010; Tonooka, 2001); however, as mentioned in chapters 1-3, these methods have been criticized, as observers may infer hierarchical organizations subjectively (Vereijken and Whiting, 1998).

MI decay and dictionary compression allow for the signatures of hierarchical organization to be evaluated from the mathematical and structural properties of sequences, including entropy (Grassberger, 2003; Lin and Tegmark, 2017) and the frequency of reoccurring combinations of elements (Nevill-Manning and Witten, 1997, 2000), without the need for observers to predefine subgoals. Thus, the methods contained within this thesis may be considered objective methods for identifying properties of hierarchical organization in sequential behaviours (Gomez-Marin et al., 2016; Sainburg et al., 2022, 2019). Power-law components of MI decay, and the differences identified between dictionaries formed during the compression of observed action sequences and Markov-generated sequences, suggest that action sequences used for nut cracking are hierarchically structured. The only analysis within this thesis which suggests otherwise is that, for most chimpanzees, the overall compression of action sequences and Markov-generated sequences were similar (however, as identified by differences in the dictionaries that underpin this compression, the pathways with which each sequence type compressed were different). During the

discussion in Chapter 3, I discussed the possibility that small sample sizes may have led to similar levels of compression across sequence types, as similar analyses in human language, and roundworm locomotion, were performed using over ten thousand elements (Gomez-Marin et al., 2016; Sainburg et al., 2022) and using systems of sequence discretization which involved a much larger possible repertoire of sequence units (e.g. over 90 different roundworm postures; Gomez-Marin et al., 2016). Therefore, the extent to which compressibility of tool-action sequences suggests that they are organized serially or hierarchically is a question that requires further investigation. As suggested in Chapter 3, processes of automated behaviour tracking, generating sequences using postures of great-ape bodies during tool-use (which would be more numerous than the functional actions I have used to describe chimpanzee behaviours) may be particularly useful for achieving such an aim (Bain et al., 2021; Bala et al., 2020; Gomez-Marin et al., 2016).

Nut cracking has previously been described to contain a hierarchical relationship between objects (Matsuzawa, 1996). During nut cracking, a nut is placed on the anvil (level 1) and then a hammer is used to strike down on this composite (level 2). The hierarchical complexity of object associations for nut cracking is supported through developmental pathways in wild chimpanzees, where individuals first interact with single objects in isolation (beginning around 1.5 years old), then begin to combine objects in pairs (at approximately 2.5 years old), until finally combining all three objects to enable nut cracking (at around 3.5 years old; Inoue-Nakamura and Matsuzawa, 1997). It is possible that this complexity in object combinations during nut cracking may be increased further by chimpanzees at Bossou, through the introduction of an additional wedge stone to support the anvil (thus increasing the total hierarchical levels of objects up to 3: wedge & anvil at one level; a nut at an additional level; and a hammer stone at the third; Matsuzawa, 1996, 1991); however, wedge-stone use is rare at Bossou, and it is unclear to what extent it is an intentional behaviour (Hayashi and Inoue-Nakamura, 2011; Matsuzawa, 1991).

It is possible that hierarchical combinations of objects could emerge through serially learnt programs of behaviour. In fact, these combinations could be produced from a completely linear program of: *grasp nut*, *place nut on anvil*, *grasp hammer*, *strike downwards on nut* (including optional repeats of this behaviour), *grasp kernel*, *eat kernel*. Therefore, whilst nut cracking has been previously theorized to require an understanding of hierarchical relationships between objects, this does necessarily demand the

sequential organization of actions to be a hierarchical aspect of primate behaviour. However, using the results contained within this thesis, I argue that, along with the organization of objects, action organization represents an additional dimension to hierarchical thinking by chimpanzees during nut cracking. I support this claim with Chapters 2 and 3 of this thesis, and also through the relationship of the results in this thesis to the wider literature. The models which I have employed to investigate hierarchical associations in primate sequential actions have found similar systems of organization in the locomotion behaviours of zebra fish (*Danio rerio*; Sainburg et al., 2020) and roundworms (*C. elegans;* Gomez-Marin et al., 2016), as well as the manual actions of *Drosophila* flies during grooming (Dawkins and Dawkins, 1976; Sainburg et al., 2020). Additionally, similar patterns of organization are found in the sequential manual actions used by humans, including during tool-use tasks (Sainburg et al., 2020; Stout et al., 2021). Thus, the hierarchical organization observed within tool-use behaviours most likely shares its origins with more basal forms of hierarchical action organization, such as for movements of limbs during grooming and locomotion. Over the course of hominid evolution, this system of organization was co-opted into the tool-use behaviours of humans and non-human apes, and continued to increase in complexity following hominin divergence from non-human apes (Stout et al., 2021; for further discussion of this topic, see section 6.4 below). I therefore predict that hierarchical organization is present across great ape tool-use, and recommend further research into the organization of sequential actions performed by apes during tool-use behaviours to confirm this hypothesis, preferably with the use of objective computational methods. Moreover, understanding whether hierarchical organization is used to organize actions in tasks which do not involve tools (such as the elaborate actions performed by gorillas during nettle feeding), are also of interest, as well as whether the tool-use behaviours of other animals, including monkeys and corvids, exhibit similar systems of hierarchical organization to those I have described for chimpanzees. Answering these questions will provide further insight into the extent to which tool-use is a domain of behaviour which requires species to possess more sophisticated systems of hierarchical thinking.

6.1.3 Nut cracking across lifetimes: development

The development of nut cracking at Bossou has been previously researched in three individuals (who were not included in my analyses), between the ages of 1-4 years old, during the field seasons of 1992-1995

(Inoue-Nakamura and Matsuzawa, 1997). These chimpanzees were observed to progress through increasingly complex combinations of objects as they aged, until nut cracking was acquired at 3.5 years (Inoue-Nakamura and Matsuzawa, 1997). For these three chimpanzees, the manual actions required for nut cracking were reported to emerge early, by 1.5 years of age, including in the case of 'correct' object manipulations, e.g. the placement of nuts on stones (Inoue-Nakamura and Matsuzawa, 1997); however, these actions were not performed in the correct sequences for tool-use until at least 3.5 years (Inoue-Nakamura and Matsuzawa, 1997). Additionally, the use of a stone for striking downwards onto a nut was reported to be rare, including at ages which preceded the emergence of successful nut cracking (Hayashi and Inoue-Nakamura, 2011). This analysis of three chimpanzees at Bossou ceased at 4 years of age, and therefore, how nut cracking behaviours changed post infancy had not been formally characterized at Bossou. This represented a key knowledge gap, and, due to the small sample size of the analysis performed by Inoue-Nakamura and Matsuzawa, the developmental pathway of nut cracking during infancy would benefit from more data from additional individuals.

Through Chapter 4, I documented the developmental pathway for nut cracking of six additional chimpanzees at Bossou, bringing the total sample size across the literature to nine. I reported a number of similarities in the developmental pathways of chimpanzees to those previously reported, including the initial use of a number of behaviours which were infrequently used by adult chimpanzees (e.g. touching objects without moving them, stomping on objects, mouthing objects); however, I also reported several differences to previous descriptions of this development. Firstly, striking using a hammer stone emerged in the repertoires of several individuals prior to the acquisition of nut cracking at Bossou (however, I did not specifically record what an individual strikes downwards onto). This finding suggests that striking using a hammer stone can emerge early in the repertoires of chimpanzees during nut cracking, but a small amount of variation was observed between individuals. Secondly, when observing the behaviours of naïve tool-users, the placement of nuts on anvils was extremely rare in my data, and only increased in frequency once individuals had reached an age where they had acquired the skill of nut cracking. This result contrasts to previous studies of nut cracking development at Bossou, where this behaviour was reported more frequently (Inoue-Nakamura and Matsuzawa, 1997). The results of my analysis mirror observations of the development of nut cracking in tufted capuchin monkeys (*Sapajus apella*), where striking with stones is

observed early, but the correct positioning of nuts on anvils takes many more years for individuals to master (Resende et al., 2008).

The analysis reported in Chapter 4 also extends the window of action repertoire development at Bossou from 1-4 years to 1-8 years, and takes a unique approach of complementing this analysis through the sampling of comparative data from proficient adults. The results of Chapter 4 therefore reveal that action repertoires not only increase while individuals are young, but are then pruned, slowly, through the juvenile period, and into adolescence and adulthood. This pruning of the action repertoire reflects the increasing efficiency with which chimpanzees are able to crack nuts over the course of their lifetimes, as also seen in the reduced number of strikes of the hammer stone used by adult chimpanzees when cracking nuts at Bossou (Biro et al., 2006). Thus, the results of this chapter contribute to a body of evidence that suggests that tool use is not a behaviour which is simply learnt at a young age, and then reperformed, but rather a skill which is refined throughout extended periods of a chimpanzee's life. Additionally, the comparison I employed between younger individuals and adults reveals that striking is one of the most common actions performed by adult chimpanzees during nut cracking. Its emergence in the repertoires of learners at an early age may therefore reflect some degree of action-imitation used by chimpanzees during skill acquisition, particularly as alternative means of exerting force (e.g. stomping, biting) were performed comparatively rarely. The early emergence of striking may reflect copying of a highly salient action performed by experienced chimpanzees during nut cracking, and aligns with previous research on chimpanzees' ability to imitate which revealed that they are more likely to copy demonstrated actions if they are associated with the manipulation of objects than those that involve only bodily movements (Myowa-Yamakoshi and Matsuzawa, 1999). Moreover, sanctuary-living chimpanzees have been anecdotally observed copying striking actions performed by other individuals during nut cracking (Fuhrmann et al., 2014). Investigating how the salience of actions influences the likelihood that they are imitated, including how conspicuous actions are from their visual and auditory cues (of which, striking using stones is both), as well as how closely related these actions are to the successful completion of a goal during tool-use task (as striking is proximate to the consumption of kernels during the overall tool-use process), are both recommended directions for future research.

Chapter 4 did not explicitly consider *how* the actions of repertoires are combined into sequences. This would be a particularly informative aspect of understanding how skills are formed and refined in great apes, including during nut cracking. MI decay analyses and dictionary-based compression have been used to characterize developmental pathways in human language (Sainburg et al., 2022). Chapters 2 and 3 demonstrated that these algorithms are highly suitable for analysing sequential structures of action in proficient nut crackers, and also identified differences between younger and older individuals from a single year of data. They therefore would be highly useful for understanding the development of grammars of action for nut cracking in chimpanzees. This analysis will be important for furthering our understanding of how predominantly asocial learning processes shape the emergence of 'grammars of actions' for cultural behaviours, especially through the perspective of chimpanzees exhibiting behavioural traditions in population-specific sequences of actions. Understanding the development of sequential relationships in ape tool use would likely be a powerful comparative model for understanding the evolutionary processes which shaped the development of human sequential behaviours, including in language, music and tool use (see section 6.4).

6.1.4 Nut cracking across lifetimes: senescence

Chapter 5 of this thesis describes how, during progressive old-age, chimpanzees at Bossou vary in the extent to which they exhibit changes in their nut cracking behaviours, including in engagement and behavioural efficiency. I therefore present this as evidence that the tool-use behaviours of wild chimpanzees are susceptible to deterioration through old-age senescence. Such a result can be expected from literature documenting cognitive and physical senescence in primates in captivity (Baxter, 2001; Corr et al., 2002; Lacreuse and Herndon, 2009; Lowenstine et al., 2016); however, without the consolidation of longitudinal data from wild primates (of which the Bossou archive is an excellent example), research into how the behaviours of individual wild primates change with old-age has been closed off to scientific investigation.

The results of Chapters 4 and 5 suggest that, for some chimpanzees, engagement with tool-use behaviours, and the efficiency with which tool-use behaviours are performed, mirror each other at either end of their lifespan. Engagement with nuts and stones begins as early as one year old, including during play and possible attempts at tool-use (Inoue-Nakamura and Matsuzawa, 1997; Myowa-Yamakoshi and

Yamakoshi, 2011); however, following the first successful tool use between 3.5 and 7 years of age, stones are used for play less frequently, and are more commonly used as tools, and with increasing efficiency (as identified in Chapter 4; but also described in Biro et al., 2006). Engagement and efficiency are stable during adulthood, until at old age when some individuals begin to engage with nuts and stone tools less frequently and efficiently, as they experience increasingly profound effects of cognitive and physical senescence.

Exactly why engagement and efficiency in nut cracking decreases with old-age for some individuals is an open question. A similar phenomena have been anecdotally described in captive apes, where apes will be less likely to engage in object-manipulation tasks with old-age (Tarou et al., 2002), thus paralleling observed reductions in tool-use engagement. However understanding the precise relationships between individuals, objects, and ageing, demands further investigation. In the case of nut cracking, this relationship may be driven by a decreased motivation to crack nuts; an inability to successfully crack nuts due to physical deterioration (e.g. sarcopenia; Lowenstine et al., 2016); or through cognitive deterioration resulting in individuals no longer recalling *how* to crack nuts using stone tools. These explanations are not mutually exclusive, and unfortunately, these hypotheses were not directly addressable through my analysis. Future research should address whether reductions in engagement and efficiency in tool-use with old-age is a phenomenon which manifests itself across different tool-use behaviours, including those of different primate species. Understanding which tool-use tasks are particularly susceptible to senescence – or whether the effects of senescence can be expected across all tool-use tasks equally – may indeed be informative to questions surrounding the mechanisms of deterioration which underlie behavioural changes.

Understanding how wild primates age is an important to a number of looming questions. Humans are living longer than ever before, with profound demographic consequences. By the year 2050, UN projections estimate that 16% of people globally will be over the age of 65 (4 of every 25 people) (United Nations, Department of Economic and Social Affairs, Population Division, 2022), and this greying population demands that we build a comprehensive understanding of - and develop preventative and therapeutic measures for - the behavioural, social and medical consequences of human ageing, for which primates offer the most translatable models of research, especially great apes. Ageing in nonhuman primates show many similarities to those of humans, including increased social selectivity (Siracusa et al., 2022), reductions in similar domains of cognition (Lacreuse et al., 2018; Lacreuse and Herndon, 2009) as well as

of similar changes in many physiological processes (Lowenstine et al., 2016). Nonhuman primates are also central to the ongoing investigation of why humans are particularly susceptible to the neurodegenerative diseases, which can have profound effects as humans experience progressive old-age (Freire-Cobo et al., 2021). Neuropathological signatures associated with Alzheimer's disease have been reported in many species of nonhuman primates over recent years, including in a number of studies on great apes (Arnsten et al., 2019; Cramer et al., 2018; Edler et al., 2021a, 2017). Yet, the explicit manifestation of Alzheimer's disease has not been recorded for a nonhuman primate, rather, nonhuman primates have only ever been documented experiencing cognitive decline which is mild in comparison to that seen in neurodegenerative disease (Edler et al., 2021b).

In Chapter 5, I identified Yo as an individual who exhibited a suite of behavioural changes in nut cracking with old-age, many of which could, in theory, be attributed to changes in cognitive processing. The profound nature of such changes for Yo could be indicative of a senescent process which is homologous with human Alzheimer's; particularly as the behavioural changes observed in Yo (disrupted action organization; repeated gathering of tool materials; etc.) could be indicative of the characteristic changes in decision-making and planning; behavioural organization; and memory, observed in Alzheimer's disease (Edler et al., 2021b). However as I previously mentioned, my analysis was not able to rule out other mechanisms underlying such changes in behaviour, such as physical deterioration. Yo died during 2020, and so determining whether behavioural changes were accompanied by pathological signatures of disease is no longer possible (Edler et al., 2017).

To understand the extent to which behavioural changes during ageing reflect pathological disease, there is the need to not only characterize behaviours such as tool-use, but also the wider behavioural repertoires of individual primates. As previously described, humans experiencing Alzheimer's disease exhibit manifold behavioural changes (Finch and Austad, 2015). Future research into primate ageing should therefore, where possible, sample multiple domains of behaviour when characterizing senescent processes (e.g. across tool-use behaviours, navigation, social interactions, communication, etc.). Profound changes across great-ape behaviours, that follow a pattern which resembles Alzheimer's disease or other forms of dementia in humans, would be more concrete evidence for the existence of such diseases in nonhuman primates.

In concert with the ageing human population, the global population of primates ageing in captivity – including zoos, sanctuaries, and research institutions - is higher than ever previously recorded (Havercamp et al., 2019; Neal Webb et al., 2019). The physical and behavioural consequences of ageing must be taken into account when formulating strategies for effective care of primates in captivity, and given the inter-individual variability observed in nonhuman primate senescence, this should include bespoke welfare initiative for individuals. In instances of best practice, artificial environments constructed for captive primates reflect their natural habitats, including both the physical and social environment (Neal Webb et al., 2019; Ross, 2020). Understanding how primates experience old-age in the wild, and especially how it influences day-to-day behaviour, will therefore be extremely informative for understanding how to design artificial environments which support the welfare of primates ageing in captivity. I suggest that understanding the dynamics of ageing and tool-use will be extremely valuable in this endeavour. Many strategies for promoting animal welfare in captivity involve the use of enrichment, including objects animals can interact with, as well as foraging tasks which reflect the natural foraging behaviours animals would perform in the wild (Talbot et al., 2023). The senescence of tool-use behaviours suggests that, with old-age, foraging tasks may become more challenging, and the motivation to engage with objects for both enrichment and foraging is less likely. Understanding the dynamics between senescence and tool-use may therefore provide a window into understanding how enrichment should be modified to promote welfare of an increasingly old population of primates in captivity.

Researching senescence in wild animals is difficult, particularly when researchers aim to sample individuals longitudinally; however, Chapter 5 demonstrates how answering such questions is possible through the use of existing long-term datasets. Many long-term sites exist for the study and conservation of wild primates, and of these sites, many have tracked the lives of primates in-situ for decades, allowing for accurate ageing from birth records, or old-age being readily deducible for individuals present at the establishment of a research site. Long-term research sites hold extensive records of demographic, ecological, and behavioural data – many spanning decades of monitoring efforts – including data on a vast range of ecologically relevant behaviours, including daily navigation and movement, activity budgets, social association data, and cultural behaviours, including tool-use. Thus, the existing data collected by long-term

research sites offer an extensive resource for answering questions surrounding senescence in nonhuman primates.

To answer these questions effectively, long-term field sites must pool data to permit the formulation of robust statistical models of wild primate ageing. The analysis I presented in Chapter 5 uses a number of models to characterize changes in behaviour with age; however, these models are largely descriptive, and were restricted to five individuals. As rates of mortality naturally increase with old-age senescence, the number of individuals living to extreme old-age in the wild at any one field site will of course also be small. There is therefore a need for wide-scale scientific collaboration between field sites to produce rigorous statistical descriptions of wild primate ageing, both within and across species. I anticipate that through collaboration, researchers will be rewarded with stimulating and novel insights into the dynamics of ageing in wild primates, with important consequences for interdisciplinary issues of wellbeing in humans, and nonhuman primates living in captivity.

6.1.5 Implications for the evolution of human sequential behaviours

The tool-use behaviours of chimpanzees are of specific interest as they offer a comparative model for understanding the evolution of human technological behaviours (Carvalho et al., 2013; Carvalho and McGrew, 2012; Haslam et al., 2009). Where similarities are identified between the tool-use behaviours of humans and chimpanzees, the most parsimonious explanation is one of a common evolutionary origin, dating back to at least the last common ancestor between these two species (Haslam et al., 2009). Conversely, differences between these species indicate that, in one lineage, a unique evolutionary process has occurred to confer distinctive behaviours in tool-use (Haslam et al., 2009). Possibly most importantly, comparative research into the tool-use behaviours of humans and chimpanzees offers a means to understand the likely pathways through which cognition for tool-use evolved, through direct investigation of behaviours of both living species. Conclusions from this research can then be compared with the archaeological record, including artefacts from the tool-use behaviours of modern humans, extinct hominin species, and living and extinct species of nonhuman primate (Haslam et al., 2009).

When considering the evolutionary trajectory of human material culture, stone-tools are particularly important. Plant-based tools, which are far more common among non-human apes, were undoubtedly a

large part of the material culture of early hominin species (Haslam et al., 2009); however, the rapid rate at which organic matter degrades ultimately removes the vast majority of such tools from the archaeological record. Lithic tools, however, persist over time, and the persistence of such tools allows for interspecies comparisons in both behaviours of living individuals, and their archaeological records (Bandini et al., 2022; Carvalho et al., 2013; Carvalho and McGrew, 2012; Haslam et al., 2013, 2009; Luncz et al., 2019). Such comparisons support the idea that for both species, percussive pounding is extremely important, and whilst obvious in the stone-tool behaviours of chimpanzees (Boesch and Boesch, 1983; Matsuzawa, 1994) and some species of monkeys (Haslam et al., 2013; Mangalam and Fragaszy, 2015; Tan et al., 2015), the percussive use of stones was also important in the evolution of technology in early hominins (Carvalho and McGrew, 2012; Faisal et al., 2010; Harmand et al., 2015; Stout et al., 2021; Stout and Chaminade, 2009). Of the stone-tool behaviours of humans, understanding the evolution of knapping (the detachment of smaller fragments of stone - “flakes” - from a larger substrate) has received particular attention (Carvalho et al., 2013; Morgan et al., 2015; Nonaka et al., 2010; Rein et al., 2014; Stout et al., 2021). Studies into the abilities of nonhuman primates have suggested that, whilst chimpanzees and capuchins do occasionally produce fragments of stones during percussive use, this generation of flakes is unintentional, and fragments are not themselves repurposed (Carvalho et al., 2013; Proffitt et al., 2016). Thus, the range of uses for stone tools may be limited in nonhuman primates by both the lack of intentional modification of stones, and the lack of reuse of stone flakes produced during the percussive combination of stone tools (Carvalho et al., 2013).

How early hominins organized actions during tool-use behaviours is another key question, with possible implications for the evolution of syntax in both tool-action and language (Faisal et al., 2010; Stout et al., 2021; Stout and Chaminade, 2009). In efforts to answer such questions, experiments have observed how modern stone-knappers recreate tools found in the hominin archaeological record, examining specifically the complexity of their action sequences (Stout et al., 2021). The result of these efforts suggests that hominin species which evolved more recently in evolutionary time produced tools which involved more elaborate systems of hierarchical organization (specifically, this study compared the organization of actions during the production of Acheulean hand-axes and Oldowan stone-tools; Stout et al., 2021). This change in complexity occurred following an extremely long technological stasis in hominin lithic technology (exact

time-spans vary, but include approximations of 1 Ma; Kimura, 2002; Semaw, 2000), and therefore, reflects a significant transition point in human evolution. The conclusions of work by Stout and colleagues are that, during this stasis, Oldowan technology was restricted in its technological complexity due to limitations of cognition, specifically for sequential organization in behaviour, and following some process of selection for more complex cognitive abilities, these limitations were alleviated, and tool-complexity increased (Stout et al., 2021); however, alternative explanations for this stasis also exist (Kimura, 2002; Semaw, 2000).

Extant primates offer a means to characterize the complexity of manual action organization in homologous systems to humans, including during tool-use behaviours. My analysis supports the theory that primates use hierarchical combinations of actions to perform tool-use behaviours. The next question to answer is: *how* hierarchical are nonhuman primate tool-use behaviours in comparisons to humans? For chimpanzees, they appear to be limited to using object combinations during tool-use which span up to three hierarchical levels (Matsuzawa, 1996); however, they may only intentionally plan to combine objects across two hierarchical levels (Hayashi and Inoue-Nakamura, 2011). Dictionary-based compression suggested that, similarly, chimpanzee action organization was limited to three hierarchical levels of organization. It is unclear what level of hierarchical organization humans would achieve during similar behaviours, particularly in comparison with very early human stone-tool technology (such as the production of Oldowan, or even Lomekwian tools; Harmand et al., 2015; Stout et al., 2021). A comparison between the organization of actions used by modern humans when reconstructing tools of early hominins, and the nut cracking behaviours of chimpanzees, would provide clarity on whether the very earliest known forms of hominin knapping required an advanced form of hierarchical cognition, or alternatively, if such behaviours are feasible using cognition which exists in nonhuman great apes, and was therefore likely a cognitive facet present in our last common ancestor. In such an instance, an Oldowan technological stasis are unlikely to be due limits on hierarchical cognition.

Whilst these comparisons would be informative, there may be methodological challenges. Comparisons of the sequential actions employed during the knapping behaviours of different hominin species are feasible as technological actions are similar across both (e.g. reorientations of the hands; striking using fast movements over short distances; flipping and rotating objects in the hand). However, the stone-tool-use behaviours of non-human primates require a different tool-kit of actions (e.g. peeling shells

from kernels, placing nuts on anvils), albeit with some overlap (i.e. striking using asymmetrical bimanual movements). The differences in the repertoire of manual actions between nut cracking and stone knapping means that direct comparisons between such systems of sequential organization, including those using the computational models included in this thesis, would be inequitable. Therefore, understanding how the hierarchical complexity of action organization during tool-use compares between non-human primates and early humans is a question which is tied to the development of methodologies which facilitate such comparisons.

These questions are not only tied to understanding the evolution of human sequential action during the production and use of tools, but may also be informative for understanding the evolution of other sequential behaviours of humans, especially language. Hierarchical organization in language has been described as paralleling the hierarchical organization of actions (Greenfield, 1991; Steele et al., 2012); however, others have argued that such behaviours show key distinctions (Coopmans et al., 2021). The existence of a domain-general neural system – situated in Broca's area – is also a focal point of current scientific debate, with some arguing that Broca's area is responsible for producing complex syntactic associations during the generation of language, manual actions, and music (Fadiga et al., 2009; Tettamanti and Weniger, 2006); however, other authors argue that the activation of this region of the brain comes from the activation of independent neural regions which are situated in close proximity (Friederici, 2020). Questions surrounding the similarity in organization of human action and language, and the existence of a possible common neural architecture for organizing both behaviours, are born from a more fundamental question: was the cognition for complex hierarchical thinking exapted from manual actions into language during the course of hominin evolution? This idea has been formulated into a number of hypotheses which share a central idea that selection for more generative tool-use behaviours favoured the evolution of more complex neural circuitry for hierarchical thinking, and at some point during hominin evolution, this more complex hierarchical cognition was exapted into communication (Kolodny and Edelman, 2018; Sainburg et al., 2020). The cognitive-hijacking hypothesis predicts that, following exaptation, the communication system produced permitted the evolution of more effective teaching behaviours, which then permitted the evolution of more complex tools, which then fed back into hierarchical thinking for linguistic syntax, and so forth to produce complex combinatorial systems across linguistic and technological behaviours (Kolodny and

Edelman, 2018; however other hypotheses do not specifically include feedback mechanisms between language and action, see Sainburg et al., 2020). The cognitive-hijacking theory is supported by transmission-chain experiments which show that gradual increases in communication between human participants, from no communication, to gesturing, to spoken language, increases the transmissibility of early hominin tool-use behaviours (Morgan et al., 2015). Furthermore, this observation has led to the suggestion that the rapid technological innovation following the Oldowan technological complex was in part through the evolution of more complex linguistic systems (Morgan et al., 2015); however the validity of this hypothesis is yet to be fully tested.

This thesis reports that hierarchical organization of behaviour is detectable in the sequence of actions produced by wild chimpanzees during nut cracking. Conversely, whilst nonrandom vocal (Leroux and Townsend, 2020) and gestural (Byrne et al., 2017; Genty and Byrne, 2010) sequences are produced by great apes, their organization appears to be readily generalizable by linear, serial chains (Byrne et al., 2017; Fitch and Hauser, 2004; Hauser et al., 2002; ten Cate and Okanoya, 2012). Thus, great ape communication appears to be much less hierarchical than great ape combinatorial action. Homologous systems in the most recent common ancestor of chimpanzees and humans would support an evolutionary scenario where action hierarchies evolve prior to those in the linguistic syntax of hominins.

6.1.6 Asocial learning of sequential manual actions and the evolution of cumulative culture

The results of Chapter 4 support the theory that the fine-grained actions used by apes during technological behaviours are acquired, for the most part, through independent innovation; however, the data I present also suggests that this process may be, at least to a small degree, mediated through the transmission of specific, highly salient actions between proficient tool-users and learners during observation. Therefore, chimpanzees likely develop sequences of actions for cultural skills largely independently, but maintain a limited capacity to imitate actions. This invites the question: what does this mean for the evolution of human culture?

The answer to this question is unclear. Humans are exceptional imitators, and in many instances have been documented performing ‘overimitation’, where during the acquisition of a novel behaviour, both the actions pertinent to the performance of a behaviour, and additional superfluous actions, are copied

(Hoehl et al., 2019). Such behaviour is observed cross-culturally (Berl and Hewlett, 2015), as well as across life stages from adulthood to childhood (Berl and Hewlett, 2015; McGuigan et al., 2011; Nielsen and Tomaselli, 2010). Thus, it may be inferred that during the course of human evolution, there was selection for an increased cognitive capacity for imitation (Heyes, 2023). The exceptional imitative abilities of humans have also been speculated to have supported the evolution of 'cumulative culture' (Heyes, 2023; Tennie et al., 2009); a distinct form of culture where the traditions of a population are innovated upon by successive generations, until ultimately, traditions emerge in populations which are more complex than any one individual could have innovated alone (Boyd and Richardson, 1996).

However, human culture is not supported by widespread imitation as a blind replicative process (Heyes, 2023). The processes which underlie human social learning are complex and manifold, and include mechanisms such as explicit teaching and communication, mindreading, and also, importantly, the use of goal emulation, a facet of nonhuman ape social learning which has been supported through numerous experimental paradigms (for two recent reviews considering culture, as well as human and nonhuman social learning mechanisms, see Heyes, 2023; and Whiten, 2017; for work on goal emulation, see Call et al., 2005; Horner and Whiten, 2005; and Tennie et al., 2010). During transmission chain experiments (such as in paradigms where participants observe and then perform the construction of a 'spaghetti tower'), participants who are permitted to observe the end-states of behaviours gain as much information about their predecessors' behaviours as those who witness the construction of towers through direct observations of their predecessors. This suggests that, even for humans, emulation is a powerful tool for the socially-mediated acquisition of behavioural strategies (Caldwell et al., 2012; Caldwell and Millen, 2008). However, explicit teaching is more effective than both processes for the transmission of more complex behaviours, such as stone knapping (Morgan et al., 2015). Therefore, the evolution of teaching (and perhaps complex means of communication that permit more effective teaching, as discussed in section 6.4, or human-specific forms of pedagogy) may have been fundamental in supporting the evolution of cumulative cultural processes in early hominins; however, other researchers argue that whilst teaching is a useful mechanism for supporting cumulative cultural processes, it may not be necessary (Zwirner and Thornton, 2015).

The cultures of wild nonhuman primates, as described thus far, are far less cumulative than those of humans, and may lack cumulative properties all together (Migliano and Vinicius, 2022). Arguments for

possible cumulative culture have been proposed for the uses of wedge stones in chimpanzee nut cracking at Bossou (Yamamoto et al., 2013), however, as previously mentioned, these behaviours are rare, and thus not readily adopted by conspecifics (Humle, 2011; Matsuzawa, 1991), and may be performed unintentionally by chimpanzees as they rotate anvils to find a stable orientation (Hayashi and Inoue-Nakamura, 2011); such a behaviour is therefore unlikely to meet the criteria for cumulative culture. The apparent lack of cumulative culture may, in-part, stem from great apes' reliance on lower-fidelity social learning mechanisms; however, other cognitive processes are likely to play a role, such as reduced cognitive flexibility in how nonhuman apes perceive the functions of tool objects (Gruber et al., 2015). A few accounts of 'teaching' have been reported in wild apes (where teaching is defined as an intentional modification of a behaviour to increase its learnability for observers), predominantly focussed on chimpanzee termite fishing (Musgrave et al., 2020, 2016); suggesting that this important social learning mechanism for cumulative culture is present in non-human great apes; however, the extent to which teaching is widespread across great ape species, and their range of behaviours, requires further research. Currently, for the nut cracking behaviours performed by chimpanzees at Bossou, no evidence of teaching has been found (Matsuzawa, 2011).

How cognitive processes, including those related to social learning, influence the emergence of cumulative cultural dynamics is therefore a question which will invite many years of further research. This not only includes research on primates, but also on species which are phylogenetically distant to humans. For example, transmission chains identify cumulative cultural processes during the formation of navigational routes in homing pigeons (*Columba livia*; Sasaki and Biro, 2017); thus, the accumulation of modifications in cultural traditions over generations is not limited to humans, and can occur in species which are '*not famous for their mental prowess*' (Heyes, 2023). The existence of cumulative cultural processes in animals which do not demonstrate particularly exceptional forms of social cognition means that cumulative cultural processes may emerge independently of complex imitation and teaching. This includes, in the case of pigeons, collective intelligence and group decision making (Sasaki and Biro, 2017). The result from Chapter 4, that sequential actions used for nut cracking are largely asocially acquired, therefore does necessarily represent an irrevocable barrier to cumulative cultural evolution in nonhuman apes (Heyes, 2023). Rather, the absence of imitation is one of many key behavioural distinctions which contribute to

disparities in cumulative cultural processes between humans and apes. The aim of comparative research in cultural cognition is now to ascertain what this extended repertoire of differences really is (Gruber et al., 2015).

6.1.7 Computational methods for characterizing sequential organization

Chapters 2 and 3 emphasized the importance of using simulated and randomized data for null comparisons when detecting signatures of hierarchical organization in sequential data. The use of simulated and randomized sequences as null comparisons is frequent in studies which employ dictionary-based compression, and have also been used for investigations of structure in language and birdsong (Sainburg et al., 2019), although not when similar models were used to evaluate the development of human speech patterns (Sainburg et al., 2022). Generating null sequences using randomization procedures and Markov models is computationally simple, particularly in the case of Markov modelling which is supported by a number of programming packages (Gagniuc, 2017; Spedicato, 2017). And so, generating data which reflects scenarios where sequential behaviours are generated by serial ordering, or by no systematic ordering at all, are readily available to researchers.

Whilst negative controls can be used for the detection of hierarchical signatures from non-hierarchical sequences, we were unable to support our analysis with use of similar methods for the detection of 'positive controls'. Positive controls could exist in the form of simulated, hierarchical data, which when passed through the methodologies used in Chapters 2 and 3, produces a result which indicates hierarchical organization. Positive controls would be extremely valuable in the case of detecting hierarchies from sequential behaviours, as they would offer further clarity on how many individuals researchers may expect to receive erroneous, null results from (such as exponential decay of MI, or dictionary-based compression that is similar to that of Markovian sequences), even if their systems of organization are hierarchical.

However, exactly how hierarchical sequences should be generated for this purpose is not clear cut. Many questions can be asked during the modelling of a hypothetical hierarchy: should all decisions lead to the formation of two (and only two) branches? If not, how many elements can be possibly organized into a single subroutine, or subgoals into larger goals? How deep should the hierarchy go? And so forth. There

are as many questions surrounding the hypothetical structure of a simulated hierarchy as there are for the possible hierarchical organizations used by animals. This fact makes the simulation of hierarchical sequences as a suitable control exceptionally difficult. Using a hierarchical model which assumes a morphological organization that is very different to an observed behaviour would be incomparable; the information between sequence elements, and the nature of their compression, predicted by the control may not reflect hierarchical organization if present.

There is no easy solution for exactly how this issue of positive controls should be addressed, and therefore I cannot recommend a concise, effective procedure. However, research into how the morphology of hierarchies influences compression, and mutual information between elements, could be key. If the morphology of a hierarchy influences information and compressibility in sequences, the process of simulating a number of hypothetical morphologies, and comparing these with real world data, may help to characterize the latent hierarchies behind many sequential behaviours in nature. This would not only include the ability to evaluate the error in detecting 'false negatives' when estimating the likelihood of hierarchical organization underpinning sequential phenomena, but may also be informative for understanding how hierarchies are themselves organized (such as through comparing compressibility, or MI decay, to sequences produced by a number of different hierarchical configurations, and observing for the closest match). I cannot say for sure whether this methodology would be useful, however I believe that future research into the mathematical and computational properties of sequences will help to understand if so.

6.1.8 Study Limitations

Many of the limitations of this thesis have been highlighted throughout this discussion, and where limitations have been identified, future directions have also been proposed. I would like to make a special note of two further limitations of my study.

This thesis focussed on the behaviours of a small number of chimpanzees at Bossou. The study of wild apes is often limited by the total available sample size, particularly when research questions demand further subsampling of communities (such as with longitudinal sampling of individuals during specific stages of life, see Chapters 4 and 5). Therefore, each of the analyses presented within this thesis are limited to between five and eight individuals. A narrow sample of individuals has permitted me to collect an extensive

body of data for each individual, and therefore analyse the structure, development and senescence of chimpanzees at an exceptional level of granularity. However, the extent to which my results may be generalized across the nut cracking behaviours of all chimpanzees requires further examination; particularly in the context of wild chimpanzee communities who exhibit culturally distinct techniques for nut cracking (Carvalho and McGrew, 2012; Proffitt et al., 2022). Detailed comparisons across sites will reveal how generalizable my results are to all chimpanzees who engage in nut cracking behaviours in the wild.

At Bossou, nut cracking behaviours are studied through the use of the outdoor laboratory. This field experiment has been exceptionally useful for generating data on how chimpanzees crack nuts using stone tools at Bossou: a behaviour which is performed at multiple locations across the home range, including during periods where the outdoor laboratory is not active (outside of the November-February field seasons). Observing nut cracking behaviours away from the outdoor laboratory can be exceptionally challenging, as chimpanzees perform these exclusively on the ground where direct observation can be obstructed by thick foliage (Matsuzawa et al., 2011). Therefore, the outdoor laboratory allows for fine-grained action coding in an arena which is cleared of foliage, and the filming of chimpanzees from multiple angles allows for the detection of subtle behaviours performed during stone-tool use. However, it is important to remember that the outdoor laboratory is not a natural ecological setting for nut cracking. Stones do not appear for chimpanzees in carefully organized matrices, and nuts are not provided in numerous piles (although they may be littered across the ground under nut trees). Therefore, the present analysis may underestimate the complexity of some aspects of wild stone-tool use by chimpanzees, such as the organization of actions during stone-tool selection and transport through forests (Boesch and Boesch, 1984; Carvalho et al., 2008). Conversely, my analysis may also overestimate the total length of sequences which are habitually performed during nut cracking behaviours, as at the outdoor laboratory a large number of nuts are provided for nut cracking. Naturally occurring nuts may occur in less numerous aggregations, and therefore, sequences of nut cracking may span shorter durations when conducted away from the outdoor laboratory. These factors may influence the overall structure of nut cracking behaviours that I have described in this thesis; however, I believe that they are unlikely to change the key messages of this thesis: that nut cracking is hierarchical; develops through exploration and pruning; and senesces with old-age.

6.1.9 Concluding remarks

This thesis demonstrates the value of computational methods for elucidating the sequential organization of animal behaviours, through a case study into the manual actions used by wild chimpanzees during one of the most complex forms of animal tool-use: nut cracking. It also provides key insight into how such behaviours are acquired and refined through an extended developmental phase, and also provides one of the first ever accounts of how senescence manifests in the technological behaviours of a non-human species with progressive old-age. The results of this thesis have broad implications, including through generating new methodological considerations for the study of animal sequential behaviours; providing information for models of the evolution of human sequential behaviours and culture; and also for research into how great apes age, which may be informative for understanding both the ageing of humans, as well as nonhuman apes living in captivity. Ultimately, this thesis sets out, at an exceptional level of granularity, models of sequential organization for stone-tool use in wild chimpanzees, and describes how these behaviours change over lifetimes. Future research into the sequential structure, development and senescence of such behaviours will be of great value, both for understanding the behaviours of animals, and for elucidating the evolutionary processes which led to the emergence of behaviourally modern humans.

6.2 References

Arnsten, A.F.T., Datta, D., Leslie, S., Yang, S.-T., Wang, M., Nairn, A.C., 2019. Alzheimer's-like pathology in aging rhesus macaques: Unique opportunity to study the etiology and treatment of Alzheimer's disease. Proc. Natl. Acad. Sci. 116, 26230–26238. https://doi.org/10.1073/pnas.1903671116

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. Sci. Adv. 7, eabi4883. https://doi.org/10.1126/sciadv.abi4883

Bala, P.C., Eisenreich, B.R., Yoo, S.B.M., Hayden, B.Y., Park, H.S., Zimmermann, J., 2020. Automated markerless pose estimation in freely moving macaques with OpenMonkeyStudio. Nat. Commun. 11, 4560. https://doi.org/10.1038/s41467-020-18441-5

Bandini, E., Harrison, R.A., Motes-Rodrigo, A., 2022. Examining the suitability of extant primates as models of hominin stone tool culture. Humanit. Soc. Sci. Commun. 9, 74. https://doi.org/10.1057/s41599-022-01091-x

Baxter, M.G., 2001. Cognitive Aging in Nonhuman Primates, in: Functional Neurobiology of Aging. Elsevier, pp. 407–419. https://doi.org/10.1016/B978-012351830-9/50028-7

Berl, R.E.W., Hewlett, B.S., 2015. Cultural Variation in the Use of Overimitation by the Aka and Ngandu of the Congo Basin. PLOS ONE 10, e0120180. https://doi.org/10.1371/journal.pone.0120180

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. Cogn. Dev. Chimpanzees 476–508. https://doi.org/10.1007/4-431-30248-4_28

Boesch, C., Boesch, H., 1984. Mental map in wild chimpanzees: An analysis of hammer transports for nut cracking. Primates 25, 160–170. https://doi.org/10.1007/BF02382388
Boesch, C., Boesch, H., 1983. Optimisation of nut-cracking with natural hammers by wild chimpanzees. Behaviour 83, 3–4. https://doi.org/10.1163/156853983X00192
Boyd, R., Richardson, P., 1996. Why Culture is Common, but Cultural Evolution is Rare, in: Evolution of Social Behaviour Patterns in Primates and Man. Oxford University Press, pp. 77–93.
Byrne, R.W., Cartmill, E., Genty, E., Graham, K.E., Hobaiter, C., Tanner, J., 2017. Great ape gestures: intentional communication with a rich set of innate signals. Anim. Cogn. 20, 755–769. https://doi.org/10.1007/s10071-017-1096-4
Byrne, R.W., Russon, A.E., 1998. Learning by imitation : A hierarchical approach. Behav. Brain Sci. 21, 667–721.
Caldwell, C.A., Millen, A.E., 2008. Experimental models for testing hypotheses about cumulative cultural evolution. Evol. Hum. Behav. 29, 165–171. https://doi.org/10.1016/j.evolhumbehav.2007.12.001
Caldwell, C.A., Schillinger, K., Evans, C.L., Hopper, L.M., 2012. End state copying by humans (Homo sapiens): Implications for a comparative perspective on cumulative culture. J. Comp. Psychol. 126, 161–169. https://doi.org/10.1037/a0026828
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). Anim. Cogn. 8, 151–163. https://doi.org/10.1007/s10071-004-0237-8
Carvalho, S., Cunha, E., Sousa, C., Matsuzawa, T., 2008. Chaînes opératoires and resource-exploitation strategies in chimpanzee (Pan troglodytes) nut cracking. J. Hum. Evol. 55, 148–163. https://doi.org/10.1016/j.jhevol.2008.02.005
Carvalho, S., Matsuzawa, T., McGrew, W.C., 2013. From pounding to knapping: How chimpanzees can help us to model hominin lithics, in: Sanz, C.M., Call, J., Boesch, C. (Eds.), Tool Use in Animals. Cambridge University Press, pp. 225–241. https://doi.org/10.1017/CBO9780511894800.015
Carvalho, S., McGrew, W., 2012. The origins of the Oldowan: Why chimpanzees (Pan troglodytes) still are good models for technological evolution in Africa, in: Domínguez-Rodrigo, M. (Ed.), Stone Tools and Fossil Bones. Cambridge University Press, pp. 201–221. https://doi.org/10.1017/CBO9781139149327.010
Coopmans, C.W., Kaushik, K., Martin, A.E., 2021. Hierarchical structure in language and action : A formal comparison. PsyArXiv 1–26. https://doi.org/10.31234/osf.io/x59un
Corat, C., Siqueira, J., Ottoni, E.B., 2016. Sequential organization and optimization of the nut-cracking behavior of semi-free tufted capuchin monkeys (Sapajus sp.). Primates 57, 113–121. https://doi.org/10.1007/s10329-015-0491-1
Corr, J.A., Martin, L.J., Boysen, S., 2002. Comparative Models of Cognitive Decline in Aging Great Apes, in: Aging in Nonhuman Primates, Interdisciplinary Topics in Gerontology. Karger, pp. 196–208.
Cramer, P.E., Gentzel, R.C., Tanis, K.Q., Vardigan, J., Wang, Y., Connolly, B., Manfre, P., Lodge, K., Renger, J.J., Zerbinatti, C., Uslaner, J.M., 2018. Aging African green monkeys manifest transcriptional, pathological, and cognitive hallmarks of human Alzheimer's disease. Neurobiol. Aging 64, 92–106. https://doi.org/10.1016/j.neurobiolaging.2017.12.011
Dawkins, R., Dawkins, M., 1976. Hierarchical Organization and Postural Facilitation: Rules for Grooming in Flies. Anim. Behav. 24, 739–755. https://doi.org/10.1016/S0003-3472(76)80003-6
Edler, M.K., Mhatre-Winters, I., Richardson, J.R., 2021a. Microglia in Aging and Alzheimer's Disease: A Comparative Species Review. Cells 10, 1138. https://doi.org/10.3390/cells10051138
Edler, M.K., Munger, E.L., Groetz, H., Raghanti, M.A., 2021b. Nonhuman primates as models for aging and Alzheimer's disease, in: Assessments, Treatments and Modeling in Aging and Neurological Disease. Elsevier, pp. 527–537. https://doi.org/10.1016/B978-0-12-818000-6.00047-0
Edler, M.K., Sherwood, C.C., Meindl, R.S., Hopkins, W.D., Ely, J.J., Erwin, J.M., Mufson, E.J., Hof, P.R., Raghanti, M.A., 2017. Aged chimpanzees exhibit pathologic hallmarks of Alzheimer's disease. Neurobiol. Aging 59, 107–120. https://doi.org/10.1016/j.neurobiolaging.2017.07.006
Fadiga, L., Craighero, L., D'Ausilio, A., 2009. Broca's area in language, action, and music. Ann. N. Y. Acad. Sci. 1169, 448–458. https://doi.org/10.1111/j.1749-6632.2009.04582.x
Faisal, A., Stout, D., Apel, J., Bradley, B., 2010. The manipulative complexity of lower paleolithic stone toolmaking. PLoS ONE 5. https://doi.org/10.1371/journal.pone.0013718
Finch, C.E., Austad, S.N., 2015. Commentary: is Alzheimer's disease uniquely human? Neurobiol. Aging 36, 553–555. https://doi.org/10.1016/j.neurobiolaging.2014.10.025

Fitch, W.T., Hauser, M.D., 2004. Computational Constraints on Syntactic Processing in a Nonhuman Primate. Science 303, 377–380. https://doi.org/10.1126/science.1089401
Freire-Cobo, C., Edler, M.K., Varghese, M., Munger, E., Laffey, J., Raia, S., In, S.S., Wicinski, B., Medalla, M., Perez, S.E., Mufson, E.J., Erwin, J.M., Guevara, E.E., Sherwood, C.C., Luebke, J.I., Lacreuse, A., Raghanti, M.A., Hof, P.R., 2021. Comparative neuropathology in aging primates: A perspective. Am. J. Primatol. 83. https://doi.org/10.1002/ajp.23299
Friederici, A.D., 2020. Hierarchy processing in human neurobiology: How specific is it? Philos. Trans. R. Soc. B Biol. Sci. 375, 1–9. https://doi.org/10.1098/rstb.2018.0391
Fuhrmann, D., Ravignani, A., Marshall-Pescini, S., Whiten, A., 2014. Synchrony and motor mimicking in chimpanzee observational learning. Sci. Rep. 4, 5283. https://doi.org/10.1038/srep05283
Gagniuc, P., 2017. Markov Chains: From Theory to Implementation and Experimentation. https://doi.org/10.1002/9781119387596
Genty, E., Byrne, R.W., 2010. Why do gorillas make sequences of gestures? Anim. Cogn. 13, 287–301. https://doi.org/10.1007/s10071-009-0266-4
Gomez-Marin, A., Stephens, G.J., Brown, A.E.X., 2016. Hierarchical compression of *Caenorhabditis elegans* locomotion reveals phenotypic differences in the organization of behaviour. J. R. Soc. Interface 13, 20160466. https://doi.org/10.1098/rsif.2016.0466
Grassberger, P., 2003. Entropy Estimates from Insufficient Samplings 1–5.
Greenfield, P.M., 1991. Language, tools and brain: The ontogeny and phylogeny of hierarchically organized sequential behavior. Behav. Brain Sci. 531–595.
Gruber, T., Zuberbühler, K., Clément, F., van Schaik, C., 2015. Apes have culture but may not know that they do. Front. Psychol. 6, 1–14. https://doi.org/10.3389/fpsyg.2015.00091
Harmand, S., Lewis, J.E., Feibel, C.S., Lepre, C.J., Prat, S., Lenoble, A., Boës, X., Quinn, R.L., Brenet, M., Arroyo, A., Taylor, N., Clément, S., Daver, G., Brugal, J.P., Leakey, L., Mortlock, R.A., Wright, J.D., Lokorodi, S., Kirwa, C., Kent, D.V., Roche, H., 2015. 3.3-million-year-old stone tools from Lomekwi 3, West Turkana, Kenya. Nature 521, 310–315. https://doi.org/10.1038/nature14464
Haslam, M., Gumert, M.D., Biro, D., Carvalho, S., Malaivijitnond, S., 2013. Use-Wear Patterns on Wild Macaque Stone Tools Reveal Their Behavioural History. PLoS ONE 8, e72872. https://doi.org/10.1371/journal.pone.0072872
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., Mercader, J., Mora, R., Petraglia, M., Roche, H., Visalberghi, E., Warren, R., 2009. Primate archaeology. Nature 460, 339–344. https://doi.org/10.1038/nature08188
Hauser, M.D., Chomsky, N., Fitch, W.T., 2002. The faculty of language: What is it, who has it, and how did it evolve? Evol. Hum. Lang. Biolinguistic Perspect. 298, 14–42. https://doi.org/10.1017/CBO9780511817755.002
Havercamp, K., Watanuki, K., Tomonaga, M., Matsuzawa, T., Hirata, S., 2019. Longevity and mortality of captive chimpanzees in Japan from 1921 to 2018. Primates 60, 525–535. https://doi.org/10.1007/s10329-019-00755-8
Hayashi, M., Inoue-Nakamura, N., 2011. From Handling Stones and Nuts to Tool-Use, in: From Handling Stones and Nuts to Tool-Use. Springer Japan, Tokyo, Japan, pp. 175–182.
Heyes, C., 2023. Imitation and culture: What gives? Mind Lang. 38, 42–63. https://doi.org/10.1111/mila.12388
Hoehl, S., Keupp, S., Schleihauf, H., McGuigan, N., Buttelmann, D., Whiten, A., 2019. 'Over-imitation': A review and appraisal of a decade of research. Dev. Rev. 51, 90–108. https://doi.org/10.1016/j.dr.2018.12.002
Horner, V., Whiten, A., 2005. Causal knowledge and imitation/emulation switching in chimpanzees (Pan troglodytes) and children (Homo sapiens). Anim. Cogn. 8, 164–181. https://doi.org/10.1007/s10071-004-0239-6
Humle, T., 2011. The Tool Repertoire of Bossou Chimpanzees, in: The Chimpanzees of Bossou and Nimba. Springer Japan, Tokyo, Japan, pp. 61–72.
Inoue-Nakamura, N., Matsuzawa, T., 1997. Development of Stone Tool Use by Wild Chimpanzees (Pan troglodytes). J. Comp. Psychol. 111, 159–173. https://doi.org/10.1037/0735-7036.111.2.159
Kimura, Y., 2002. Examining time trends in the Oldowan technology at Beds I and II, Olduvai Gorge. J. Hum. Evol. 43, 291–321. https://doi.org/10.1006/jhev.2002.0576

Kolodny, O., Edelman, S., 2018. The evolution of the capacity for language: The ecological context and adaptive value of a process of cognitive hijacking. Philos. Trans. R. Soc. B Biol. Sci. 373. https://doi.org/10.1098/rstb.2017.0052

Lacreuse, A., Herndon, J.G., 2009. Nonhuman Primate Models of Cognitive Aging, in: Bizon, J.L., Woods, A. (Eds.), Animal Models of Human Cognitive Aging. Humana Press, Totowa, NJ, pp. 1–30. https://doi.org/10.1007/978-1-59745-422-3_2

Lacreuse, A., Parr, L., Chennareddi, L., Herndon, J.G., 2018. Age-related decline in cognitive flexibility in female chimpanzees. Neurobiol. Aging 72, 83–88. https://doi.org/10.1016/j.neurobiolaging.2018.08.018

Leroux, M., Townsend, S.W., 2020. Call combinations in great apes and the evolution of syntax. Anim. Behav. Cogn. 7, 131–139. https://doi.org/10.26451/abc.07.02.07.2020

Lin, H.W., Tegmark, M., 2017. Critical behavior in physics and probabilistic formal languages. Entropy 19, 1–25. https://doi.org/10.3390/e19070299

Lowenstine, L.J., McManamon, R., Terio, K.A., 2016. Comparative Pathology of Aging Great Apes: Bonobos, Chimpanzees, Gorillas, and Orangutans. Vet. Pathol. 53, 250–276. https://doi.org/10.1177/0300985815612154

Luncz, L.V., Gill, M., Proffitt, T., Svensson, M.S., Kulik, L., Malaivijitnond, S., 2019. Group-specific archaeological signatures of stone tool use in wild macaques. eLife 8, e46961. https://doi.org/10.7554/eLife.46961

Mangalam, M., Fragaszy, D.M., 2015. Wild Bearded Capuchin Monkeys Crack Nuts Dexterously. Curr. Biol. 25, 1334–1339. https://doi.org/10.1016/j.cub.2015.03.035

Matsuzawa, T., 2011. Education by Master-Apprenticeship, in: The Chimpanzees of Bossou and Nimba. Springer, Tokyo, Japan, pp. 201–208.

Matsuzawa, T., 1996. Chimpanzee intelligence in nature and in captivity: Isomorphism of symbol use and tool use, in: Great Ape Societies. pp. 196–212.

Matsuzawa, T., 1994. Field Experiments on use of Stone Tools in the wild, in: Chimpanzee Cultures. pp. 351–370.

Matsuzawa, T., 1991. Nesting cups and metatools in chimpanzees. Behav. Brain Sci. 14, 570–571. https://doi.org/10.1017/S0140525X00071417

Matsuzawa, T., Hulme, T., Sugiyama, Y., 2011. The Chimpanzees of Bossou and Nimba.

McGuigan, N., Makinson, J., Whiten, A., 2011. From over-imitation to super-copying: Adults imitate causally irrelevant aspects of tool use with higher fidelity than young children: From over-imitation to super-copying. Br. J. Psychol. 102, 1–18. https://doi.org/10.1348/000712610X493115

Migliano, A.B., Vinicius, L., 2022. The origins of human cumulative culture: from the foraging niche to collective intelligence. Philos. Trans. R. Soc. B Biol. Sci. 377, 20200317. https://doi.org/10.1098/rstb.2020.0317

Morgan, T.J.H., Uomini, N.T., Rendell, L.E., 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. Nat. Commun. 6, 4–11. https://doi.org/10.1038/ncomms7029

Musgrave, S., Lonsdorf, E., Morgan, D., Prestipino, M., Bernstein-Kurtycz, L., Mundry, R., Sanz, C., 2020. Teaching varies with task complexity in wild chimpanzees. Proc. Natl. Acad. Sci. U. S. A. 117, 969–976. https://doi.org/10.1073/pnas.1907476116

Musgrave, S., Morgan, D., Lonsdorf, E., Mundry, R., Sanz, C., 2016. Tool transfers are a form of teaching among chimpanzees. Sci. Rep. 6, 1–7. https://doi.org/10.1038/srep34783

Myowa-Yamakoshi, M., Matsuzawa, T., 1999. Factors influencing imitation of manipulatory actions in chimpanzees (Pan troglodytes). J. Comp. Psychol. 113, 128–136. https://doi.org/10.1037/0735-7036.113.2.128

Myowa-Yamakoshi, M., Yamakoshi, G., 2011. Play Behaviors Involving the Use of Objects in Young Chimpanzees at Bossou, in: The Chimpanzees of Bossou and Nimba. Springer Japan, Tokyo, pp. 231–240.

Neal Webb, S.J., Hau, J., Lambeth, S.P., Schapiro, S.J., 2019. Differences in Behavior Between Elderly and Nonelderly Captive Chimpanzees and the Effects of the Social Environment. J. Am. Assoc. Lab. Anim. Sci. 58, 783–789. https://doi.org/10.30802/AALAS-JAALAS-19-000019

Nevill-Manning, C., Witten, I., 1997. Identifying Hierarchical Structure in Sequences: A linear-time algorithm. J. Artif. Intell. Res. 7, 67–82.

Nevill-Manning, C.G., Witten, I.H., 2000. On-line and off-line heuristics for inferring hierarchies of repetitions in sequences. Proc. IEEE 88, 1745–1755. https://doi.org/10.1109/5.892710
Nielsen, M., Tomaselli, K., 2010. Overimitation in Kalahari Bushman Children and the Origins of Human Cultural Cognition. Psychol. Sci. 21, 729–736. https://doi.org/10.1177/0956797610368808
Nonaka, T., Bril, B., Rein, R., 2010. How do stone knappers predict and control the outcome of flaking? Implications for understanding early stone tool technology. J. Hum. Evol. 59, 155–167. https://doi.org/10.1016/j.jhevol.2010.04.006
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, Jonathan.S., Pacome, S.S., Luncz, Lydia.V., 2022. Identifying functional and regional differences in chimpanzee stone tool technology. R. Soc. Open Sci. 9, 220826. https://doi.org/10.1098/rsos.220826
Rein, R., Nonaka, T., Bril, B., 2014. Movement pattern variability in stone knapping: Implications for the development of percussive traditions. PLoS ONE 9, 1–27. https://doi.org/10.1371/journal.pone.0113567
Resende, B.D. de, 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. Dev. Sci. 11, 828–840. https://doi.org/10.1111/j.1467-7687.2008.00731.x
Ross, S., 2020. Chimpanzee Welfare in the Context of Science, Policy and Practice, in: Chimpanzees in Context. The University of Chicago Press, Chicago, pp. 552–584.
Sainburg, T., Mai, A., Gentner, T.Q., 2022. Long-range sequential dependencies precede complex syntactic production in language acquisition. Proc R Soc B 289:, 2020.08.19.256792. https://doi.org/10.1098
Sainburg, T., Mai, A., Gentner, T.Q., 2020. Long-range sequential dependencies precede complex syntactic production in language acquisition. bioRxiv 2020.08.19.256792.
Sainburg, T., Theilman, B., Thielk, M., Gentner, T.Q., 2019. Parallels in the sequential organization of birdsong and human speech. Nat. Commun. 10, 1–11. https://doi.org/10.1038/s41467-019-11605-y
Sanz, C.M., Morgan, D.B., 2010. The Complexity of Chimpanzee Tool-Use Behaviors, in: The Mind of the Chimpanzee: Ecological and Experimental Perspectives. The University of Chicago Press, pp. 127–140.
Sasaki, T., Biro, D., 2017. Cumulative culture can emerge from collective intelligence in animal groups. Nat. Commun. 8, 15049. https://doi.org/10.1038/ncomms15049
Semaw, S., 2000. The World's Oldest Stone Artefacts from Gona, Ethiopia: Their Implications for Understanding Stone Technology and Patterns of Human Evolution Between 2·6–1·5 Million Years Ago. J. Archaeol. Sci. 27, 1197–1214. https://doi.org/10.1006/jasc.1999.0592
Siracusa, E.R., Negron-Del Valle, J.E., Phillips, D., Platt, M.L., Higham, J.P., Snyder-Mackler, N., Brent, L.J.N., 2022. Within-individual changes reveal increasing social selectivity with age in rhesus macaques. Proc. Natl. Acad. Sci. 119, e2209180119. https://doi.org/10.1073/pnas.2209180119
Spedicato, G.A., 2017. Discrete Time Markov Chains with R. R J.
Steele, J., Ferrari, P.F., Fogassi, L., 2012. From action to language: Comparative perspectives on primate tool use, gesture and the evolution of human language. Philos. Trans. R. Soc. B Biol. Sci. 367, 4–9. https://doi.org/10.1098/rstb.2011.0295
Stout, D., Chaminade, T., 2009. Making tools and making sense: Complex, intentional behaviour in human evolution. Camb. Archaeol. J. 19, 85–96. https://doi.org/10.1017/S0959774309000055
Stout, D., Chaminade, T., Apel, J., Shafti, A., Faisal, A.A., 2021. The measurement, evolution, and neural representation of action grammars of human behavior. Sci. Rep. 11, 13720. https://doi.org/10.1038/s41598-021-92992-5
Talbot, C.F., Reamer, L.A., Lambeth, S.P., Schapiro, S.J., Brosnan, S.F., 2023. Meeting Cognitive, Behavioral, and Social Needs of Primates in Captivity, in: Robinson, L.M., Weiss, A. (Eds.), Nonhuman Primate Welfare. Springer International Publishing, Cham, pp. 267–305. https://doi.org/10.1007/978-3-030-82708-3_12
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, 1–25. https://doi.org/10.1371/journal.pone.0124733

Tarou, L.R., Bloomsmith, M., Hoff, M., Erwin, J., Maple, T., 2002. The Behavior of Aged Great Apes, in: Aging in Nonhuman Primates, Interdisciplinary Topics in Gerontology. Karger, pp. 209–231.
ten Cate, C., Okanoya, K., 2012. Revisiting the syntactic abilities of nonhuman animals: Natural vocalizations and artificial grammar learning. Philos. Trans. R. Soc. B Biol. Sci. 367, 1984–1994. https://doi.org/10.1098/rstb.2012.0055
Tennie, C., Call, J., Tomasello, M., 2010. Evidence for Emulation in Chimpanzees in Social Settings Using the Floating Peanut Task. PLoS ONE 5, e10544. https://doi.org/10.1371/journal.pone.0010544
Tennie, C., Call, J., Tomasello, M., 2009. Ratcheting up the ratchet: on the evolution of cumulative culture. Philos. Trans. R. Soc. B Biol. Sci. 364, 2405–2415. https://doi.org/10.1098/rstb.2009.0052
Terrace, H.S., 2005. The simultaneous chain: a new approach to serial learning. Trends Cogn. Sci. 9, 202–210. https://doi.org/10.1016/j.tics.2005.02.003
Tettamanti, M., Weniger, D., 2006. Broca's area: A supramodal hierarchical processor? Cortex 42, 491–494. https://doi.org/10.1016/S0010-9452(08)70384-8
Tonooka, R., 2001. Leaf-folding behavior for drinking water by wild chimpanzees (Pan troglodytes verus) at Bossou, Guinea. Anim. Cogn. 4, 325–334. https://doi.org/10.1007/s100710100110
United Nations, Department of Economic and Social Affairs, Population Division, 2022. World Population Prospects 2022: Ten Key Messages. (Summary), World Population Prospects 2022. United Nations.
Vereijken, B., Whiting, H., 1998. Hoist by their own petard: The constraints of hierarchical models. Behav. Brain Sci. 21, 705–705. https://doi.org/10.1017/S0140525X98451744
Whiten, A., 2017. Social Learning and Culture in Child and Chimpanzee. Annu. Rev. Psychol. 68, 129–154. https://doi.org/10.1146/annurev-psych-010416-044108
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.
Zwirner, E., Thornton, A., 2015. Cognitive requirements of cumulative culture: teaching is useful but not essential. Sci. Rep. 5, 16781. https://doi.org/10.1038/srep16781