Primate Archaeology: Comparative models for the evolution of primate technical cognition through tool-use

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Abstract

The field of Primate Archaeology is concerned with (A) understanding the origins and development of tool use in non-human primates, and (B) the implications of a general primate model for understanding human technical and cognitive development. Cross-species comparisons, however, remain distinctly anthropocentric in nature. The metaphysical commitments of Neo-Darwinist frameworks reinforce an inherent assumption that cognition is something which takes place in the head, influenced but apart from the body and environment. Assuming psychological discontinuity of this kind, comes at the expense of taking phylogenetic, bodily and environmental differences seriously – a considerable problem when we consider the diversity of primate tool using species which a comparative model must include. In an attempt to overcome issues of heterogeneity and anthropocentrism, this thesis explores the potential of the Material Engagement Theory as a means of re-conceptualizing complexity and causal cognition in Primate tool use, and as the basis of a methodological framework suitable for cross-species comparison. Case-studies of the three living lithic-using non-human primates are compiled and compared, demonstrating the emergent, processual nature of technical cognition as a fundamentally non-individualistic phenomenon co-constituted by the environment and others. General patterns are discussed with reference to theories of technical evolution. The findings of this thesis suggest current hypotheses of primate human and non-human technical evolution, as long as they maintain a separation between mind and matter, cannot accurately account for the role of tool using in cognitive development. To better integrate mind with materials, future research must shift its focus away from the brain, body, and environment, and towards the diachronically shifting, dynamic spaces between.

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List of Acronyms

ASS	Field site of Assirik, Senegal
BOS	Field site of Bossou, Guinea
BUD	Field site of Budongo, Uganda
CCF	Coupling constitution fallacy
EM	Extended mind hypothesis
FBV	Field site of Fazenda Boa Vista, Brazil
GOM	Field site of Gombe, Nigeria
GOU	Field site of Goualougo, Republic of Congo
KIB	Field site of Kibale, Uganda
LOP	Field site of Lope, Gabon
MAH	Field site of Mahale (M group), Tanzania
MAK	Field site of Mahale (K group), Tanzania
MET	Material Engagement Theory
NHP	Non-human Primate
PCA	Principal components analysis
PNY	Field site of Piak Nam Yai, Thailand
PP	Parity Principle
SDC	Field site of Serra da Capivara, Brazil
SHE	Method of analysing variance (following Shott, 2010)
SRY	Field site of Sam Roi Yot, Thailand
TAI	Field site of Taï, Côte d'Ivoire

1.1 Primate Archaeology: behavioural models for a cognitive past

Tool use and the evolution of complex causal cognition remain topics of key interest in cognitive archaeology, and primate comparisons a vital means of insight into an otherwise invisible hominin behavioural past (Gärdenfors & Lombard, 2018; Lombard & Gärdenfors, 2017; McGrew et al., 2019; Vaesen, 2012; Wynn et al., 2011). The last 30 years has seen a significant increase in socio-biological and Neo-Darwinist approaches to animal behaviour and cognition, with anthropocentric notions of culture having expanded to recognise the socially distributed nature of animal behavioural traditions (Laland & Galef, 2009; Ottoni, 2015; Tomasello, 1994; Whiten et al., 1999; Whiten et al., 2003), marking both a de- and re-emphasis of hominin psychological exceptionality (Povinelli, 2000; Penn and Povinelli, 2007; Vaesen, 2012b; Dean *et al.*, 2014). Whether used to justify such exceptionality or to deny it, there remains an overriding agenda in which hominin cognition is seen as 'to be explained' and primate behaviour as 'to be used as explanation'. This distinction alienates modern primate behaviours from their own evolutionary contexts and re-entrenches the historical line between 'us' *modern* humans and 'them', *primitive* primates (Shennan, 2001). Despite relative phylogenetic closeness there remains great distance and variation between primate species'. Indiscriminate use of like-with-like analogy risks placing undue emphasis on convergently developed homoplasies while diminishing the role of species' unique experience and evolutionary history (Barrett, 2015; Barton, 2006; Sayers & Lovejoy, 2008).

The relatively new field of Primate Archaeology (Carvalho, Sousa and Matsuzawa, 2007; Haslam *et al.*, 2009, 2017) seeks to address the anthropocentrism of existing primate comparative models while providing a comprehensive, holistic approach to the general evolution of primate

(including hominin) technical behaviour. While previous work in Primate Archaeology has focused on development of methods for recognising archaeological signatures of Non-human primate (hereafter NHP) tool behaviours (Haslam *et al.*, 2013; Visalberghi *et al.*, 2013; Benito-Calvo *et al.*, 2015; Proffitt *et al.*, 2016; Luncz *et al.*, 2019; Pascual-Garrido, 2019; Arroyo *et al.*, 2021), mapping NHP tool site formation (Carvalho *et al.*, 2008; Mendes *et al.*, 2015; Haslam, Pascual-Garrido, *et al.*, 2016; Luncz *et al.*, 2016; Falótico, Spagnoletti, *et al.*, 2017), and on establishing the antiquity of NHP lithic tool use (Mercader, 2002; Mercader *et al.*, 2007; Haslam, Luncz, *et al.*, 2016; Falótico *et al.*, 2019), less attention has been directed to the potential issues of deeper anthropocentrism embedded in key conceptual and evolutionary frameworks.

1.2 Dualisms prepackaged: methodological problems with conceptual issues

Anthropocentric characterisations of tool using as sapient, and Sapiens as a tool user, embody two older questions in the philosophy of psychology: 'what is it to be human?', and 'do animals have minds?' – the two historically taken to be mutually exclusive. Aristotle and St Aquinas, for example, thought humans unique in their ability to think rationally, animals only instinctually (Andrews, 2014); Kant described animals as unconscious prisoners of impulse (Kant, 2001; Fisher, 2017); Heidegger, as poor in the world (Heidegger, 1927/1996); Wittgenstein, as thinking but thoughtless (Wittgenstein, 1953; Glock, 2017); and Descartes, as soulless and mechanistic (Cottingham, 1978). In Man the Tool-Maker, Oakley's (1956, p. 2) argument that "the real difference between what we choose to call an ape and what we call man is one of mental capacity" extends to both tool making and language as criterions of humanity, so that they too have become intuitively (if not explicitly) representative of these common themes of difference; in particular, the capacity for conceptual thought as a capacity apart from conscious perception (cf. Morgan, 1894), and for the capacity for free-will, or intent, as a motivation apart from impulse, or instinct (cf. Darwin, 1880; Romanes, 1912).

Situating animal tool performances in the context of this anthropocentric narrative is methodologically problematic. Influenced by Thorndike (1911) and Pavlov's (1927) theories of associative learning and conditioning, ethological studies of animal behaviour have typically avoided assuming agency, or attributing mental states to animal minds, rejecting anthropomorphic inference and the subjectivist approach (e.g. Darwin, 1880; Romanes, 1912), in favour of a positivist methodology grounded in the establishment of reliable connections between environmental stimuli and adaptive behavioural responses (Tinbergen, 1951, 1963; eg. Lorenz, 1952, 1965).[1] Behaviourist frameworks, as popularised by Watson (1913) and Skinner ('radical behaviourism': 1938), subvert mentalism by approaching cognition *as* behaviour, which is understood as instinctual and species-specific - providing use in their particular evolutionary context. Animal 'minds', are characterised materialistically as their "tendencies to behave physically in a certain way" (Bunnin and Yu, 2004, p. 414), and 'intelligence', as the capacity to perform complex behaviours built on chains of contingent S-R associations acquired through practice. Cognitivist ethological approaches, though often presented as a theoretical anti-thesis to behaviourism because they accept the existence of internal mental states (and thereby the potential for anthropocentric inference), can be seen as a theoretical extension - retaining functionalist and Neo-Darwinian evolutionary frameworks, but exchanging associationism for rule-based representational theory (Costall, 2004). Rather than taken as *a priori* to tool performance, discernment of 'mental processes' is grounded in the difficult discrimination between successful internal representation of external causal relations (i.e. causal reasoning) and effective causal exploitation (Visalberghi and Limongelli, 1994; Tomasello and Call, 1997; Povinelli, 2000; Penn and Povinelli, 2007); 'intelligence', in the degree to which a tool behaviour can escape the bounds of fixed or modularly inherited response (Seed and Byrne, 2010; Call, 2013; Hunt, Gray and Taylor, 2013).

[1] Morgan's canon argues that "In no case may we interpret an action as the outcome of a higher psychical faculty, if it can be interpreted as the outcome of one which stands lower on the psychical scale"

For Primate Archaeology, sitting at the junction between anthropocentric cognitive archaeology and primatology, methodological issues with anthropomorphism feed into broader conceptual issues: a general reluctance to make assumptions on behalf of animal minds diverting necessary conversation *about* technical cognition, *around* the subject.[2] As the wider biological context reveals both 'tool use' and 'cognition' are inherently unstable concepts (Preston, 1998; Bayne et al., 2019) which, despite intuitive simplicity, evade strict definition. Framed as *the use of an object to fulfil a given function*, 'tool use' can, and has been, applied to cover an inordinate range of behaviours; from New Caledonian crows shaping and using Pandanus probes (Holzhaider et al., 2010; Hunt, 1996; Hunt & Gray, 2004); to female water-striders using copulating males as living floats (Pierce, 1986); to, in extremis, a fungus parasitizing the leaves it sits on (Lestel and Grundmann, 1999). Though not all would agree with all these examples, breadth of more widely accepted animal tool behaviours nevertheless subsumes an equal variety of brains, bodies, and thereby cognitive processes, which may differ substantially both between and within species, and from one epistemological approach to another. The last 30 years has seen significant paradigm shifts both in anthropocentric cognitive archaeology and in philosophy of mind, with classic anthropocentric, mentalist, accounts of cognition and the mind increasingly challenged by 4E theories, variously arguing for a view of the mind as embodied by the organism, embedded in the world, and distributed beyond the individual (Chemero, 2009; Clark, 1997; Dunbar et al., 2010; Hutchins, 1995; Edwin Hutchins, 2005; Sutton, 2006; Varela et al., 1991; Wilson, 2002). Commonly understood as an umbrella term for *information processing* (Rowlands, 2009; Shettleworth, 2010), 'Cognition' has been ecologically extended (not simply metaphorically) from a process of individual, internal representation, to include a variety of social, cultural, behavioural, material, and plant processes (Shettleworth, 2010); from group decision making in bacteria and baboons (Adler &

[2] In the 2009 article *Primate Archaeology*, for example, Haslam et al. (2009) write that the archaeological significance of tool use is not what it *is,* so much as what it *does*, and what it leaves behind that can tell us about the minds and intentionality of past tool users. Tool use is ultimately defined by its adaptive value, and thereby the Neo-Darwinian framework, without due acknowledgement of how this framework affects archaeologists' ability to interpret the science the project develops.

Wuno-Wai, 1974; Barrett & Henzi, 2005), to volatile signalling in trees (Wu and Baldwin, 2009; Garzón and Keijzer, 2011).

While 4E theories have gained significant ground in primatology (Barrett et al., 2007; Barrett & Henzi, 2005; Dunbar et al., 2010; Johnson, 2000; Johnson & Oswald, 2001; Mangalam & Fragaszy, 2016; Mosley & Haslam, 2015), their application remains conservative, constrained by ongoing commitment to the Neo-Darwinian evolutionary framework, and its own inherent set of metaphysical assumptions.[3] With 'cognition', for lack of broader consensus, having become 'whatever cognitive scientists study' (Allen, 2017) - a "gesture towards a domain of investigation" (Bayne et al., 2019, pR611) - approaches to primate technology, in their explicit assumptions about 'what' and 'where' tool behaviour is and takes place, implicitly beg the same questions of technical cognition and the mind. Commonly accepted ethological definitions which, wishing to avoid anthropocentric over signification of animal tool performances in favour of exploring evolutionary function or adaptive advantage, attempt to bound tool use *a-cognitively,* as an individualistic physical phenomenon adjacent to, yet apart from, the body and environment (Hall, 1963; Van Lawick-Goodall, 1971; eg. Beck, 1980; Shumaker, Walkup and Beck, 2011), circularly reinforce the implicit analogous assumption, that technical cognition can be similarly bounded - as something taking place in the brain, causally constrained by, yet constitutively detached from, body, environment, and others (Tomasello and Call, 1997; Povinelli, 2000; Seed and Byrne, 2010; Vaesen, 2012; Lombard, Högberg and Haidle, 2019; Seed and Call, 2019).

1.3 The problem of Primate modelling: finding patterns in heterogeneity

For Primate Archaeology, as Barrett (2015) argues, even without inference of causal representation or intentionality, retaining a brain-bound view of cognition risks repeating

[3] '4E' cognition – a set pf theories which argue, variously, for an embodied, embedded, enactive, and extended view of cognition which goes beyond the brain. Further elaborated upon in chapter 2.

anthropocentrism of a more insidious kind. The assumption that these theories "capture some essential quality of cognitive processing not tied to one species, but applied generally across the board and to all brains", leaves organisms' physical being and sensory systems at the periphery of explanation (Barrett, 2015, p32). This is problematic if we consider that a significant challenge to our understanding of the origins of tool use by means of primate modelling lies in overcoming the extreme degree of heterogeneity therein – a challenge only exacerbated if that heterogeneity is not taken seriously. Estimates suggest the primate order encompasses over c.600 extant species and numerous extinct ancestor or 'dead-end' species, entailing a huge range of bodies, environments, and ecologies, spanning an evolutionary context of approximately 81-87 million years (Martin, Solico and Tavare, 2007; Perelman *et al.*, 2011). Though a long shared evolutionary history and suite of shared biological features might make NHPs, and specifically the Great Apes, the default palaeoanthropological comparator (Elton, 2006), not all or even the majority of primates are tool users. While captive tool use is more common, habitual tool-using in the wild is rare, reported among Burmese long-tailed macaques (*M.f.aurea*: Gumert et al., 2019; Gumert & Malaivijitnond, 2012; Malaivijitnond et al., 2007), capuchins (*Sapajus spp.*: Fragaszy et al., 2004; Moura & Lee, 2004; Visalberghi & Fragaszy, 2010; Waga et al., 2006); orang-utans (*Pongo spp.*; Meulman & van Schaik, 2010; van Schaik et al., 1996), and chimpazees (*Pan troglodytes spp.*: McGrew, 2004; Sanz & Morgan, 2007; Whiten et al., 2001); and less frequently among wild populations of gracile capuchins (*Cebus capucinus*: Barrett et al., 2018), bonobos (*Pan paniscus*: Hohmann & Fruth, 2003) and gorillas (*Gorilla spp.*: Breuer et al., 2005; Greuter et al., 2013; Kinani & Zimmerman, 2014). Only three species customarily (*sensu* McGrew, 1992, p. 180) exploit lithic tools in the wild, making them suitable for more direct comparison with tool using by early hominins, these species are: Burmese long-tailed macaques, robust (or brown) capuchins (*Sapajus libidinosus*), and western chimpanzees (*Pan troglodytes verus*).

The NHP tool-using species are phylogenetically distant and ecologically and socio-ecologically diverse, suggesting evolutionary convergence rather than a pan-primate technical

propensity (LeFebvre, 2013; Panger, 2007; Reader, et al., 2011). Where phylogeny is closest, proximate mechanisms and adaptive function may differ: McGrew (1993a), for example, found no consistent pattern in the frequency of tool using by ape species and postulated correlates of tool behaviour, including absolute brain size, encephalisation quotient (Jerison, 1976), and brain structural asymmetry; hand length indices, thumb length, and thumb opposability; and diet, and terrestriality. Adding significant complication, the adaptive function of NHP tool use also remains unclear (Biro, Haslam and Rutz, 2013), muddied by the diversity of contexts and modes in and by which NHP tool using takes place. NHP tools are used in the intimidation and defence of and against predators and rivals; in seeking attention and the performance of social displays; for comfort, to sanitise and to medicate; and most commonly, in the extraction and processing of food resources (for a review see Shumaker et al., 2011) – with no single context unique or ubiquitous to a sub-order, family, or genus. Where context is consistent, neighbouring groups of the same species may perform differing patterns of tool behaviour independent of ecological explanation, preferentially selecting differing materials (Luncz, Mundry and Boesch, 2012; Gruber *et al.*, 2015; Visalberghi *et al.*, 2017; Luncz *et al.*, 2019; Pascual-Garrido, 2019) targeting differing food resources/social responses (Boesch & Tomasello, 1998; Boesch, 2010; Ottoni & Izar, 2008), and even using techniques altogether idiosyncratic to the given site (e.g. Falótico & Ottoni, 2014; Yamakoshi & Sugiyama, 1995). Testing of ecological hypotheses as explanations of extractive tool use (e.g. Fox et al., 1999; Rutz & St Clair, 2012) has also yielded inconsistent results (Sanz and Morgan, 2013; Koops, Visalberghi and Van Schaik, 2014): tool using at some NHP sites correlating with necessity (Yamakoshi, 1998; Moura and Lee, 2004; Bogart and Pruetz, 2011), at other sites, with opportunity (Nishie, 2011; Spagnoletti *et al.*, 2011; Falótico, Spagnoletti, *et al.*, 2017), and at several sites, with no strict correlation either way (Hernandez-Aguilar, Moore and Pickering, 2007; Gumert, Kluck and Malaivijitnond, 2009; Sanz and Morgan, 2013; Falótico, Siqueira and Ottoni, 2017). With so few empirical data unambiguously linked with the adaptive significance of tool behaviours (extractive or otherwise), Biro et al., (2013)

suggest “we may more fruitfully put our efforts into identifying those aspects of tool use that are promoted, or depressed, by an animal’s physical abilities and surroundings”.

1.4 Finding the mind in matter: Neo-Darwinist narratives and a dualistic ‘mark of the cognitive’

From the Archaeological perspectives of wishing to both extrapolate cognition from material remains and model past hominin cognitive/behavioural evolution using primate comparisons, where we place the mind matters (Malafouris, 2013a, 2019). Mentalist approaches to cognition and agency not only limit our ability to interpret the minds of past hominin tool users, with archaeologists simultaneously restricted to interpretation of materials as the remnants of past minds while prevented from accessing past minds themselves, they also dictate the narratives which can be reconstructed. Both cognitivist and Neo-Darwinian frameworks, for example, assume that since cognition precedes action, cognitive capacity must precede behavioural adaptation. This assumption has led to a dualistic ‘mark of the cognitive’, and a narrative in which material objects are used as markers of cognitive development, stepping stones in a gradual accrual of cognitive and behavioural features along a timeline from ‘primitive’ to ‘modern’ and ‘complex’ (Ambrose, 2001; Bar-Yosef, 2002; Henshilwood et al., 2002, 2009; McBreaty & Brooks, 2000). While this kind of perspective provides a valuable insight into the *when* and *where* of cognitive development, it pre-determines the field of potential answers available for *how* and *why* (Malafouris, 2010; Roberts, 2016). The result is an image of psychological ‘modernity’ which is static, fully-realised, and evolved within, yet in isolation of, a passive external material world (Latour, 1993; Malafouris, 2010, 2013a; Roberts, 2016) – a metaphorical ‘brain-in-a-vat’ (Putnam, 1981).

The use of primate comparisons, rather than serving to question this narrative, has only served to reinforce the ‘modernity problem’. Of the many putative scenarios offered to explain technical evolution, the two most influential theories are the ecological (or sensori-motor)

intelligence (Parker and Gibson, 1977; Gibson, 1986; Byrne, 1997) and the social intelligence hypotheses (Jolly, 1966; Humphrey, 1976; Byrne and Whiten, 1988; Dunbar, 1998). Whilst these two theories have traditionally been considered as rival hypotheses, current evidence supporting a mosaic view of primate cognitive evolution suggests that they are better construed as complementary (Rosati, 2017). The ecological intelligence hypothesis argues that primates developed larger brains to solve the complex cognitive demands of resource exploitation; specifically geo-temporal distribution of resources (spatial memory) and extractive foraging problems (causality and complex manipulation skills). In this scenario tool-use is part of the mechanism by which selection drives increasing intelligence, giving an adaptive advantage in times of high resource competition and/or food scarcity. The social intelligence hypothesis, in contrast, argues that primate brains evolved to cope with the cognitive demands of increasingly complex social networks. Primate social networks are characterized by their relative complexity and correlated encephalisation (Dunbar, 1998; Dunbar et al., 2010). Group living (and Machiavellian political manoeuvring), cooperative breeding, and social learning, are all socially intelligent strategies that could provide an individual with an adaptive advantage. In this hypothesis, tool-use behaviour is less a driver of intelligence than it is a secondary adaptation, enabled by selection acting directly on domain-general cognitive processes contributing primarily to social intelligence. Despite the obvious opposition, the key difference in seeing tool-use as either cause or effect means that the two theories are not mutually exclusive and there is no reason why they could not be seen as two sides of a mutually reinforcing process (Rosati, 2017). Neither scenario, however, actually accounts for what motivates tool use in the first place, nor how the intellectual skills imputed to give adaptive advantage come about: the study of primate technology suffers from the same assumption that technical evolution takes place anatomically, in the brain, with technical cognition scalarly or modularly accrued, and intelligence a matter of relative ecology/socio-ecologies. In the teleonomic functionalism of the Neo-Darwinian framework, we are always one step behind (O'Grady, 1984).

1.5 Scope, outline, and aims

This thesis applies a Material Engagement Theory framework in order to explore complexity and causal cognition in the tool using behaviour of non-human primates, with implications for the evolution of early hominin technologies. Case-studies of the lithic using non-human primates are used to argue for a fundamentally non-individualistic, and multi-temporal view of material agency, cognition, and technical cultural processes. Finally, cross-species comparison is used to identify broader patterns of primate and early hominin technical becoming.

Chapter 2 begins by expanding upon and exploring how our understanding of tool use as a behavioural phenomenon affects and is affected by individualistic views of cognition and agency, and how these characterisations, in turn, affect the interpretive potential of archaeological and ethological records. The latter half of the chapter considers how Material Engagement Theory targets the mentalist paradigm, and identify the key implications of a radically embodied, enactive framework for approaches to technical cognition in Primates. Building from the theoretical position established in Chapter 2, Chapter 3 develops a practical framework for applying material engagement theory to Primate tool use in a manner suitable for cross-species comparison. The first half of the chapter focuses on reorienting Haidle's (Haidle, 2009, 2010; Lombard and Haidle, 2012; Lombard, Högberg and Haidle, 2019) cognigram method outside the brain to provide a means of quantifying behavioural complexity, while also laying out broader contextual measures of repertoire richness and diversity to be taken at both the group and species level. The latter half of the chapter considers the phenomenological experience of tool users, and learners, drawing together theories of enskilment, enactive social cognition and the skilled intentionality hypothesis to re-interpret Lombard & Gärdenfors (Lombard and Gärdenfors, 2017; Gärdenfors and Lombard, 2018) evolutionary model of causal cognition in terms of emergent perceptual and bodily skill. The method outlined in Chapter 3 is applied in Chapters 4, 5, and 6 to case-studies of each of the lithic tool-using NHPs, drawn from the existing literature: *P.troglodytes* at Bossou, Guinea; *S.libidinosus* at Serra da

Capivara, Brazil; and *M.f.aurea* at Piak Nam Yai, Thailand. Though similar themes are present throughout all the case-studies, each species is used to emphasise a particular aspect relevant to understanding the nature of tool use as an ecology of agency: chimpanzees, education by master-apprentice and the co-constitution of emergent techniques; capuchins, patterns of material deposition and the development of canonical affordances; and macaques, the role of resource distribution, opportunity and risk in constituting affordance relevance. Finally in Chapter 7, the case-studies are compared in the context of each species' broader tool-behavioural catalogue. The first half of the chapter gives a quantitative analysis, with results then discussed in the context of the broader themes highlighted by the qualitative descriptions provided in each case-study, in the second half. The overall aims of the thesis are (1) to consolidate existing primate archaeological theory with more pragmatic, non-anthropocentric approaches to material agency and cognition, (2) to develop a practical framework for approaching cognition in cross-species comparisons, and (3) to gain insight into the nature and dynamics of tool use as a particular mode of mutualistic becoming with the environment, and the implications this has for our understanding of hominin technical evolution.

2.1 Introduction

The last 15 years have seen a shift away from the traditional internalist view of cognitivism with cognition since being described as embodied (Lakoff and Johnson, 1999; Gallagher, 2005; Chemero, 2009), enactive (Varela *et al.*, 1991; O'Regan and Noë, 2001; Thompson, 2005; Hutto and Myin, 2013), distributed (Dunbar et al., 2010; Hutchins, 1995, 2005; Kirsh, 2006; Rowlands, 2010; Sutton, 2006) and extended (Clark and Chalmers, 1998; Clark, 2008). While these views are increasingly incorporated into human and NHP studies of technical evolution, often as a means of contextualising species-specific modes of cognition and behaviour, their application remains conservative, constrained by dichotomous assumptions inherent to their Neo-Darwinian frameworks.

Material engagement theory (hereafter MET), though encapsulating many of the same concepts, sets itself apart from other work on philosophy of mind and cognition with its specific focus on material culture and engagement; encouraging a bridging of the mind-material gap, in order to recognise the primacy of material interaction in processes of species psychological *becoming* in and *with* their environments (Malafouris, 2004, 2008, 2009, 2013, 2015, 2016, 2019; Malafouris & Renfrew, 2010; Renfrew, 2004). Taking cognition to be embodied in a radical sense, i.e. constituted by both body *and* environment, MET develops the three interrelated hypotheses of extended mind, enactive signification (Malafouris, 2013a) and material agency (Knappett and Malafouris, 2008; Malafouris, 2008), to call for a re-orienting of the boundaries of the mind and a recognition of the material dimensions of cognition (Iliopoulos and Garofoli, 2016).

Continuing from the introduction, the following section reviews issues in common between cognitivist archaeological and primatological approaches to tool use, then explores how the

methodological principles of MET target the mentalist paradigm. The implications of the MET framework for approaches to NHP tool use are explored through three inter-related working definitions taken from the MET literature:

1. *Metaplasticity*, the flexible integration of things and plastic brains/bodies which describes the ongoing becoming of the mind.
2. *Thinging*, defined as the act of cognitive prosthesis, or the ability to think *with, through and about* things.
3. *Creative thinging*, the creative force which drives human engagement with materials and the discovery and bringing forth of meaning in the world.

2.2 Tools, techniques, and technology: Issues with dualism

Tool use is a concept historically defined by its dualisms, concomitant with the cognitivist division between mental and physical phenomena: as 'an extra-somatic adaptation to the environment' (Childe, 1933) tool use belongs exclusively to neither internal nor external; it is biologically functional and intelligent; 'a need satisfying behaviour of the individual' (Sahlins, 1972, p. 186), and a core marker of cultural traditions (Mauss, 1936; Latour and Lemmonier, 1994; Bensa and Creswell, 1996; Whiten *et al.*, 1999).[4] Though motivated by different research agendas, anthropocentric and ethological approaches to tool use which maintain a separation between mind and body nevertheless share this 'bifurcated' (following Latour, 2014, p. 507) approach; converging upon an evolutionist perspective which emphasises function and technical efficacy of external pragmatic gesture while maintaining the primacy of 'higher-order' internal mental processing (Haidle, 2014; Tomasello & Call, 1997; Vaesen, 2012; Wynn, 1993).

[4] Defining the *chaîne opératoire,* Bensa & Creswell (1996, p.127-128) write that "La manière dont sont imbriquées les chaînes est culturellement définie, ou plus exactement définit une culture particulière".

For Ingold (1993, 2000), the externalisation of technique amounts to a conflation of the technical with the mechanical, and a "'machine-theoretical' cosmology" (Ingold, 2000, p. 314) that has subsequently led the Standard view of tool use to characterise technique as utilitarian, individually practiced, and in binary opposition to science (or intellectual method), which is in turn seen as societal and fundamentally expressive. Early conceptual and methodological development of the *chaîne opératoire*, for instance, characterises technique as an operational sequence of mechanical actions, priorly conceptualised, and organised according to a mental schema arrived upon by internal reasoning (Brezillon, 1968; Sellet, 1993);[5] the standardisation and complexification which occurs with Acheulean tool forms has consequently been interpreted as indicative of the 'operator's' ability to work to a 'mental template', shaped in part by shared cultural norms (Deetz, 1967; Dibble, 1987; Gowlett, 1979, 1984; Isaac, 1972; McNabb et al., 2004; though see Wynn, 2004).[6] Although significant effort has gone into integrating the physical and social aspects of technique (Lemmonier, 1992; Latour and Lemmonier, 1994; Sillar and Tite, 2000), the influence of machine-rhetoric is still present in contemporary analysis in both archaeology and cultural primatology - maintained in the frequent distinction between physical, 'biomechanical', or 'sensori-motor', intelligence relating to individual technique, and the separate but inter-dependent mental representation of method relating to socially transmissible 'tradition' (eg. Mosley & Haslam, 2015; Parker & Gibson, 1977; Pelegrin, 2005; Vaesen, 2012; Wynn, 1993).

To both the Standard and Neo-Darwinian view, tools are considered subject to technological determinism, selective forces which for similar functions produce homologous shapes, forms, or behavioural patterns: "comparable to biological determinism, with as much overlap, as many exceptions, but with as much clarity in the ensemble" (Leroi-Gourhan, 1943, p. 334). At the same

[5]It is recognised that this is very much a generalisation. *Chaîne opératoire* has many nuanced interpretations (not all of which relate to artefact production) and has become an umbrella term to a number of parallel concepts such as operational sequence, and in lithic analysis, reduction sequence (*cf.* Brezillon, 1968; Pelegrin et al., 1988; Schiffer, 1976; Sellet, 1993).

[6] 'Mental templates' is another nebulous term with numerous understandings which refer to more than one aspect of technique/are used as a proxy for a number of different mental capacities: for a review see Chase (2016).

time, most functions are multiply-realisable to the extent that function shapes, but cannot make, tool form – "whoever does the task must at some point make a choice" (Wynn, 1995, p. 14). For Leroi-Gourhran (1943), tools are the objectification of technical tendency (*la tendance*) in local facts (*degrés du fait*) at a specific time and location. Take, for example, a technical solution to a problem which has reappeared independently multiple times or in multiple locations such as use of a probe tool in the predation of army ants by chimpanzees (McGrew, Pruetz and Fulton, 2005; Möbius *et al.*, 2008; Pascual-Garrido, 2019): the tendency is for a long, thin, flexible probe of either bark or herbaceous material, while variation in local facts might depend upon a number of ecological, social, and idiosyncratic stylistic factors, such as site of predation (i.e. at the nest or mound), ant species (and aggression), material availability, individual and/or cultural preference, each affecting inter- and intra-site-average tool lengths.

A cognitivist interpretation of tools and techniques as the by-product of internal cognitive processes overlooks the fundamentally 'active' nature of tool *using*, and diminishes the importance of materials and subjective experience as formative aspects of those same processes. The Standard view of technology assumes 'necessity is the mother of invention' (Pfaffenberger, 1992), and *ipso facto*, that technical form follows function; but also that function as *aboutness* follows mental intent. A tool might signify mental intent, yet to the cognitivist, would not constitute that which it signified: a hammer might signify the intent to apply force but the knowledge of 'heaviness', 'hardness', and the 'know-how' to use the hammer (i.e. proper technique) is supposed to come not from the hammer or its use, but from the mind of its user – as if these concepts could be understood without ever having been 'substantiated' through the lifting of an object (Renfrew, 2001): "technique appears to be given in the operational principles of the tools themselves, quite independently of the experience of their users" (Ingold, 1993, p. 433). The presupposition that these 'mental' aspects must come from an influence beyond the natural environment necessitates that there *be* something other than the external, circularly reinforcing the metaphysical invocation of an internal realm of symbolic representation in which signification of concepts precedes physical experience (Renfrew,

2001; Henare, Holbraad and Wastell, 2007). Conflation of the parallel dualisms inherent in cognitivist concepts of tool use causes an epistemological paradox: despite tool and technique being two components of the same conceptual unit, tool use is interpreted as materially representative of, yet behaviourally in-opposition-to, mentally constructed and socially meaningful 'Culture'. On the one hand, tools and techniques are treated as the static, teleological manifestations of internally represented problem-solving processes; and on the other, processes such as subjective agency and individual experience, in many accounts denigrated to secondary phenomena "expressed only in the last *degres du fait*" (Audouze, 2002, p. 284).

2.3 Reconceiving perceiving: Radical embodiment, affordance, enactive cognition, and material agency[7]

MET's radically embodied and enactive approach takes its starting point in Ecological Psychology (Gibson, 1963, 1979) and the phenomenological approaches of Merleau-Ponty (Merleau-Ponty, 1945/2012) and Husserl (1931/2012), breaking down the distinction between stimulus, thought and action to argue that cognition and agency are processes grounded in situated action. For Merleau-Ponty (1945/2012) and Husserl (1931/2012), perceiving is fundamentally tied to being, being to intentionality, and intentionality with the capacity for action (as an organism's primary means of achieving intent), so that the sentience of the world is seen as in its relation to the perceiver's own particular mode of *being-in-it* (following Heidegger, 1927/1996). For example, a fish might perceive the world in terms of its ability to swim; a bird, to fly; prey, to hide; and a predator, to kill. Mouse and elephant experience the same mass as heavy or light; distance as large or small; and time as long or short, because that is how those features of the environment relate to their particular means and mode of being.

[7] This section and the following sections (2.4-2.5) contain work published in Mosley (2020)

The notion of perception as relative to the perceiver is central to J.J Gibson's (1979) theory of affordances, which argues that perception of the environment occurs *directly*, in terms of its situational affording of an organism's physical capabilities, and without the need for mental representation (Shaw, Turvey and Mace, 1982; see also Chemero, 2009). Although there are many interpretations of what an 'affordance' actually *is* – including by Gibson over the course of his career - the interpretation of 'affordance' adopted here, is as a quasi-ontology: affordance is taken as neither a property of the organism, nor of the environment (cf. Turvey, 1992), but as a possibility for action arising from their situational complementarity (cf. Stoffregen, 2003). Understood in this sense, the environment may simultaneously afford many things to many perceivers: for example, a field of daisies might afford pollination to a bee; nesting material to a fieldmouse; and making daisy-chains to children; as a glass might afford drinking orange juice in the morning, water in the afternoon, and beer evening. To use an analogy from quantum physics: in the phenomenon of quantum super-positioning, prior to observation, a quantum particle may exist in more than one location at once – it is only in the moment of observation that its single location is determined. Prior to perception, the environment affords an almost infinite number of possibilities for action – but it is only in action *as* perception, in the compatibility between organism and environment which occurs in the moment of affordance solicitation (i.e., action), that the world is meaningfully revealed. The most important aspects of affordance are that it points both ways, to the organism and environment (Gibson, 1979, p. 129), and that it looks forward and back in time, perception and agency co-constituted by their ongoing mutuality. The relevance of a perceived affordance is as rooted in the organism's species biology and own past socio-material experience (Costall, 1995, 2012) as it is routed by the perception-action/intention-action coupling occurring in the moment of affordance solicitation (Baber, Parekh and Cengiz, 2014).

Radical enactivism (Varela *et al.*, 1991; Hutto and Myin, 2013, 2017), though differing in several of its core assumptions, converges strongly with Ecological Psychology (hereafter EP) in both its non-representational view of cognitive processes and its treatment of organisms and

environments as reciprocal, co-constitutive aspects of a single dynamic cognitive system.[8] Where EP is primarily focused on the investigation of generic agency [or the 'ecology of agency' in affordance (Costall, 2008)], enactivism "[emphasises] the participatory engagement of the [acting organism] in the situation" (Szokolszky *et al.*, 2019, p. 378). Grounding perception in sensation, cognition is seen to occur when environmental interaction causes a feedback loop between dynamic neural activity and the organism's sensorimotor contingencies (Varela *et al.*, 1991; O'Regan and Noë, 2001): 'meaning', more than discovered (as *per* EP), is seen as actively created – or as Malafouris (2013a) argues, '*brought-forth'* in the lived experience of agential action.

From an MET perspective, J.J Gibson's theory of Affordance and theories of radical enactivism are important for several reasons. Firstly, because they characterise perception and agency as active, experiential processes of skilful environmental engagement *through which* cognition and intent are *enactively* and *emergently substantiated* (following Renfrew, 2001). Secondly, cognitive processing, rather than an essential quality of being constrained within the brain (and without the body or environment), is recognised as a *fundamentally* heterogenous process founded in organismic-environmental co-determination and mutualistic transaction: Species unique perceptual and motor capacities are placed at the fore-front of explanations, rather than the periphery. With the body taken *as* the brain, intention is seen as in action, and to act seen as to perceive. Further, since affordance is distributed evenly across the organism and environment, cognitive processes are considered co-constituted by the two; agency is seen as lying in the-between, not a property of 'who' or 'what' (mind or material), but a matter of 'when' (Malafouris, 2013, p51).

[8] It has been pointed out to the view of affordance I adopt is perhaps more in keeping with the radical enactivist view (e.g., Hutto & Myin, 2013, 2017) than with Neo-Gibsonianism (e.g., Turvey, 1992); however, as Baggs & Chemero (2021) argue, I do not see that the two views are necessarily mutually exclusive. There is no reason why we should not be able to consider ecological information (about affordances) as a property of the environment to be able to discuss *potential* affordances relative to an *ideal* organism; provided it is acknowledged that ecological information can exist in a *meaningful* sense, only in the precise moment of affordance solicitation by a *real* organism.

2.4 Metaplasticity: perceptual learning and enskilment as developmental processes of mutualistic becoming with materials.

The temporality of agential processes and historicity of affordance perception are aspects of EP which hold relevance for MET's own developmental framework with regards to understanding how the mind as an agential perspective develops. From an EP perspective, to the extent that cognition and action occur in the world and alter the relationship between organism and environment through their occurrence, organisms' perceptual 'lenses' and the landscape of available affordances are in a state of constant flux (Adolph, 2020; Adolph & Kretch, 2015; Rietveld & Kiverstein, 2014). Mind and the meaningfulness of direct perception are perpetually incomplete (Gibson and Pick, 2000; Oyama, 2000), while change (or lack of change arising from change) is viewed as primary: "we gain our understanding from change and becoming" (Gibson, 1994, p. 71; also cited by Szokolszky *et al.*, 2019, p. 373).

A similar notion of ongoing change within the organism/environmental system brought about through action, as the creative source of variation, is central to the MET related hypothesis of metaplasticity, which views 'mind' as a non-linear, transactional process of mutualistic *becoming* with the environment. Adopted from the neuro-scientific literature, where the term describes behaviourally dependent higher-order synaptic plasticity (Abraham and Bear, 1996), in the context of the MET framework, 'metaplasticity' expresses the transformative nature of material engagement in the recursive relationship between mind and materiality. As material engagements lead to novel modes of *being*, so they engender novel ways of thinking and perceiving, which in turn shape, scaffold, and constrain the pathways for future environmental interaction. In the same sense that our material engagements and modes of materiality can produce short-lived or profound long-lasting effects for ourselves and our environments, metaplastic processes are threaded across multiple inter-connected timescales (Malafouris, 2015), and it is in the unravelling of these

timescales that we can best understand tool use as a phenomenon extended beyond a single performance, individual, or generation.

2.4.1 Evolution and skill acquisition in the context of a developmental framework: gene/cultural co-constitution, interaction as transaction, and the ontogenetic niche.

At the organismic level, Malafouris (2010, pp. 52–53, 2013a, pp. 40–41) grounds metaplasticity in theories of neuro-constructivism (Quartz and Sejnowksi, 1997; Mareschal *et al.*, 2007) and developmental systems theory (Griffiths and Stotz, 2000; Oyama, 2000; Oyama, Griffiths and Gray, 2001; Griffiths *et al.*, 2010), using concepts of 'extended inheritance' and 'parity' between internal and external resources to argue for 'mind' as a kind of 'probabilistic epigenesis' (Gottlieb, 2002, 2007). Though phenotype is still understood to predispose a particular 'form of life' (Wittgenstein, 1953; Rietveld and Kiverstein, 2014), individuals' perceptual capacities are essentially shaped by their own situated experience and practice. In so much as the environment may enhance or constrain the shape of neurological and physical development, organisms are seen not as inheriting 'minds' *per se,* but the "ability to develop a mind" (Griffiths and Stotz, 2000, p. 31). This view marks a significant departure from adaptationist Neo-Darwinist views of organisms as having evolved to 'fit' a particular environmental niche and of tool-use as an intelligent behavioural response to selective environmental pressures. With the relationship between organism and environment viewed as dynamic and mutually constitutive, rather than static and unilinearly causal, focus is shifted from the active role of the organism in its *selective* environment [i.e. niche construction theory (Odling-Smee, Laland and Feldman, 1996, 2003; Laland, Odling-Smee and Feldman, 2001)], to its role (and the role of its material engagements) in shaping the *ontogenetic* environment (Stotz, 2014, 2017; West et al., 1988). In the acquisition of tool behaviours, the development of technical cognition and individual technique, while predisposed by the organism's genetic propensity for particular modes of environmental engagement (i.e. the field of affordances

to which an animal is initially receptive), is ultimately determined through the real-time process of environmental engagement as it unfolds (i.e. the affordances which the organism is solicited by and the possibilities for future action this produces).

Further contrary to the Neo-Darwinist approaches (e.g. Boyd & Richerson, 1985; Boyd & Richerson, 1995; Cavalli-Sforza & Feldman, 1981), within the MET framework no separation is made between genetic and cultural modes of transmission or between evolutionary and developmental processes; the relation between differing metaplastic timelines being viewed as one of transaction as opposed to interaction (Malafouris, 2010). Organisms are not alone in their worlds and the ontogenetic niche is an environment inherited from and constantly developed by the skilled practices of others (Mauss, 1936; Leont'ev, 1981; West, King and Arberg, 1988), the materiality of their praxis redistributing materials around the landscape and directing attention (deliberately or inadvertently) towards critical aspects of method, influencing the perceptual significance of relevant functional affordances and particular modes of engagement relative to others (Gibson, 1979; Ingold, 2001). In the transaction between developing minds and materials, the shaping of perception is both a process of enculturation and of cultural production through which artefacts, via their material permanence, can become the focus of enduring, and cumulative, social influence (Costall, 1995, p. 471)). With each act of material engagement feeding back into the broader meshwork, the development of technical proficiency and idiosyncratic technique becomes a negotiation of individual place among the broader constellation of conspecifically available technologies (Lave and Wenger, 1991; Gowlland, 2019).

2.5 Thinging: materially constituted causal cognition, and tool use as enactive prosthesis.

The understanding perception as a skilful form of 'interactive engagement' with the environment enables a re-framing of causal cognition – typically treated as the representation of

causal relationships (Kronenfeld, 2014; Lombard and Gärdenfors, 2017; Bender, 2020) - as the direct perception of causality via changes in the environment-organism system, and *the interactive means by which animals become receptive to solicitation by the effective affordances of objects.* At its most basic level, causal perception facilitates enskilment (i.e. the development of bodily/perceptual skills) via the discovery of basic object and target object affordances (e.g. 'grip-ability' or 'consume-ability') by direct proprioceptive handling, or perhaps by observation of a conspecific's object manipulations. This understanding of causal cognition as a mode of active probing of the external world also extends to tools as continuous prosthetic parts of the perceptual process; a notion expounded by Malafouris (Malafouris, 2014, 2016, 2019) in the concept of *Thinging*, as the skilful ability to think *with* and *through,* as well as about objects. Echoing Clark & Chalmers' (1998) 'parity principle',[9] Malafouris (Malafouris and Renfrew, 2010; Malafouris, 2013a) argues that as causality shifts beyond the skin, so too does the transactional boundary between organism and environment where cognitive processes take place. Tools, as and where they function to alter scope and or effectivity of bodily skills, are considered active extensions of the perception-action cycle, and as constitutive parts of the agential process (Mangalam & Fragaszy, 2016; Smitsman, 1997; Smitsman & Bongers, 2012).

J. J. Gibson (1979, p. 36) alludes to this co-constitution in referring to tools as a "special kind of detached object" (Susi & Ziemke, 2005, p11), which once attached, are no longer environmental objects; suggesting that through causal constitution, a continuum of organism and tool exists such that any goal intended by the user, is intended by the tool also. Though likely intended to mean 'when in use', Gibson's use of the term 'attachment' is ambiguous, allowing for a conflation between the organism as the source of the physical manipulation involved in tool use, and as the primary source of functional intent. This latter characterisation of technical agency is one which is common among the categorical exclusions made by operational definitions of tools use (Parker and Gibson,

[9] The parity principle states that any external process which were it to take place within the brain, would be considered cognitive, should be given equal cognitive (constitutive) status (Clark & Chalmers, 1998).

1977; eg. Beck, 1980; Shumaker, Walkup and Beck, 2011), and to weaker approaches to Extended Mind theory (Clark and Chalmers, 1998), which originate functional intent (and cognition) within the user, extending (or leaking out) to the tool. Tools' agency is viewed as essentially 'mediative', existing only within the moment of use and when adjacent to the tool user. Instances of 'proto-tool use' (i.e. tools either not held in the hand, or still fixed to a substrate), for example, are typically excluded from operational definitions on the basis that they lack an active agent of change; that is, the object which would otherwise be considered to exert a causal mechanical effect does not do so as a physical extension of the 'user', but, being either static or fixed (i.e. not directly manipulated), is considered a passive element of the broader environmental context (following Parker and Gibson, 1977). The distinction between environmental objects 'acted-with' when attached and 'acted-upon' when detached is thus indicative of a broader conceptual dichotomy between organism and environment, which locates technical agency with the individual and extends to tools by virtue of their direct physical and causal connection. Where exclusion of proto-tools reflect assumptions about who or what might make an agent, the exclusion of constructions reflects assumptions about how and when agential processes unfold. Traps, for instance, often share their mechanical functions with analogous tool forms (e.g. a snare trap shares its function and much of its mechanism with a lasso), but are excluded on the basis that it is the trap-ee, rather than the trapper, which is assumed to be responsible for the activation of the trap's function and thereby its final 'effective orientation' (Preston, 1998). The distinction is interesting for two reasons: firstly, because it suggests an assumption that technical agency can be neither constituted by, nor extended to, objects of change (even if they do something the user 'intends'); and secondly, because it establishes the technical agency of functional objects, or their 'tool-ness', as a temporal condition constrained within the moment of their active physical connection with the user. While this latter assumption may suit an ethological context, methodologically in the sense that tool objects are identified by virtue of their use [i.e. may be considered purposive without impugning representation or intent (following Visalberghi & Fragaszy, 2012)], and unproblematic in the sense that the majority of animal curated

tool objects are modified ad hoc, frequently perishable, and infrequently reused (i.e. may not exist far beyond their use); it does not suit an anthropocentric context in which objects' tool-ness maybe associated with recognisable tool forms, persistent beyond their attachment and use.

In contrast, the MET framework takes a fundamentally non-anthropocentric approach to attachment and cognitive extension: rather than an extendible property of the user, technical agency is tied with overall causality (or pragmatic effect), an emergent product negotiated by the whole organism-tool-environmental system (Ihde & Malafouris, 2019, p. 4). In Malafouris' (2013) example of the Blind Man's Stick (see also Merleau-Ponty, 1962; Bateson, 1973), long-term use results in the blind man's brain treating his walking stick as a part of his body, resulting in a sensory 'transparency' or 'phenomenological osmosis' (Leder, 1990) whereby he is able to see *through* it. As the man's body schema is extended to incorporate the stick; so the stick acts *'inwards'*, facilitating a reorganisation of the man's primary visual cortex to process haptic stimuli.[10] Since the stick is vital to this neural re-routing, which could not exist in its absence, the two are not simply causally-coupled, but are mutually constitutive, together forming a new "material-mind hybrid" and a new pathway of cognition which could not be explored were a boundary drawn between the two (Latour, 1993; also cited by Roberts, 2016). Rather than an act of cognitive extension, the attachment involved in cognitive prosthesis is mutualistic: it is as much incorporation of the tool as a material object into the bodily skills of the user, as it is incorporation of the tool using organism by the tool (following Gilbert et al., 2015; Parisi, 2019).

Mutualistic incorporation, as opposed to pure extension, implies a more gradual temporality in which perceptual transparency is not immediately apparent, but an emergent quality the user to

[10] There is ongoing debate in the field of neuroscience of the differences between extension and incorporation (Martel *et al.*, 2017; Parisi, 2019). The stance taken here is that though the two may be different in terms of how they alter the perception of bodily-ownership (e.g. de Vignemont, 2017: *working-body* versus *protective-body schemas*); the phenomenology of *causal* agential experience is continuous between the two – with extension a temporary form of co-constitution which may, through extended engagement lead to skilful incorporation, in which true agential transparency is achieved.

some degree 'works-toward': in Heidegger's (1927/1996) theory of equipment, unfamiliar objects are argued to *present-themselves* to *Dasein* as present-at-hand (i.e., as opaque, or without use), only becoming ready-at-hand (i.e., as transparent, or 'something-in-order-to') as the perceiver's degree of familiarity increases. Ihde (Ihde, 1979, 1990) too, relates a similar idea with the phenomenological concept of 'technics', defined as the "symbiosis of artefact and user *within a human action*" (Ihde, 1990, p73, emphasis added), in which through time and an extended period of habituation (following Bourdieu, 1977) users come to experience the causality of their tools as extensions of the agential self, their skilled tool actions as epistemic as they are pragmatic. A new pair of glasses, for example, are present to the user; their weight is felt on the face, and the user is aware of looking through the glass. With time, however, the feeling of the glasses recedes until the user is no longer conscious of their presence: the phenomenological experience which at first might have been described as [user → glasses → world] becomes [(user + glasses) → world]. If enskilment is a process of explorative material engagement whereby affordances arise then, for MET, skilled tool use (i.e. incorporation) is the *cultivated* perceptual ability to be solicited by the appropriate affordances of a given tool task as they arise; to direct attention away from the boundary between body and tool to the functionally meaningful relationship created between [body + tool] and the environment. Importantly, as with all other forms of enskilment, the process of skilful incorporation is a function of practical engagement: as Ingold (2000) argues, the process of enskilment is one "in which learning is inseparable from doing, and in which both are embedded in the context of a practical engagement in the world" (p416).

2.6 Creative thinging: discovery in improvisation and making as material-mind flow

Referring specifically to the kind of thinking which takes place *through* making, Malafouris describes *Creative thinging* as a process of attentive enactive discovery and a "combination of world-involving and world-revealing bringing forth" (Malafouris, 2014). While the concept further

emphasises the transactional nature of material engagement articulated by the concept of *thinging,* it also expressly highlights the integral role of creativity in human *being* and in past hominin *becoming* (Gell, 1998; Ingold, 2010b, 2012; Malafouris, 2013a, 2014, 2019; Walls and Malafouris, 2016). Contrary to classic cognitivist approaches to tool-making which isolate and prioritise the ecology of the creative space as an internal problem-solving process which is subsequently projected over matter (e.g. 'mental templates' or *chaine operatoire*), MET understands the creative mind as the hylonoetic space in-between 'mind' and matter arising *through* the dynamic interplay of methods and materials: "if the origin of the creative process can often be found within the mind, it is not because mental or neural representations inside the head precede or supervene upon its physical realisation in matter; rather, it is because the creative mind is already a mixture of neural and material qualities… and thus is not limited by the skin" (Malafouris, 2014).

Simondon (and subsequently Ingold, 2012, p. 433) conveys the hylonoetic nature of making via the metaphor of clay brick-manufacture, in which clay is pressed into a wooden mould and dried or fired to produce a standardised brick-shape. The brick is produced as much by the compressive force of the mould acting against the clay, as it is the expressive force of the clay pressed against the mould; it's form, rather than made, is taken, arising not from the physical imposition of the mould as an ideal template, but from the compatibility of clay and mould negotiated at the moment of their meeting (Ingold, 2012, p. 433). Applying the same concept to technique (as opposed to material form), Keller & Keller's (1991, 1996) ethnographic accounts of blacksmithing demonstrate the fluidity, and improvisational nature of skilled practice. Though the skilled blacksmith approaches their task with an embodied anticipation of proper method (as a rough procedural outline learned though past engagements), as they engage with the materials each movement with the hammer invites the next, the nature of the immediate task unfolding with each strike and every reaction of the metal, with each novel constraint and every affordance that they present. Technique becomes a matter of embodied improvisation – a seeking of stabilisation of form which can only be achieved through the attuning of perception to the flow of the material as it is revealed through action

(Ingold, 2010a). The organic configuration of actions (or *know-how*) brought together in technique is what Keller and Keller (1996) term the 'constellation of knowledge', characterised by Ingold as an emergent set of dynamic relations – not a network, but a 'meshwork' of lines, tensions, and material flows which together constitute the ecology of the creative space (Ingold, 2012).

For MET, the significance of *creative thinging* goes, with the lines of meshwork, beyond a single tool form, tool maker, or technique, to capture the way in which humans and things "entrap" and 'entangle' (following Hodder, 2012) one-another (Malafouris, 2014, p143). Tool using, making, and enskilment are constant *metaplastic* processes of transformation, presenting an unfolding and refolding of material engagements upon the world (Deleuze and Strauss, 1991), and a drawing of material skills around the body in patterns of ever-increasing complexity and mutual dependence.

2.7 Criticisms of MET

As Chakrabaty (2018) points out, in adopting a radically embodied and extended approach, Malafouris could be accused of conflating causality with constitution: the coupling-constitution fallacy (hereafter CCF) argues roughly that 'though *x* maybe coupled with *y, x* and *y* are not necessarily constitutive of either x or y' (Adams and Aizawa, 2010b). However, as Kagan and Lassister (2013) write, this not a claim made by the extended mind hypothesis (nor by MET), and even when more accurately restated as 'although *x* is coupled with *y*, *x* and *y* are not necessarily constitutive of *z*' (Adams and Aizawa, 2010a), this and other formulations of the CCF argument are guilty of begging the question by taking the initial assumption that causal coupling cannot ground constitution relations as self-evident. In fact, the constitution argument espoused by EM (*sensu* Clark, 2010; Clark & Chalmers, 1998) does not suggest that all causal relations *must* infer constitution at all, but refers to a particular kind of relation in which some element (or elements) of a system act dynamically with others to produce a novel whole. For example, notes within a

symphony are causally coupled to form the larger body of music, which may be beautiful. The notes, though perhaps singularly unbeautiful, are in their coupled context, by extension, also beautiful. If the initial statement of the CCF is disregarded in favour of a positive thesis, specifying how and when causal coupling is constitutive (i.e. a mark of the cognitive like the parity principle), it is possible to reconsider how and when external resources are constitutively cognitive (Piredda, 2017). It is to this end that MET is "systematically concerned with figuring out the causal efficacy of things in the enactment and constitution of cognition" (Malafouris, 2014, p203).

At the opposite end of the critical spectrum, MET has been critiqued from a Baradian perspective for its dialectical thinking (Govier, 2019) - in particular, the dialectic between mind and matter evoked in the concept of creative thinging, in the context of which Malafouris describes the creative idea as both an "inseparable mind-matter moment", and "a dialectical formation in action" (2014, p145). For Govier (2019), this dialectic relationship is problematic in the sense that it implies inter-action between separate entities as asymmetrical opposing forces, and consequently, a linear causal chronology (i.e. that effect *follows* cause), whereas Barad argues that things, causes and effects, are "in-phenomena" (Barad 2003, p815: also cited by Govier, 2019, p53). This criticism does, however, seem slightly unfounded, appearing more concerned with semantics than substance - as Govier (2019) admits, in archaeology dialectics is used more informally to describe processes of mutualistic co-constitution and entanglement, which is clearly the sense in which it relates to creative thinging (see previous section). In reality, the metaplastic, transactional notion of agency developed by the MET framework seems broadly complimentary (if not wholly compatible) to Barad's (2003, 2007) own open-ended, intra-active notion of 'agential realism', and as equally aimed at challenging the very 'causal unilateralism' Govier (2019) critiques.

2.8 Summary: implications for a theory of Primate tool using

MET is a theory primarily relating to human cognition, the metaplasticity of the human brain, and unique propensity for creative material engagement – far beyond that of any other primate (living or extinct). Where this might cause issues of resolution for other frameworks, which maintain a primacy of mind over matter, propagating an additional dichotomy between and non-human, the shift in focus from function to process makes the MET framework an ideal candidate for cognitive comparisons, and a valuable means by which to approach non-human technical cognition also.

As outlined in this chapter, MET argues for a rejection of cognitivism and other forms of substance dualism, and the view of cognitive processing *within* the head and *without* body and environment as sufficient for effective behaviour. A weak interpretation of embodied cognition allows that the body and environment are causal to cognition – the mind still represents and thinks about the world, but the ability to represent is secondary, and dependent upon the minds' being embedded in it (van Gelder, 1995, p. 380). Body and environment are peripheral constraints put upon a theory of inner cognitive organisation and processing which still remains largely compatible with cognitivism (Clark, 1999, p. 348). Though MET allows that external representation may occur as a part of material engagement, it rejects the view of minds as being solely constituted by internal representations of the external world. In so doing, MET essentially argues that difference can be 'of the world' rather than 'of its representation', taking the significance of the body and being-in-the-world as ontological such that the body *is* the mind (Malafouris, 2013a). It is only with this assumption (i.e. of cognitive constitution) is accepted, that the notion of the environment as a part of the cognitive system, and its implications, can be fully realised. For inter-species comparisons, this means recognising that:

- Functionally different cognitive processes performed by different species are underwritten by fundamentally different cognitive processes, produced by, and producing, fundamentally different minds.

- Complex cognitive capacities (and in particular metacognition) are emergent *through* the development of physical skills and novel materialities, and are not their precursor.

- Tools and tool-associated materials the constitutive parts of technical cognitive processes and understanding their materiality is vital to understanding how these processes come to be.

- Techniques are fundamentally non-individualistic: they are co-constructed by and with others and their material engagements, past and present.

- Perception of technical affordance relevance (i.e. the likelihood of solicitation by one affordance over another) is ecologically grounded, and enactively developed through material engagement throughout the enskilment process to optimize the adaptive, energetic, and/or simply affective risk-benefit ratios of that situational context.

- To understand the nature of a species' technical cognition, research focus should be shifted towards understanding the nature, temporality, and degree of changes to the organism-environmental system incumbent through its enskilment and tool-using processes (i.e. the metaplastic effects of its risks and/or benefits, and of its movement of materials around the landscape).

3.1. Introduction: Case Study Methodology

Previous methodologies have split tool use into three inter-related categories:

1. Macro-level technology: group patterns and demographic spread of tool 'traditions'
2. Ontogeny: learning mechanisms, the development of technique, and behavioural transmission between individuals.
3. Micro-level methods: causal cognition in operational sequences, and object relationships.

The MET framework (as outlined in chapter 2) combines the three, taking a radically embodied approach to cognition which sees technique as co-constructed through the ontogenetic development of skill within a technological system of structured action affordances and socio-material interactions.

Here it is recognised that it is only by considering tool use within a theoretical framework appropriate to cross-species comparison – i.e. one in which technical behaviour and cognition are rooted within species' unique diachronic physical, cultural and ontogenetic contexts - that the NHP record may offer a valuable source of insight into broader themes of human and NHP technical evolution. This chapter therefore aims to explore the application of complexity theory as a means of quantifying behaviour and causal cognition, outlining a method by which to characterize species specific *modes* of material engagement which is subsequently applied in the following three case-study chapters; one for each of the lithic tool using NHPs; chimpanzees (*P.troglodytes*), tufted capuchins (*S.libidinosus*), and Burmese long-tailed macaques (*M.f.aurea*).

To maintain the holistic approach of MET, each case-study will have a micro and macro component. The micro-level component uses the visual interpretation afforded by Haidle's (2010, 2014) cognigram method, accompanied by a deep ethographic description of behaviour and causal

cognition. The macro-component will discuss these relative to the broader field of species technical behaviour. Site selection is included in this chapter in section 4.3; however, the source materials used to construct the operational sequences for each species are cited by behaviour in their relevant case-study chapters.

The mathematical concept of complexity (Chaitin, 1966, 1975; Kolmogorov, 1968) and the works of Haidle (2010, 2014), and Lombard and Gärdenfors (2017; Gärdenfors and Lombard, 2018), are integral to the development of this methodology.

3.2 Complexity Theory & Behaviour

There is an intuitive assumption in Palaeoanthropology that 'complex' must be synonymous with 'greater derived' (Sambrook & Whiten, 1997, p191), but what is it to be 'complex'? What is it that makes one tool use behaviour more or less complex than another; and how does that complexity cost or benefit an individual? Further, how does complex cognition relate to complex tool use: does complexity beget complexity?

To identify and explore complexity requires a working definition of the phenomena. This section adopts Chaitin's (1966, 1975) 'algorithmic' model which defines complexity as being proportional to the minimum amount of information needed to describe a system. Chaitin's model divides a sequence into the fewest common factors necessary to predict a systems subsequent state and from these, forms the minimal program (Chaitin, 1975; see also Sambrook and Whiten, 1997). It is the length of this minimal program (i.e. the longest chain of unpredictable, non-repetitive parts) which implies its relative complexity: the longer the more complex.[11]

A review of previous attempts to compare the complexity of human and non-human tool using demonstrates 'Complexity' can be quantified by a number of aspects. These include the various functional parts of the tool (Oswalt, 1976; McGrew, 1987; Westergaard, 1995; Perreault *et*

[11] Also known as 'Boolean complexity' (see (Feldman, 2000, 2006)

al., 2013); the number of mechanical actions in an ethogram (Byrne and Byrne, 1993; Byrne, Corp and Byrne, 2001); the hierarchical relationships between objects (Lashley, 1951; Parker and Gibson, 1977; Matsuzawa, 1996); and the cognitive load required to process them (Coolidge and Wynn, 2005, 2007; Haidle, 2010). The majority of these approaches adopt a model of complexity comparable to Chaitin's, the 'minimal program' being taken as the minimum number of units describing the focus aspect: Oswalt's (1976) techno-unit system, for example, describes 'more complex' as 'greater number of functional units' whilst Matsuzawa's tree system describes it as 'greater number of object relationships' (Matsuzawa, 1996).

Whilst these approaches can offer useful insights into the quantitative differences between behaviours and objects, taken in isolation, they produce reductionist and one-dimensional views of tool use in which tool and technique are conceptually divorced. In a hierarchical model, minimal programs strung together display patterns of predictability describable as sub-routines in a derivative minimal program. Provided the organisation of subroutines is neither entirely periodic nor entirely random, there will always be the potential for higher levels of descriptive minimal patterns. It follows that an intuitively complex system will display a greater degree of hierarchy and will arise from an optimum between chaos and order. This hierarchy is critically important when the model is applied to a behavioural context. To take a one-dimensional view of complexity would be to create a system which reaches its maxima with increasingly random behaviour. As Byrne *et al*. (2001, p526) point out, it is the "evolution of richly patterned behaviour" which necessitates explanation; random behaviour is by definition inexplicable.

Further, by taking technical complexity as a proxy for cognitive complexity (and intelligence), an inherent assumption is made that longer minimal programs are the theoretical optimum. This becomes particularly problematic when individual-level behavioural measures of technical complexity are used, such as 'operational sequence' length (Lemmonier, 1993).[12] A longer minimal

[12] See also 'chaîne opératoire' and 'reduction sequence' (Leroi-Gouran, 1964; Shott, 2003)

program may indicate a base-level for the intelligence prerequisite to solving a given problem, however, the reverse assumption that intelligent behaviour creates longer programs contradicts the intuitive assumptions that tools, as problem solving devices, should reduce physical or cognitive effort through use, and that efficiency of tool use is optimised when the operational sequence length is at its minima; complexity in this latter sense, being an undesirable trait. This being the case, though complexity in the number of tool use behaviours in a given repertoire may be the product of either necessity or intellectual/ecological opportunity (or both), complexity in the behavioural facets of individual tool behaviours should only be considered as the product of necessity.[13]

By understanding that complexity can be multi-dimensional, we can begin to explore the multiple scopes which make tool use behaviour complex. From a MET perspective, this includes understanding how material interaction contributes to the balance between different aspect modes: for example, it can be predicted the complexity of hierarchical object relationships will correlate with the complexity of the operational sequence length, if only because each additional object requires at least one additional action. Similarly, though objects may support increased length of the operational sequence by directing attention, there may be a limit at which material can no longer prop working-memory,[14] necessitating modulation of behavioural chains and so it should also be predicted that as overall behavioural complexity increases, so should hierarchical complexity, so that the length of the lowest hierarchical level stays relatively the same (Baddeley, Thomson and Buchanan, 1975; Haidle, 2010; Mathy and Feldman, 2012). Here, it is suggested that all facets of complexity be studied as individual, yet interacting 'agents' of an *emergent* complexity (Heylighen, Cilliers and Gershenson, 2007) which describes the system as a whole.

[13] Functional necessity: complexity which cannot be otherwise avoided. This includes performative functionality such as performative signalling of 'difficulty', 'exclusivity', or 'authenticity' associated with a more complex technique – for example, deliberate 'ornamentation' of the production technique in biodynamic viticulture.

[14] Evidence demonstrates short term memory has limited capacity (Miller, 1956; Cowan, 2001).

This study therefore builds its method from the five-step 'cognigram' method constructed by Haidle (2010, 2014; Lombard and Haidle, 2012; Lombard, Högberg and Haidle, 2019). This method of behavioural coding was selected for the hierarchical potential of its specific form of *chaîne opératoire* approach, which includes several aspect measures of complexity (expanded upon below). A disadvantage of the method, however, is that the cognigram, as its name would suggest, was initially designed to infer past cognition and behaviour from artefacts observed in the present, and the model makes several cognitivist assumptions problematic for a radically embodied and comparative framework which must consider yet supersede cognitive and other inter-species imbalances. Given this conflict, there must be several important diversions from this method in terms of use and interpretation. The MET framework rather than being considered in opposition to such a methodology, should be seen to highlight its potential value as a means of visualising the cognitive system, "by directing attention away from the extraction of mental templates, and onto the situated field of relationships through which sensorimotor knowledge involved in making is built between generations" (Walls, 2015, p3). No behavioural algorithm can be taken in isolation, and each should instead be seen as entangled within the meshwork of other behaviours and material relationships (Ingold, 2010a; Hodder, 2011, 2012). Techniques are one part of this meshwork, co-constructed across generations and constantly re-emergent in action (Walls, 2016).

3.3 Selection of Study Sites

Chimpanzee tool studies have benefitted significantly from the animal cultures debate, with cultural 'panthropology' having become a subject in its own right (Whiten, Horner and Marshall-Pescini, 2003). Long term data is available for multiple sites, with extensive efforts having been made to class, categorise, and compare technical behaviours between sites and with other ape species (Wynn and McGrew, 1989; Whiten *et al.*, 1999, 2001; Sanz and Morgan, 2007; Gruber, Clay and Zuberbühler, 2010; Wynn *et al.*, 2011; Meulman and Van Schaik, 2013). A recent review by

McGrew (2017) lists a total of 120 *Pan troglodytes* field sites with the earliest long-term studies having begun in the 1960s in Tanzania and Uganda.

There were numerous sites which could have been selected to use for the chimpanzee case-study, however, the technological repertoire for Bossou [as reported by Humle (2011)] was chosen on the basis that (1) the chimpanzees are habituated, and clear behavioural descriptions are available for the majority of tool behaviours, (2) nut-cracking is present and customary, (3) the tool-repertoire does not appear functionally specialised [as at Ngogo (hygiene oriented) or Goualougo (extractive foraging oriented)], and (4) the site, like the capuchin and macaque sites, was semi-provisioned and in close proximity to human settlement, which although unideal in the sense that behaviour is likely subject to anthropogenic influence, offers an example of chimpanzee tool use in a similarly semi-wild setting. By selecting a site which is non-specialised and at which nut-cracking is present it is hoped Bossou provides an image more representative of general chimpanzee tool use while maximising the chance of behavioural overlap with the other species. To situate Bossou within the technological constellation of chimpanzee technologies, and for macro-comparison, this study uses the chimpanzee technological repertoires for Taï, Assirik, Goualougo, Lopé, Gombe, Mahale (M and K), and Kibale as reported by Sanz & Morgan (2007).

In contrast, a comprehensive tool use catalogue of the same scale using the same ethographic comparative framework has yet to be published for either *S.libidinosus* or *M.f.aurea* (although see McGrew *et al.*, 2019); tool behaviour being a far more recent discovery in both species. In order to construct the *S.libidinosus* and *M.f.aurea* repertoires, a literature review was conducted of publications reporting novel tool use at the main long-term study sites for each species: Serra da Capivara and Fazenda Boa Vista, for *S.libidinosus,* and Piak Nam Yai and Koram islands, for *M.f.aurea*. A primary site was selected as the repertoire for comparison, however, discussion of material and causal cognition makes use of studies from the non-selected sites where necessary. Key sources are listed in each case study chapter.

The primary choice of capuchin site was simplified by the fact that Serra da Capivara (hereafter SDC) has a substantially larger reported tool repertoire than Fazenda Boa Vista (hereafter FBV), providing greater opportunity for cross species comparison of similar behavioural traits. However, it is recognised that the SDC repertoire may represent an anomaly in terms of the more species-typical pattern of tool expression, for which the FBV repertoire may be a better representative. Factors which may have led to the specific behavioural dynamics at SDC are discussed within the case-study (Chapter 5) and the repertoire of FBV is included in the meta-species comparison (Chapter 7).

As there was little difference in terms of the number, type of tool behaviours present, or the ecologies of the macaque sites, either site could have been used. Piak Nam Yai (hereafter PNY) was selected on the basis that (1) nut cracking is present and customary, and (2) the majority of sources reporting tool use as novel behavioural traits came from this site, whereas the behavioural data from SRY primarily explores the ontogeny of tool using and social learning, and (3) the SRY site is irregularly provisioned and highly subject to a higher level of anthropogenic disturbance (Tan, 2017) - tourist boats with buckets of bananas being an almost daily occurrence during peak season (personal observation). It should be noted on this third point that PNY is also subject to anthropogenic disturbance (Gumert, Hamada and Malaivijitnond, 2013); however, it was considered to be less of an impacting factor in tool behaviour since the macaque population of PNY, although bordering human settlement, remains as yet unhabituated. Lack of habituation was not considered a significant issue given that detailed reports of the tool using behaviour have been recorded through off-shore observation and video recording (e.g. Tan *et al.*, 2015).

3.4 Micro-level Comparison: Technique without context

This section aims to clarify the cognigram method and how it will be used to achieve the objectives of this thesis. The hierarchical levels at which technique will be coded are elaborated

upon below, with the example algorithm, Figure 1 (p58). All behavioural algorithms were diagrammatised using the free-source version of the graphical interface design tool, Figma (www.figma.com, 2019).

3.4.1 Hierarchical Level 1 – Classification of *Focal Complexity*

Each column represents a cognitive part of the technical system of a given tool behaviour, or a system focus. The left-most column signifies the actor and each subsequent column to its right, an environmental object. The *focal complexity* of a technique is taken as its total number of focal columns, including the subject, which together comprise a dynamic cognitive system.

3.4.1.1 Active and passive foci

An important diversion from the original method is in the treatment of foci as active or passive. Recognising that tool use represents a dynamic system in which subject and object/s are mutually constitutive, all foci are considered active, though their degree of influence, and constitution, may change through time. As the algorithm does not represent an active real-time process, there is no need to make the distinction between 'objects' and 'tools'. This is because the algorithm only becomes a 'technique' at its point of completion and as such, there is no need to state that the material changes from 'object' to 'tool' at its point of use. This avoids both implying the subject intends to use the object as a tool, without denying the tools constitutive role in bringing forth that intent, and confusion with subjects simply picking up and then discarding items.

3.4.1.2 Object order relationships

Bridges between columns (as at actions 6, 7 & 8a in Figure 1, p.58) show *object order relationships* (following the system proposed by Fragaszy *et al.,* 2005; see also Visalberghi and Fragaszy, 2012). Spatial relationships can be either static or dynamic. A static spatial relationship is one which does not change over time, whereas a dynamic spatial relationship requires monitoring,

either because use of the tool moves the target item, or because the target item moves of its own accord (in the case of invertebrate/vertebrate prey). Spatial relationships may be either sequential or simultaneous.

As material engagement theory views the direction of agential influence to be mutualistic, bridges reflect the direction of the physical effect (in other words, 'object moves with relation to'). For example, a hammer influences a nail because it affords striking the nail, but the nail also influences the hammer, since it affords striking in a particular manner. However, in the object order relationship and action 'strike', the hammer can be said to 'strike with relation to the nail'.

3.4.1.3 Hierarchical affordance relationships

The identification of subjects "perception of needs" which is included in the original cognigram method will be excluded. Haidle would describe the initial impetus for chimpanzee ant dipping as "recognise feeling of hunger" (2014, p4). This may be true but its inclusion makes impossible inferences into the mind of an animal actor and its mental states. Instead, in order to recognise the mutuality of objects and subject, the initial state of each focus shall be described as either its 'effectivity' (in the case of the subject), or 'complementarities' from which affordances arise through interaction (Turvey, 1992). A diagram of the hierarchical affordance relationships is included for each behaviour (following van Leeuwen, Smitsman and van Leeuwen, 1994, Figure 1, p176). Complementarities and effectivities are represented in the circular blocks at the top of each column and together signify the nodal relationships between objects, incorporating Matsuzawa's (1996) notion of object hierarchy.

3.4.2 Hierarchical Level 2 – Classification of *Behavioural Complexity*

As in an ethogram, the method is described as the parsimonious minimal sequence of common-denominator, or 'critical' actions required to complete a task, not including individual

stylistic differences, descriptions of manual laterality or interruptions to the task-specific behaviour (such as interaction with a conspecific or scanning for predators). In this sense, the operational sequences visualised represent the general method, as a distributed process of problem-solving between the actor and the environment. Pure epistemic actions are included in the diagrammatised algorithms to accord with their thick descriptions where relevant. However, to account for differences in the reporting of NHP explorative behaviours between species and sites, and to aid fair comparison with technical methods extrapolated from archaeological artefacts in isolation of a behavioural model, pure epistemic actions are excluded from calculations of operational sequence length and behavioural complexity unless they form the last action of an algorithm – for instance, in the example algorithm (Figure **1** p.58, action 9 is not counted, though action 10 is.

3.4.2.1 Action Unit Size

The original cognigram method defines its minimal units as "all individual action steps that must be taken to solve the different [sub-routines] and satisfy the basic [algorithm]" (Lombard and Haidle, 2012, p.240). As this remains open to subjective interpretation, the minimum unit having previously been interpreted as minutely as individual motor-actions (Byrne and Byrne, 1993), here the minimum unit for action is taken as: any *unbroken phase of system focus*. For instance, as in the example Figure, "grip hammer" is taken to be behaviourally distinct from "strike with hammer" as the two cannot be conflated without failing to account for the change of direction in object influences between the plank, the nail and the hammer, and therefore the change in system focus.

3.4.2.2 Placement of action-units

Action-units appear in the respective column of the object physically coupled with or directly manipulated by the subject. For example, in Figure 1 (p.58) and Table 1 (p.59), action 1 - "select nail" - belongs to the column representing the nail; action 6 – "strike the nail with the hammer" - belongs

to the column representing the hammer (active coupling), the column representing nail (active focus of the subject-hammer coupling), and the column representing the plank (active focus of the subject-hammer-nail coupling). Actions are displayed in the order in which they are reported to most likely occur, moving from top to bottom. The *behavioural complexity* is taken as the minimal number of critical action units required to complete a given method of achieving the super-ordinate affordance.

3.4.2.3 Search phases

To avoid attributing similar mental states to non-humans, discovery of objects will be described as 'discover/select/or detach item' unless an active and directed search behaviour (e.g. skilled foraging, Johnson and Bock, 2004) is reported in the literature. Similarly, "selection" should not imply either material 'selectivity', rational choice, or causal reasoning on the part of the subject, unless it is described as so in the accompanying thick description.

3.4.3 Hierarchical Level 3 – Classification of *Sequence Complexity*

Actions are grouped into sub-routines, or 'phases', based on shared sub-goals or problems. Break-points occur between phases where either a sub-goal has been achieved and there is a shift of focus, or where the next action is not predictable and the actor may or may not continue on to the next phase, giving insight into the ways in which material interaction acts as a prop for attention. For example, in Figure 1 (p.58) the overall goal, or super-ordinate affordance is to be able to hammer a nail into a plank of wood. This can be broken down into the sub-goals: acquire nail (Phase II: Component acquisition), acquire hammer (Phase III: Tool acquisition) and use the hammer (Phase IV: Active tool use). It is again noted that the goal is held not by the individual, but is brought forth through the dynamic interplay of focal aspects within the system.

3.4.4 Hierarchical Level 4 – Classification of *Modules* and *Iterations*

Iterations within the sequence are recorded as mid-phase breaks. These are points at which the actor may repeat, return, or skip ahead to a section of the algorithm. The natural repetition of sub and sub-sub-routines within the overall sequence demonstrates behavioural flexibility and can provide insight into how the actor may transfer technical knowledge learned from the "constellation" of technologies and technological knowledge present at a group-level, into individual techniques via the situational affording of action (Dougherty and Keller, 1982; Keller and Keller, 1991; also cited by Sinclair, 2014).

Illustrating this same concept on a hierarchical level above sequence complexity, modularity can be used to describe *groups of phases* which appear (without significant modification) repeatedly, or in the operational sequence of more than one variant. This includes groups of phases which act towards a common affordance that is not the super-ordinate affordance of a composite variant/sequence of chained variants, including secondary tool use (see Section 3.5.4.2 Associative tool use). *Modular complexity* is calculated as the total number of modules comprising a given variant. High modular complexity indicates increased potential for cross-context skill transfer, more complex technological and conceptual modularization, and an entangling of technical/material networks as tool use becomes distributed through time and beyond individual effort (Ingold, 2010a; Hodder, 2011, 2012).

Figure 1 Example algorithm and diagram showing the hierarchical affordance relationships involved in a Handyperson stabilising a wooden plank by means of a hammer and nail

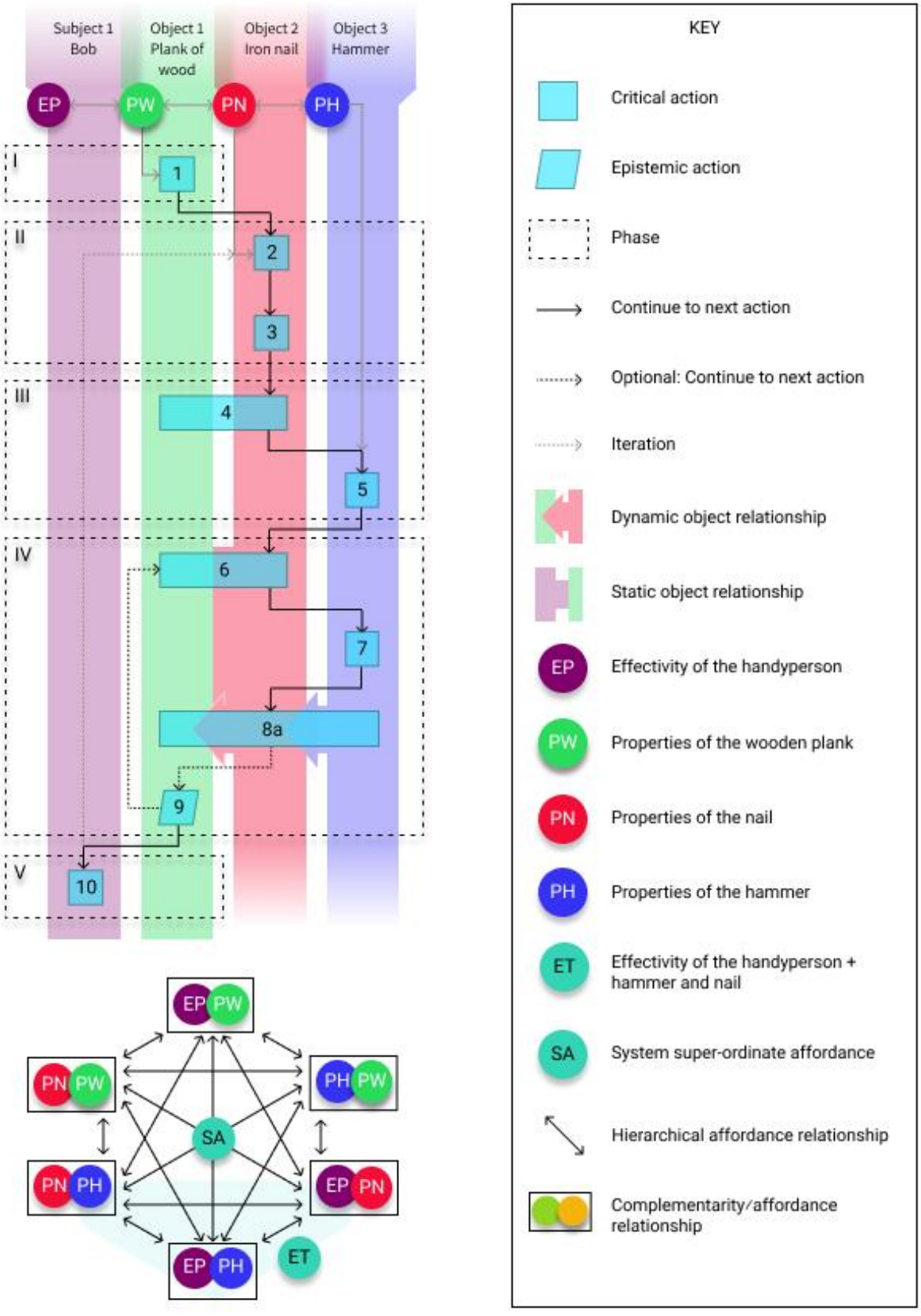


Table 1 Behavioural key to the example algorithm

Phase I: Arrival at the site

1. Discover a loose plank

Phase II: Tool acquisition (1)

2. Search for a nail
3. Select a nail
4. *Optional: Pick up and transport the nail to the plank*

Phase III: Tool acquisition (2)

5. Select the hammer from a worn tool-belt

Phase IV: Active tool use

6. Place the nail relative to the loose plank
7. Grip the hammer
8. (a) Hold the nail in place with one hand

   (b) With the free hand, strike the nail into the wooden plank with the hammer, repeatedly
9. *Epistemic: Wiggle the nail*

Iteration: If the nail remains loose, repeat from 6

Phase V: Completion

10. *Epistemic: Admire the fixed plank*

Iteration: If the super-ordinate affordance remains relevant, repeat from 2

Table 2 Complexity scoring for the example algorithm

Complexity	Coded as	Score
Focal	Total number of focal columns	4
Behavioural	Total number of critical actions (including all optional actions and the final action if epistemic)	9
Sequence	Total number of phases	5
Modular	Total number of modules	1
Technical	Total number of modifications applied to tool objects	0

3.5 Macro-level Context: Criteria for inclusion into repertoires and classification of tool variants

3.5.1 Things in the mind's mesh

Building context, repertoire *richness* is taken as the total number of discrete technical variants present within a population. To provide an arbitrary limit to the behavioural comparison, this chapter adopts St Amant & Horton's (2008, p1203) definition of tool use as "the exertion of control over a freely manipulable external object (the tool) with the goal of (1) altering the physical properties of another object, substance, surface or medium (the target, which may be the tool user or another organism) via a dynamic mechanical interaction, or (2) mediating the flow of information between the tool user and the environment or other organisms in the environment". Following other comparative studies, objects used in play are not included into the repertoire unless they are used to solicit a reliable response. Nest-building behaviours are also excluded on the basis nest-building is not generally considered to be tool use (Sanz and Morgan, 2007; Meulman and Van Schaik, 2013). Accidental, anecdotal and idiosyncratic technical variants are included in order to represent the flexible and innovative nature of tool use (St Amant and Horton, 2008; Stout and

Chaminade, 2009). Technical behaviours were only included if they were part of the natural tool using repertoire of a site, and not if they were exhibited only when artificially or experimentally induced.

Where possible, and with the aforementioned limits, technical variants were coded in accordance with the ethographic descriptions catalogued by Whiten *et al.* (Whiten *et al.*, 1999, 2001), and addended by Sanz & Morgan (2007). However, in a departure from Whiten *et al.* (1999, 2001), following Sanz & Morgan (2007), variants were not discriminated on the basis of material selectivity. Thus, technologies such as 'nut-cracking', which following Whiten *et al.,* (1999, 2001) would be classed as four discrete variants (wood hammer, wood anvil; wood hammer, stone anvil, etc.), are, under this classificatory system, counted as only one variant irrespective of the possible combinations of material aspects – these are instead given in the thick description accompanying each algorithm, recognising that the materiality of tool use is an important marker aspect in disentangling the physical and social factors affecting primate affordance recognition, for example, when material selectivity reflects a conformity to cultural norms (Luncz, Mundry and Boesch, 2012; Luncz and Boesch, 2014). Whiten *et al.* (1999) likely made the distinction for this very reason, to identify putatively 'cultural' material preferences in chimpanzee tool use; but in so doing, the authors create a system which presupposes that for other variants, material selectivity is not cultural, despite evidence to the contrary (Pascual-Garrido, 2019). No methodological distinction was therefore made to avoid both the artificial inflation of variant richness, and an over-emphasis on the importance of particular tool types.

Similarly, technologies for which more than one technique is reported (e.g. 'leaf fold', 'leaf sponge', 'leaf spoon') are counted only once *unless* the alternative technique/s result in the performance of an alternative *functional mode* (see Section 3.5.3.2 Functional mode), for example, the exertion of a cutting force in place of a pounding force (e.g. 'nut-crack' versus 'hatchet').

Finally, composite modular sequences of otherwise independent variants are classed as novel variants only when the sub-modules act towards a super-ordinate affordance which targets the same focal aspect. For example, in Chapter 5, the SDC variants 'pound open' and 'expel' may be chained to form the novel composite variant 'open and probe' as both sub modules act towards the breaking down of the same encasing matrix. In contrast, although the SDC variants 'dig' and 'nut crack' (Chapter 5, Section 5.2.1) may often occur in sequence, their composite is not classed as a novel variant since each sub module acts towards the breaking down of a separate encasing matrix, the former targeting an encasing substrate, and the latter, an encasing shell. This distinction only relates to variant classification and should not be confused with categories of tool 'association', which are expanded upon further in Section 3.5.4.2 Associative tool use on p71.

Seven additional variants were identified which did not sufficiently match any of the behavioural descriptions provided by either Whiten *et al.* (1999, 2001) or Sanz & Morgan (2007); their descriptions are as follows (the full species-by-species catalogue is shown in Appendix 1, Tables 1-3):

'Axe-hammer': use of the point of a small stone tool in a pick-like motion, to chip at and/or crack sessile prey attached to a large or fixed substrate (Gumert, Kluck and Malaivijitnond, 2009).

'Hatchet': use of a flat stone held perpendicular to the ground to pound open and/or "cut dry branches… cactuses… or tubers" (Mannu and Ottoni, 2009, p245). Mannu & Ottoni (*ibid*) describe the action pattern as similar to that for the behavioural variant 'nut-crack'.

'Palm-sap collect': the sequential performance of 'pestle-pound' and 'leaf sponge' in which a palm petiole is used to pound and deepen a hole in the apical meristem of palm tree, followed by the insertion of vegetation, chewed and used to collect fluid from the hole (Yamakoshi and Sugiyama, 1995).

‘Pound open’: use of a pounding stone tool to “break open dead wood, conglomerate rock or cement, or to detach wooden sticks, or the bark of living tree trunks (presumably in search of invertebrates or other edible items” (Mannu & Ottoni, 2009, p245).

‘Stone pound’: purposive percussion of an immobile or embedded rock with a hammer stone (“stone banging”, Moura, 2006; Mannu and Ottoni, 2009).

‘Self-poke’: rubbing, poking, or scratching of the self with the distal end of a thin plant or stick tool, used for grooming or for self-stimulation (adapted from the functional mode “scratch”, Sanz & Morgan, 2007, p423).

‘Toothpick’: “precise placement of one end of a thin plant tool into the mouth, held in position against a tooth or the gum, followed by rapid side-by-side movement of the tool and its inspection once withdrawn from the mouth” (Haslam and Falótico, 2015).

Although each catalogue must be considered specific to its species, and site, representing the full technical constellation of skilled knowledge and abilities within which a variant is developmentally realised; in order to aid macro-comparison between species, functionally similar variants retain the same names. For example, though ‘nut-crack’ appears in all species’ repertoires, being functionally similar, the three variants should not be considered interchangeable. Species typical behaviour is elaborated upon in the thick description of each variant.

3.5.2 Social distribution

To explore the populational distribution of material cognition, variants are coded by their *populational frequency*. Coding for this aspect describes the degree of behavioural canalization into the group technological repertoire and follows the criteria laid out by Whiten *et al*. (1999), by which populational frequency is classified as customary (C), habitual (H), idiosyncratic (I), absent (O), or unknown (?) – customary and habitual tools are classed as ‘frequent’, and idiosyncratic or absent as

'infrequent'. It is noted that in other repertoire comparisons, there is often a distinction made between genetically derived and culturally salient behaviours (Whiten *et al.*, 1999, 2001; Krützen, Willems and Van Schaik, 2011; Meulman and Van Schaik, 2013). Since this seems a somewhat unnecessarily dichotomous interpretation of the nature of material culture, and Culture large, that is at odds with the more holistic approach of MET, no such distinction is made. For this reason, the coding category 'ecological explanation' (Whiten *et al.,* 2001, p1488) is not included. Instead, ecological and other factors which might influence the perception and relative relevance of tool affordances, including sex bias, mode of social learning, and the potential for behavioural conformity, are discussed in the thick descriptions.

3.5.3 Modes of *Thinging*

To explore the functional orientation of material engagement in each species technology, that is the kind of technical affordances to which a species is most susceptible to solicitation, variants are further classified in terms of their functional context, mode, and causal function.

3.5.3.1 Functional context

Functional context describes the nature of the problem a given variant responds to, with problems broadly grouped by subsistence, hygiene, or social problems. Tools in which doubt remains over function, or which did not fit into subsistence, hygiene, or social categories, are classified as other. Subsistence problems are subdivided into foraging and extractive foraging problems; the latter defined as problems which involve the extraction of an edible item from an inedible matrix (Meulman & van Schaik, 2013), and the former defined as all other, non-extractive subsistence problems. This definition of 'extractive' foraging differs subtly from some used by other authors, notably those which define extraction as tool assisted access to otherwise manually inaccessible resources (e.g. Sanz & Morgan, 2007, p43). As in Meulman & van Schaik's (2013) method, this is in order to avoid the inclusion of all tools which extend the user's reach; distinguishing between

behaviour such as the use of a branch to draw another otherwise out of reach branch closer, and more intuitively *extractive* behaviours such as use of a twig to pull ants from a nest. This distinction is most important in cases where the inedible matrix visibly hides the resource, the extraction of these resources presenting a potentially more cognitively challenging problem (Boesch, 2013). It should also be noted that here, extractive foraging is not considered equal to destructive foraging, which typically involves the partial or complete destruction of the inedible matrix (Terborgh, 1983). The distinction between extractive and destructive foraging is made to avoid excluding tools which in no way result in breakdown of the inedible matrix, for example, probing of a rock crevice with a stick.

3.5.3.2 Functional mode

To assess *functional mode,* tool variants are further compiled into tool-activity categories adapted from Shumaker *et al*. (2011, Table 1.1 on p13-14), modified here in Table 3 (p.66). Functional mode describes how a function is achieved; the action the tool affords and the intent it draws forth. For example, for the functional mode 'cut' (e.g. in use of a saw to cut wood), intent 'to incise' is brought forth in the action of drawing a sharp-edged tool across a surface. The tool's affordance is its 'draw-ability' but this is only relevant in the context of the particular tool task.

Several variants were coded with a primary and secondary functional mode, for instance composite variants involving the sequential use of more than one tool, and compound tools. These multiple functional modes were not factored into calculations of overall repertoire richness, in which variants were counted only once irrespective of function; however, they were counted independently in calculations of repertoire diversity, made using the method of 'SHE' analysis outlined by Shott (2010).

Table 3 Definitions of 15 functional modes of tool-use, adapted from Shumaker et al. (2011, table 1.1, p14)

Functional Mode	Description
Throw	Propelling an object through open space. Force is transferred at a distance by means of the user's own energy
Drag	Pull an object while walking or running; the object remains in contact with the substrate
Wave	Move an unattached object repeatedly up and down or side to side
Club	Agonistically strike another organism with an object.
Pound, Hammer	Forcefully strike an object or prey item with a second relatively hard object (the tool)
Pry, Apply Leverage	Apply force to an object, using a fulcrum
Dig	Excavate the substrate
Jab, Penetrate	Use the distal end of the object to push another object or organism away, or to forcefully puncture or perforate a surface or inanimate object.
Reach	Use an object to touch or retrieve another object, either when the user's prehensive structures are too short, or to avoid touching the target object. The tool is held throughout use.
Insert and Probe	As in Reach, but when the target object is embedded in a hole or behind a restricted opening
Scratch, Rub	Move an object across a bodily surface, often repeatedly, applying pressure.
Absorb	Soak up and contain fluid
Wipe	Displace and remove fluid by application of force
Affix, Apply, Drape	Attach a fluid or an object to the body, a surface, or another organism without adhesive
Bait, Entice	Manipulate an object so as to elicit a reliable response from another

Table 4 Definitions of 7 causal functions, adapted from Shumaker et al. (2011, table 1.1, p13-14)

Causal function	How does the tool alter the user's effectivity?
Extension of the users reach	Use of the tool object results in a physical and perceptual extension of the users reach through peri and/or extra-personal space. The tool may be used to bring objects closer and to keep objects at distance.
Amplification of the user's mechanical force	Use of the tool object results in either a transformation (usually an increase) of the mechanical force of the user, and the physical impact which can be applied to a target.
Creation or augmentation of a signal value	Use of the tool object enhances the values of social signals or displays made by the user. This may include the ability to perform/the creation of novel signals and displays.
Effective control of a liquid or of small solids	Use of the tool object enables more effective control of a liquid substance, or of small solids (e.g. fine sand)[15].
Concealment	Use of the tool object results in effective camouflaging of the user against their environment from either predators, prey or conspecific others.
Enhancement of bodily comfort	Use of the tool alters the user's affective potential. This may include reduction in the perception of pain, an increase in the perception of pleasure, or the restoration of a neutral perceptual state of well-being.
Representation of reality	Use of the tool results in the direct creation of a material sign.

[15] McGrew (2013, supplementary material) includes effective management of "soft" solids.

3.5.3.3 Causal function

Causal function describes the constitutional role of the tool in the new 'effectivity' arising from the dynamic coupling of [user + tool] in the context of tool use. Returning to the cutting tool example, its causal function is to amplify the mechanical force of its user; in this case producing a cutting or shearing force. It is through the causal function of the cutting tool and its 'draw-ability' that the super-ordinate affordance – the target item's 'cut-ability' – becomes realisable. Shumaker *et al.* (2011, Table 1.1 p13-14) outline 7 'causal functions' of tool use (here *causal functions*) which are shown in a modified form below, in Table 4 (p.67). As for functional mode, variants were coded for primary and secondary causal functions; again, to calculate repertoire richness, variants with more than one causal function were counted only once, but independently in calculations of repertoire diversity.

3.5.4 Modes of creative *thinging*

A key aspect differentiating human and NHP tool use is the former's capacity for reflexive innovation and cumulative culture (Heyes, 1993; Tomasello, 1994; Boyd and Richerson, 1995; Whiten, Horner and Marshall-Pescini, 2003; Dean *et al.*, 2014; though see Schofield *et al.*, 2018); specifically, the persistent ability to combine "cultural knowledge with beneficial modifications" (Dean *et al.*, 2014, p284), otherwise known as the 'ratchet effect' (Tomasello, 1994) - or, as Malafouris writes: "to scaffold the ecology of our minds, shape the boundaries of our thinking and *form new ways to engage* and make sense of the world" (2014, p140). To explore creative material engagement in tool use and the inventiveness of different species' technologies, tools are considered as modifiable objects: objects which may be crafted, and which may be associate

Table 5 Definitions of 6 modes of tool manufacturing, adapted from Shumaker et al. (2011, Table 1.1 p14) and Oswalt (1976)

Classification		Description
Reshaping	Detachment	Detachment of a raw material to form a tool, from its fixed connection to a substrate or to a larger object. Includes: detachment of grass stems, dislodging of inorganic material.
	Reduction	Reduction of the tool's over all mass to produce a more functional form. Includes: clipping of the tool in order to shorten length, removal of leaves or flakes to reveal a core tool form, and uprooting or detachment of the tool from an attached substrate/medium.
	Replication	Production of at least two functionally similar structures as a single functional part of a tool form.
Association	Linkage	Juxta-positioning of two physically distinct forms which act in direct combination. In this manufacturing step, the bringing together of two objects creates a novel functional relationship but not a novel tool form.
	Conjunction	The conjoining of physically separate functional aspects into a singular compound form. In this manufacturing step, the conjoining of two objects creates a novel tool form, but not necessarily a novel function.

Table 6 Definitions of 4 kinds of associative tool use adapted from Shumaker et al. (2011, Table 1.2, p19).

Association	Description
Tool Set	Two or more tools are used sequentially, usually each in a different mode, to achieve a single outcome. The outcome could not be achieved unless all tools used are done so in sequence. This includes tools used as part of a composite variant and those used in the sequential performance of two or more independent variants.[16]
Compound[17] Tool	Two or more tools are used simultaneously, usually each in a different mode, to achieve a single outcome
Meta-tool	A tool used simultaneously with one or more other tools to increase the effectivity of those other tools, with the former working directly on the latter during the latter's use. Meta-tools are a subset of compound tools.
Secondary Tool	Tools which are used to acquire, make or structurally modify another tool, but which are not used in the active tool use phase of a given algorithm[18]. Manufacture of secondary tools forms a separate modular variant.

[16] Original differs subtly from McGrew's (1993, p159) definition of tool set, which entails a higher degree of inclusiveness. Modified accordingly.
[17] Original outline uses the term 'composite'. Modified to avoid confusion with composite variants.
[18] Original defines secondary tool use as manufacture and structural modification of another tool, but not acquisition without modification.

3.5.4.1 Tool crafting and *technical complexity*

All variants were scored for *technical complexity* - here defined as the total number of action units describing the manufacturing of all primary tools (following Perreault *et al.*, 2013). This methodology was adopted in favour of Oswalt's (1976) 'techno-unit' system in the hopes it might provide a resolution more suited to NHP tool use (for primate/human technical comparisons using the techno-unit system, see McGrew, 1987; Westergaard, 1995). *Tool manufacture* is defined as by Schumaker *et al.,* as "any *structural* modification of an object or an existing tool so that the object serves, or serves more effectively, as a tool" (2011, p11 emphasis included in original). Each manufacturing action is counted only once, therefore reflexive modifications to the tool, such as adjusting of tool length after-the-fact, are not counted towards technical complexity unless it is the first occurrence.

To further aid comparisons between species, manufacturing is also coded in accordance with the classificatory system outlined below in Table 5 (p.69), which combines Oswalt's (1976) principles of artefact reduction with Shumaker *et al.*'s (2011) modes of tool making. Detachment *is* included as a manufacturing mode, however, in the algorithms, as detailed in Section 3.4.2.3 Search phases, the act of detachment is for many variants taken as the act of material selection. This means detachment does not appear as its own action in the operational sequence, though the other manufacturing behaviours do.

3.5.4.2 Associative tool use

Shumaker *et al.* (2011, Table 1.2, p. 19) outline 6 forms of associative tool use ("tools used in any combination to achieve an outcome", *ibid*). The forms relevant to this thesis are outlined in, Table 6 (p.70) below. The category "sequential", which Shumaker *et al.* (2011, Table 1.2, p19) define

as tools used to acquire other tools was excluded on the grounds that the name is confusing ('sequential' also appears in the definition of 'set' in Table 6, p.70), and that the splitting from 'secondary' tool use seems unnecessary. The categorical definition for 'secondary' tool use was modified to accommodate this change. In agreement with McGrew (2013, supplementary material, p6), the constraint that tools forming a compound tool not be used to modify one another is dropped as over-restrictive.

3.6 Means and degrees of constitution

3.6.1 Thick descriptions of causal reasoning

One means of observing how material shapes cognition is in the ways in which it constitutes causal cognition. This section uses the implications of MET theory outlined in Chapter 2 to re-develop Lombard & Gärdenfors' (2017; Gärdenfors and Lombard, 2018) seven-stage evolutionary model of causal reasoning from an internalist framework to one recognising the primacy of material interaction. The seven grades expand Woodward's (2011) three-stage model of causal learning, and are ordered based on their presumed level of detachment from egocentric learning (some grades being parallel to each other). Hypothetically, the first level is the simplest, the seventh, the most developmentally complex – which, in this regard, is considered to mean *sapient*. A list of behavioural proxies for each grade is given in Table 7 (p.80).

3.6.1.1 Grade 1 – Individual causal reasoning

The first, and most basic, level of causal reasoning remains largely as formulated by Lombard & Gärdenfors (2017, p3); as an individual's understanding of the link between their actions and the causal effects of those actions through direct perception. In other words, individuals experience their own agency as they act. Direct material interactions (i.e. without a tool intermediary) are

inherently epistemic, and through proprioceptive and manipulative interactions with objects, individuals are able to learn about object affordances.

Individuals with grade 1 causal cognition are able to perceive the super-ordinate affordances of some tool objects, but are as likely to be solicited by irrelevant tool affordances as they are relevant ones. For example, an individual could perceive that a golf club affords hitting a golf ball off a tee, but that individual would be as likely to strike the ball by the handle as by the club-head. Thus, individuals are capable of learning and exploiting tool using affordances, but success is a matter of trial-and-error learning. Grade 1 tool users develop inflexible techniques and are unable to efficiently adjust to the changing parameters of the tool task.

3.6.1.2 Grade 2 – Cued dyadic-causal reasoning

The second grade also remains largely unchanged; with individuals at this level able to directly perceive the causality of other's actions – Lombard & Gärdenfors (Lombard and Gärdenfors, 2017) suggest through mirror-neuron activation. Combining phenomenological notions of intentionality *in action* (Merleau-Ponty, 1962; Husserl, 1931/2012) with interactive and enactive cognitive theory (for a review of IR social cognition, see Gallagher, 2015); grade 2 can be understood as an individual's ability to experience the agency manifest in conspecific action. From an MET perspective, information about object affordances is emergent in observed conspecific material interactions. As with grade 1, individuals are able to perceive the super-ordinate affordances of some tool objects, but depending on the level of their observation of and familiarity with the behavioural model, are as likely to be solicited by irrelevant tool affordances as they are relevant ones during the tool using process (e.g. Froese and Leavens, 2014; Froese, 2015). For instance, an individual unfamiliar with chopstick use might observe from others use that chopsticks are for eating with, but when attempting to use them themselves, apply inappropriate technique (say, skewering their food) or use them for an inappropriate food medium (say, soup). Individuals are capable of

learning tool using affordances, including the critical actions of a tool method, through observation alone. However, success remains a matter of trial-and-error learning since, like Grade 1, Grade 2 tool users develop inflexible techniques and are unable to efficiently adjust to the changing parameters of the tool task.

3.6.1.3 Grade 3 – Conspecific mindreading

In its original formulation, grade 3 describes the ability to infer the mental states of others by observing their actions. Although for the observer, the cause of the action is not directly perceived, knowledge of inner states is used as a hidden variable for cause; for example, an individual recognises that the aggressive actions of another could be motivated by hunger, tiredness, or anger. Lombard & Gärdenfors also include self-mindreading or self-awareness in this grade, which, they argue, entails the ability to perform mental time travel, as well as basic episodic and working memory (2017, p3-4).

However, in a MET framework, in which mental states are corporeal and transparent as opposed to incorporeal and opaque, and in which intent is in action as opposed to in the brain; there is no difference between this level and the newly formulated grades 1 and 2. Therefore, to reframe this grade in a manner useful to this thesis, here the 'mind' subject to 'reading' at grade 3, is the organism + tool system. Taking extended, embodied and enactive concepts of tool use as a distributed, goal-oriented version of the agential process, in which the material tool is a constitutive part of a dynamic system of agency (Ingold, 2000; Baber, Parekh and Cengiz, 2014), grade 3 conspecific mind-reading is re-interpreted as an individual's ability to perceive of another's tool using as an extension of their agency.

In this sense, others' material interactions involving tools not only provide information about tools' affordances as environmental objects (grade 2 causal cognition), but also about tools' relevant

affordances in the context of super-ordinate affordances of tool using tasks (i.e. tools' functional modes and causal functions). For instance, not only does an individual discern from another's use of a pepper pot, that the pot affords adding pepper to their meal; they are also able to discern the nested affordances, e.g. that the lid of the pot affords removal prior to the top of the pepper pot affording twisting left. This ability would enable high-fidelity learning of technical methods as a base-line from which to develop efficient technique; however, as in grade 2, efficiency in the degree and focus of imitation would still be subject to individual familiarity with social conventions. The critical actions of tool using tasks and how to achieve them would be emergent in observation of others tool using, but the reflexive symbiosis of tool and user described in Ihde's technics (1979) would still require individual practice and long-term engagement to achieve.

The ability to achieve symbiosis of tool and user, through extended engagement and the development of skill, is reliant upon grade 3 self-mind reading; i.e. the ability to perceive of the tool as an agential extension of the self. Material interaction provides information about the relevance of tool functional affordances (functional modes) in the context of the super-ordinate affordances of tool using tasks. As skill increases, the phenomenological perceptual barrier between the agency of the individual and the agency of the tool object begins to dissolve (at this level, in peri-personal space). Through long-term engagement, development of skill enables a fluidity of action and perception *through* the tool during the tool using process. As a result, technique becomes flexible and the user is able to quickly adjust to changing parameters of the tool task as they occur.

With respect to mental time travel, the skilled intentionality framework (Rietveld and Kiverstein, 2014; Kiverstein and Rietveld, 2015; van Dijk and Rietveld, 2017; Bruineberg, Chemero and Rietveld, 2019) allows us to consider 'higher cognition' and 'imagination' as forms of embodied anticipation – forms enabled by the skills and regularities of a socio-material environment associated with a particular 'form of life' (see Section 2.3). In this sense, the skilled ability to recognise functional modality enables modularisation of the behavioural sequence such that the curation and

manufacture of tools may be performed in embodied anticipation of the situational affording of their use.

3.6.1.4 Grade 4 – Detached dyadic-causal reasoning

At grade 4, 'detached dyadic-causal reasoning', an individual has the capacity to infer past agency from perceivable cues in the present. For example, the removal of a strip of bark from a tree leaves a long-lasting visible scar which may be perceived long after its cause. Understanding what caused the scar and the motive behind it, Lombard & Gardenfors (2017, p4-5) argue, relies on the ability to simultaneously represent both the current perceptual state and the imagination of an individual removing the bark.

A non-representational account of the same kind of causal cognition is given by Bruineberg, Chemero, and Rietveld (2019) in their concept of 'general ecological information'; defined as "any [perceived] regularity in the ecological niche between aspects of the environment, *x* and *y*, such that the occurrence of aspect *x* makes the occurrence of aspect *y* likely" (p5237). For example, because, in experience, it is perceived that fire *tends* to occur with smoke - there is no smoke without fire; smoke is a causal proxy for fire even when fire itself is not sensorially present.

Considering tool use we can expand upon this using the concept of canonical affordances (*sensu* Costall, 2012, 2014), which, like general ecological information, considers that the wider social framework within which individuals develop influences their perception of, and ability to be solicited by, affordances. Because we do not simply arrive into a world of objects and affordances, but are in effect introduced to them (Leont'ev, 1981; also cited by Costall, 1995); through long-term interaction, particular objects come to afford particular normative uses – e.g. a mug is *for* drinking from – which are discovered through the process of enskilment (Ingold, 2000).

Objects associated with canonical affordances are enactive signs (Malafouris, 2013b); material objects which embody their affordances whether or not those affordances are, or have ever been, solicited (Borgo and Vieu, 2006, 2009; though see Kassel, 2010). In this sense, long-term exposure to and engagement in material interactions such as tool using may produce enactive signs, perhaps in the form of the tool object or its debris. Interaction with these material signs produces information about tool functional and super-ordinate affordances, with the past intent implicit in the object. Tool use indicative of this level of causal cognition is likely to take place immediately upon arrival at a site, and with few to no proprioceptive behaviours prior to use.

3.6.1.5 Grade 5 - Non-conspecific mindreading

This grade follows the same logic of grade 3 (Section 3.6.1.3, p.74), but in this case the observed other is a non-conspecific. At grade 5, individuals demonstrate an ability to perceive of non-conspecifics' tool use as extensions of the observed non-conspecifics' agencies. As the tool is a perceived as part of the intentional agent, non-conspecific's material interactions not only provide information about tool affordances as environmental objects, but also tool affordances in the context of the super-ordinate affordances of tool using tasks (i.e. tool functional modes and causal functions). This should enable transmission of technological behaviours from observations of non-conspecific others. As in grade 3, the critical actions of tool tasks, and even how to achieve them, would be emergent in the observation of others' tool using; but a reflexive symbiosis of tool and user would still require individual practice and long-term engagement to achieve.

It might be questioned whether it is worth separating conspecific and non-conspecific modes of causal cognition into distinct categories. On the one hand, since there is the potential for greater difference in the underlying bio-mechanical systems of individuals of different species than between those of the same species, mirror neuron activation during observations of non-conspecifics is less likely and may require extended periods of learning through observation and

association - hence, the attribution of agency to the non-conspecific other and any tool they wield should be considered more developmentally complex. On the other, heterospecific social learning is not uncommon, the information produced by non-conspecifics in some cases being more ecologically adaptive than that produced by members of the same species (for a review of heterospecific social learning see Avarguès-Weber, Dawson and Chittka, 2013). While much of this behavioural transmission is likely to involve associative learning and emulative rather than imitative processes (Tomasello, 1996; Penn and Povinelli, 2007; Huber *et al.*, 2009), evidence shows prolonged species association, for example in the human domestication of dogs, drives the development of specialised sensory systems leading to a convergence of communicatory skills, including sensitivity to hetero-species perceptual capacities and affective states (Call *et al.*, 2003; Riedel *et al.*, 2008; Udell, Dorey and Wynne, 2011; Turcsán *et al.*, 2015), leading to the perception of non-conspecific behaviour as involving conspecific-like agency.[19] In recognition of their potentially differing (though probably similar) processes of development, the analytical distinction between grades 3 and 5 causal cognition is retained.

3.6.1.6 Grade 6 – Inanimate causal reasoning

Grade 6, inanimate causal reasoning, involves ascription of causal roles to inanimate objects even where the causes of change are not perceived. Causation at this level is understood in terms of force dynamics, in particular force transmission as an extension of the agential self (Wolff, 2007; Povinelli, 2010; also cited by Gärdenfors and Lombard, 2018, p3).[20] Unlike the previous grades of causal cognition, no animate agent needs to perform an action to produce the force behind a perceived cause. However, for an individual to discover information about object affordances and tool super-ordinate affordances still requires them to engage in material interaction. Here,

[19] Prolonged species association includes phylogenetic and/or ontogenetic developmental associations.
[20] 'Force' is as broadly meant as in the original (see Gardenfors & Lombard, 2018, p4), consistent with 'effectivity' (*sensu* Turvey and Shaw, 1979; Turvey, 1992) or 'power' (*sensu* Witherington, 2019).

information describing the functional affordances of forces produced by inanimate objects is emergent in the application of counterforce; with individuals experiencing inanimate objects as agential in relation to their own agency.

By extrapolation, this includes object agencies which act *with* the agential self, with the former experienced as an extension of the latter even through extra-personal space - as a kind of agential momentum. Since individuals with causal reasoning ability up to grade 5 are only able to perceive tools as extensions of the self through peri-personal, but not extra-personal space, they are be able to solicit the super-ordinate affordances of projectile tools, but would be extremely limited in their degree of successful use, relying predominantly on trial and error learning. Striking of an aimed target would take multiple attempts and would be extremely inefficient while striking of a moving target with any degree of reliability would be almost impossible. In contrast, at Grade 6, material interaction provides information not only about the super-ordinate affordance of projectile tasks, but also about relevant tool affordances in the context of those tasks - for example, the proper technique to compensate for a projectile's heft, over a given distance. With practice, reliable striking of an aimed target would be possible even in more difficult scenarios like hunting of mobile prey (Gärdenfors and Lombard, 2018).

3.6.1.7 Grade 7 – Causal network understanding

The most developmentally complex grade of causal cognition, grade 7 'causal network understanding', describes the kind of technical reasoning typically thought to be 'uniquely' human, in which individuals are able to think *about* not just *through* objects. This level relies on 'higher cognitive' capabilities and abstract inferential abilities, including the ability to relate domain-specific causal node sets to constitute inter-domain causal networks; "aspects of all the previous [grades of causal cognition] can be integrated and/or mapped onto each-other in never-ending patterns of recursion and complexity" (Lombard and Gärdenfors, 2017, p6). At this level individuals are able to

Table 7 Behavioural proxies for seven grades of causal cognition

Grade of causal reasoning		Evident in
1	Individual	Explorative, purely epistemic actions. Inability to respond effectively to changing parameters in the tool task. Inflexible, 'unintelligent' tool use.
2	Cued dyadic	Low fidelity transmission of method. Populational distribution of technical variants. Education of attention.
3	Self or conspecific mindreading	Fewer purely epistemic actions made by skilled tool users. Effective response to the changing parameters of the tool task, for example, modulation of force during tool use. Material selectivity, matching appropriate tool materials to a task. High-fidelity transmission of method. Populational distribution of technical variants. Teaching through active attention direction.
4	Detached dyadic	Immediate and canonical tool reuse without prior proprioceptive interactions with the tool, or observation of the previous tool user.
5	Non-conspecific mindreading	Transmission of technical behaviours between species.
6	Inanimate	Tool use in extra-personal space, e.g. projectile use. Tool manufacture in which functional aspects are connected through a binding material, e.g. hafted spears.
7	Causal network understanding	Tools with stored forces, e.g. traps, bow and arrow sets. Cumulative ratcheting of technologies. Complex tool kits; tools with specialised functions. High degree of modularisation including secondary tool use. Increased artefact entanglement. Discursive teaching.

At this level individuals are able to bring together otherwise disparate, or domain-specific, skills developed through various modes of material interaction, in order to realise shared super-ordinate affordances, for example, the creation of a fire-set through the combination of a bow (the ability to apply torque) and drill piece (the ability to apply friction) together produce the ability to produce heat. Gärdenfors & Lombard (2018) include indirect force transmission as an aspect of grade 7 causal cognition; in principle because the ability to store force for indirect transmission must be combined with some ability by which that force is released. In a bear trap, for instance, elastic potential energy is stored in the spring mechanism when the trap is set open; but to release the restorative force requires activation of the trap's trigger (i.e. the ability to apply leverage), releasing the spring.

As Kiverstein and Rietveld (2018) show, this kind of cognition is not necessarily 'representation hungry', but is continuous with 'lower cognition'. If, following Varela (1999), we take individuals to be constituted by their aggregate abilities for sensorimotor engagement with the environment, abilities inter-related by their grounding in socio-material practice;[21] then the environment can be considered as a rich (and structured) landscape of affordances (Rietveld and Kiverstein, 2014; Kiverstein and Rietveld, 2018, p153). As individual causal networks become more complex (in number of skills and degree of entanglement), so does the environment they are able to be solicited by (Kiverstein and Rietveld, 2018, p153). Perhaps the best example of this level of causal network understanding is cumulative culture, in which causal nodes may be related with causal nodes and causal networks with causal networks to create meta-networks beyond the scope of an individual's life-time (Dean *et al.*, 2014). Creative engagement in cumulative culture involves not only the ability to connect familiar bodily skills in novel ways, but also the ability to imagine and generate forms of engagement which could not have been generated relative to the pre-existing

[21] Varela (1999, p10) uses the terms 'micro-identity' to describe a 'readiness-for-action' (here ability/skill); and 'micro-world', for the specific lived situation to which readiness corresponds. The individual is thus comprised of multiple micro-identities. For Varela, skilled interaction with the world, including complex social practice, is always immediate, direct, and transparent – "our lived world is so ready-at-hand that we have no deliberateness about what it is and how we inhabit it" (*ibid.,* p9).

ecology of mind (Boden, 1996; Malafouris, 2014, following Boden, 1994). Relational manipulation at this level is not only of objects and skills as substance, but also of objects and skills as enactive signs.

3.6.2 Degrees of material constitution – Metaplasticity at the evolutionary time-scale

Finally, having concluded that all tools as environmental objects, are to some degree constitutive to cognition in Chapter 2, it is worth considering the ways in and degrees by which their constitutive roles vary. For Greif (2017), the degree to which a given external resource constitutes a cognitive process, is the degree to which it alters the functioning of the system it is a part of in scope, effectivity, efficiency or reliability. The ontogenetic aspect of this is already somewhat included in considering grades of causal cognition – for example, in skilled tool-use indicative of grade 3 causal cognition, the tool is inherently greater constitutive to the cognitive process than in un-skilled tool use typical of grade 1, since it results not only in the emergence of a novel [tool + user] agential perspective by which to probe the environment, but also since the fluidity of skilled tool use is by definition more effective than unskilled. This section focuses on the long-term meta-plastic effect of tool using variants as constitutive parts of organismic and phylogenetic processes of *becoming*.

At this scale, *minimal constitution* is the supplementation of a pre-existing ability of the organism with a novel, tool assisted process to better achieve the same goal.[22] Depending upon demographic distribution, minimally constitutive variables have the potential to affect the adaptive fitness of individuals, sub-groups, or entire populations; however, the adaptive value of these variables does not lead to species specialisation. In contrast, a tool using process is considered *maximally constitutive* when either (1) it enables the establishment of a novel function previously and otherwise unavailable to the organism; or (2) the adaptive significance of a tool using process is significant enough to drive species behavioural specialisation. Direct substitution of a pre-existing

[22] In so much as tool use alters the scope, range, or effectivity of the behaviour.

ability with a tool-assisted function (in which there is no change in scope, range, or efficiency) is not considered constitutive, unless the original ability is no longer functioning properly so that scope, effectivity, or reliability of that ability is impaired; in which case, being comparable to maximal constitution in terms of effect, the tool use is *strongly constitutive*.

3.7 Summary

This chapter has argued for a multi-faceted theory of 'complexity' in action and tool use, where complexity in behavioural technique may mean the inverse of technological complexity. To quantify these multi-facets, the cognigram method has been shifted outside the head and reframed as the balancing of systematic agency in tool use as a dynamic, environmentally situated process. Enactive, embodied, and extended concepts have been used to reformulate notions of causal cognition within a MET framework which identifies behavioural proxies for cognitive skills.

While the approach outlined may offer a promising means of cross-site and cross-species comparison as a means to explore the phenomenology of technical cognition in NHPs; there remain several points of potential weakness. Firstly, success or failure of the method is largely dependent upon the quality and consistency of behavioural reporting; which in reality, varies substantially in style and method between sites and species. Further, as noted, coding of the cognigram method is also open to subjective differences in unit size and identification. While this is less of a problem within the thesis (provided consistency is maintained); researcher subjectivity makes cross-study result comparisons prone to error through artificial inflation or deflation of complexities. The hierarchical level at which complexity is measured should provide some level of shielding this effect. By taking the focus away from single aspect measures, comparisons of emergent complexity should put the focus on complexity as an emergent phenomenon rather than as a phenomenon amenable to direct 1:1 comparison.

The utility of conceptualising causal cognition as pragmatic is three-fold. Firstly, in avoiding the need for mental representation, it subverts the impossible task of distinguishing between representation of causal relationships from the exploitation of relationships which so happen to be causal. Secondly, in so doing, it allows that the kinds of information about affordances, emergent in material engagement, may differ from individual to individual, from species to species, and even intra-individually from time *x* to time *y*; which, thirdly, highlights the metaplastic temporality of causal cognition – allowing that causal cognition is a developmental process in which an organism must often 'learn-to-learn' (Adolph and Kretch, 2015; Adolph, 2020).

Case Study 1: Material engagement, tool-use and technical cognition amongst chimpanzees (*P.t.verus*) at Bossou, Guinea

4.1 The Case Study Site of Bossou and its place amongst the wider chimpanzee technical repertoire

The chimpanzee study-site of Bossou (7°38'N, 8°29'W) is situated 6km from the Nimba mountains, in the Republic of Guinea, on the border with Cote d'Ivoire and Liberia. The study-site was established in 1976 and tool-use has been observed there since 1979 (Sugiyama and Koman, 1979b, 1979a; Sugiyama, 1981). The site itself is relatively unique amongst the long-term study sites in both its proximity and relationship with humans, the village of Bossou being home to c.2,500 people, and resources often being shared between human and chimpanzee communities with little conflict (Bryson-Morrison et al., 2017; K J Hockings et al., 2009; Kimberley J. Hockings et al., 2015; Humle, 2011b). In terms of its ecology, Bossou is located c.550m above sea-level and surrounded by small hills of primary and secondary forest. Climate has two seasons, with a dry season between November and February, and a wet season from March to October (Humle, 2011b). Since 1976, the local chimpanzee (*P.t.verus*) population has ranged between 23 and 7 individuals, the population having become semi-isolated and no females having transferred into the community for four decades (www.greencorridor.com).

4.1.1 The Bossou repertoire and its place amongst the wider chimpanzee technical repertoire

Wild chimpanzees perform a wide range of technical behaviours (N = 41), with significant differences in repertoire size and diversity between study-sites. Repertoires ranged from 5 tool variants at Lope, to 22 at Bossou. Shown in Table 8 (p87), Repertoire richness, heterogeneity, and evenness were calculated for both chimpanzee site repertoires by variant functional modes, and by variant causal functions using the SHE archaeological assemblage analysis outlined by Shott (2010),

demonstrating that besides being one of the richest repertoires in total number of tool forms, the Bossou repertoire is also among the more diverse. Technological repertoires at Taï, Goualougo, and Gombe were all of a comparable size, with c.20 technical variants at each site. However, Taï exhibits a greater number of customary and habitual behaviours (N = 15) compared to Bossou's 12; a substantial proportion of the Bossou repertoire being either idiosyncratic or anecdotal reports of one-off behaviours (N = 10). Taking frequency of behavioural expression into account, the Bossou repertoire appears typical of chimpanzee tool-use, its greater size reflecting the spontaneous, innovative, and often transient mode of technical material engagement characteristic of the wider chimpanzee technical context.

Wild chimpanzee repertoires are predominantly oriented towards the subsistent context with 54.7% of 128 total variants from across all sites directed to extractive or non-extractive foraging (49.2%, N = 63; and 5.5%, N = 7, respectively), whilst social, hygiene, and other contexts made up 21.1% (N = 27), 18.75% (N = 24), and 5.5% (N = 7), respectively. A list of variants comprising the Bossou repertoire is shown in Table 9 (p.88), adapted from the list of behaviours reported by Humle (2003, 2011c), along with the key sources used to construct behavioural algorithms. Subsistent variants comprise the largest portion (72.7%, N = 16), with approximately half the total Bossou repertoire being classed as extractive foraging variants (63.6%, N = 14). 18.2% of Bossou variants were classed as social (N = 4), 4.5% as Hygiene (N = 1), and 4.5% as other (N = 1). Given bias in contextual orientation, it is unsurprising that Humle (2011c) reports the four most frequently observed tool behaviours at the site, all take place in an extractive foraging context, nut-cracking being the most frequently observed behaviour (accounting for 0.36% of sum-total observation time), followed by ant-dipping (0.51%), pestle-pounding (0.07%), and algae-scooping (0.03%). Of all Bossou variants,46.4% had a causal function which extended the user's reach (N = 13); 25% amplified mechanical force (N = 7); 14.3% augmented the value of a social signal (N = 4); 10.7% enabled effective control of liquids and small solid objects (N = 3); and 3.8% (N = 1) improved bodily comfort .

Table 8 Richness and diversity of chimpanzee repertoires, values calculated from the data presented in Humle (2011), Whiten et al. (2001) and Sanz & Morgan (2007)

Site code	BOS	TAI	ASS	GOU	LOP	GOM	MAM	MAK	KIB	BUD
Total variants	**22**	20	6	19	5	19	12	9	9	7
Complex variants	**2**	**2**	0	1	0	1	1	0	0	0
Customary or Habitual	12	**15**	4	8	4	12	7	7	7	6
Present or Anecdotal	**10**	5	2	11	1	7	5	2	2	1
S(functional mode)	11	**12**	3	10	4	10	8	6	7	7
H(functional mode)	2.01	**2.22**	0.87	2.09	1.33	1.97	1.77	1.42	1.89	1.95
E(functional mode)	0.68	0.77	0.79	0.80	**0.95**	0.72	0.74	0.69	0.94	1
S(causal function)	**5**	**5**	3	**5**	4	**5**	**5**	4	4	4
H(causal function)	1.34	**1.53**	0.80	1.40	1.33	1.50	1.44	1.17	1.31	1.26
E(causal function)	0.76	0.92	0.74	0.81	**0.95**	0.90	0.84	0.80	0.93	0.88

- Bold font denotes the highest score for a given category

Table 9 Technical variants observed at Bossou since 1979, following Humle (2003, 2011c)

	Tool variant	Populational frequency	Key reference/s
Subsistants	Algae scoop	Customary	Matsuzawa *et al.* (1996), Humle *et al.* (2011)
	Ant-dip (single/wipe)	Customary	Sugiyama *et al.* (1988), Sugiyama (1995b), Humle & Matsuzawa (2002), Humle (2003, 2006)
	Ant fish	Present	Yamamoto *et al.* (2008, 2011)
	Anvil prop	Habitual	Matsuzawa (1991b)
	Branch haul	Present	Sugiyama & Koman (1979b)
	Dig	Present	Sugiyama (1995b, 1997)
	Expel	Customary	Humle (2003)
	Fluid (honey) dip	Customary	Ohashi (2006)
	Insect pound	Present	Sugiyama & Koman (1979b)
	Leaf sponge (fold/spoon)	Customary	Sugiyama (1995a), Tonooka (2001), Biro et al.(2006)
	Nut hammer	Customary	Sugiyama & Koman (1979b), Matsuzawa (1994), Biro *et al.* (2006)
	Palm sap collect	Present	Sugiyama (1994)
	Pestle pound	Customary	Sugiyama (1994), Yamakoshi & Sugiyama (1995), Yamakoshi (2011)
	Resin pound	Present	Sugiyama & Koman (1979b)
	Sponge push-pull	Present	Sugiyama (1995a)

- Bold font denotes a variant involving complex and/or sequential tool-us

Table 9 cont. Technical variants observed at Bossou since 1979, following Humle (2003, 2011c)

Functional Context	Tool variant	Populational frequency	Reference
Subsistence	Termite fish	Present	Humle (1999), Ohashi (2006)
Social	Aimed throw	Customary	Sugiyama & Koman (1979b), Humle (2003)
	Branch drag	Habitual	Humle (2003)
	Club	Customary	Humle (2003)
	Leaf clip	Customary	Sugiyama (1981)
Hygiene	Leaf cushion	Present	Hirata *et al.* (1998)
Other	Investigatory probe	Habitual	Ohashi (2006)

- Bold font denotes a variant involving complex and/or sequential tool use

It is worth noting that almost all idiosyncratic tool innovations, with the exception of leaf-cushion, are reported to take place within the subsistent context.

4.2 Cognigrams and thick descriptions

To reduce repetition, in the following sub-sections (4.2.1-4.2.12) variants are grouped by functional context, and, where there are many, sub-grouped by similar target resources and/or tool forms. Each section begins with brief behavioural descriptions of the technical variants included in the group/sub-group, accompanied with their respective cognigrams, and is followed by a section on general investigation of causal cognition considered on a section by section basis. This format will continue through the other case-study chapters 5 (Section 5.2) and 6 (Section 6.2). Sub-groupings are arbitrary, for ease of presentation only, and do not factor into the quantitative analysis which is presented at the end of each case-study chapter, or in the cross-species comparison presented in Chapter 7.

4.2.1 Subsistents used in the predation of insects and their nests

Predation of social insects is common among chimpanzees, and tool-assisted foraging of ants and termites is customary among many wild communities (McGrew, 1974; Sugiyama and Koman, 1979b; Goodall, 1986; Humle, 1999; Whiten *et al.*, 1999, 2001; McGrew, Pruetz and Fulton, 2005; Sherrow, 2005; Sanz and Morgan, 2007). At Bossou, 5 variants are used in the context of social insect predation, and 1, in the processing of insect products; these include 'ant dip', 'open and probe', 'ant fish', 'termite fish', 'insect pound', and 'fluid dip'.

Ant dip 'Ant-dipping' is customary at Bossou, and has two behavioural techniques: one-handed "direct-mouthing" ['ant-dip (single)'], and two-handed "pull-through" ['ant-dip (wipe)'] (Humle,

2003, 2011).[23] A typical episode begins with removal of leaf litter and/or topsoil by hand, followed by insertion of a modified probe tool of twig, stem, or bark, into a nest cavity or migrating ant trail (*Dorylus spp.*). The inserted probe is moved in short sideways movements, sweeping up the ants as they climb and attack the probe. Once covered in ants, the probe tool is extracted and run either through the closed fingers of the free hand, which wipes the ants into the mouth ('pull-through' technique), or sideways through the lips ('direct-mouthing') (Humle & Matsuzawa, 2002; Yamakoshi & Myowa-Yamakoshi, 2004). Figure 2 (p. 92) describes ant-dipping as a single perception-action module, in which the single super-ordinate affordance (i.e. predation of ants by means of a probe tool) is seen to arise from the dynamic interplay of three focal aspects, including: the chimpanzee, an organic material which forms the probe tool, and the ant prey. 2 spatial relationships have been counted towards objects order: 1 static (between probe and nest entrance), and 1 dynamic (between probe and ant prey). The minimal operational sequence is comprised of 7 critical actions (maximum = 11), in 4 phases. Sugiyama et al. (1988) report at least 3 modifications (besides detachment) either observed or inferred from probe tools recovered at the site, including: adjustment of tool length by biting of the distal tip, removal of excess bark, and stripping of excess leaves – all 3 modifications have been classed as reductive reshaping.

Dig and probe Sugiyama et al. (1988, p. 59) speculated that one tool recovered from the site of recent ant-dipping activity may have been used as a digging stick to remove topsoil prior to use of probe tools, or to open and expand the ant-tunnel, a further report by Sugiyama (1995b, p. 197) appearing to confirm the earlier conjecture: during one observed ant-dipping episode, an old female chimpanzee was seen "pounding or digging the earth with a long stick". The stick, which was left behind with a number of ant-dipping wands was reported to differ from the latter in all its characteristics: the 'digging stick' was longer and thicker - "a straight, hard branch… [with] one edge

[23] Techniques are named following McGrew (1974)

Figure 2 Cognigram for the Bossou variant 'Ant dip'

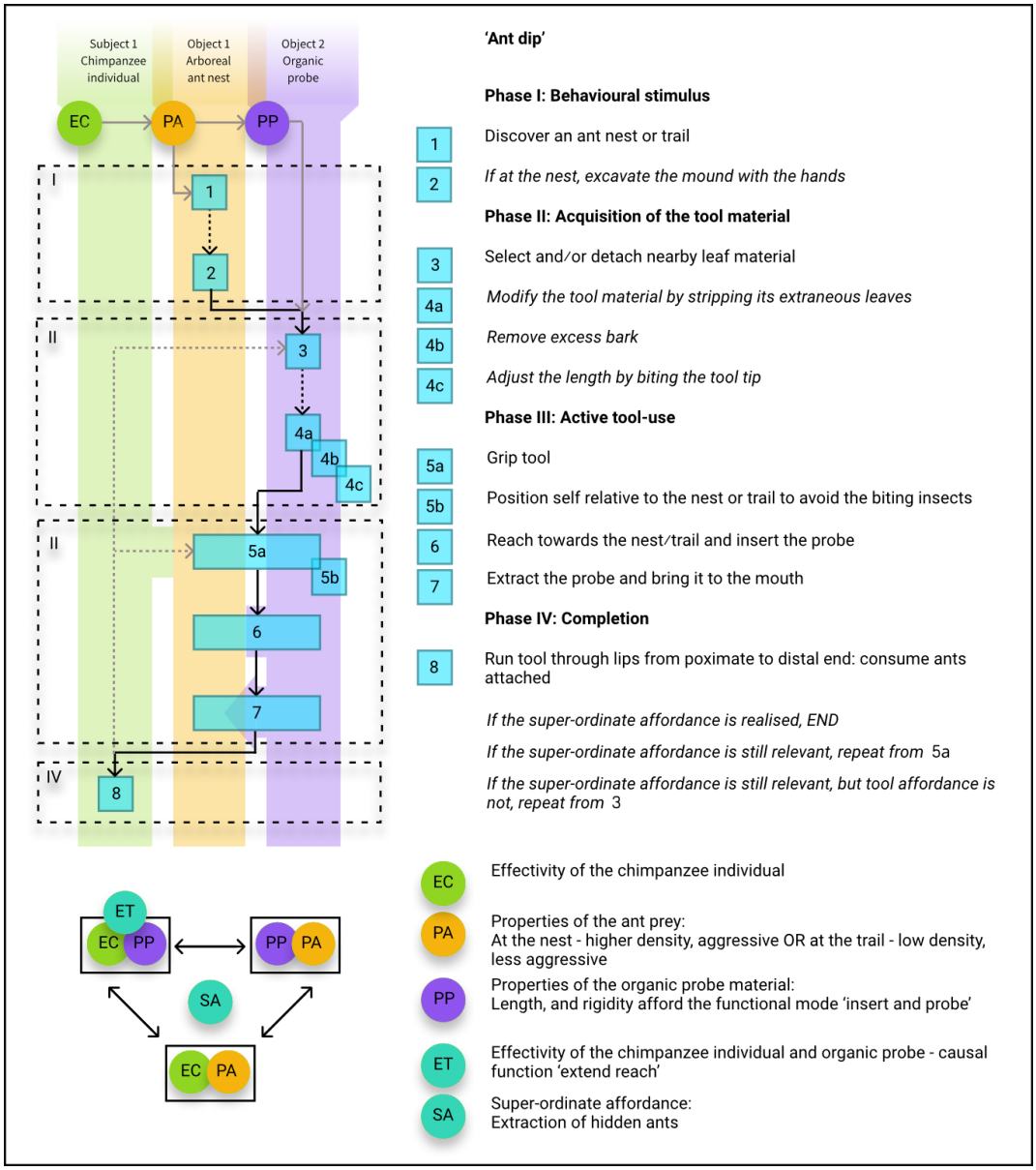
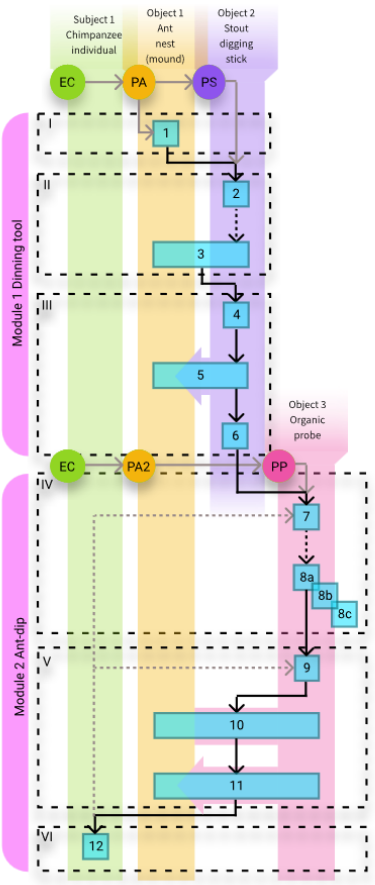
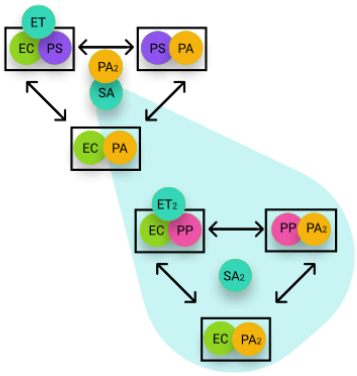


Figure 3 Cognigram for the Bossou variant 'Dig and probe'





'Dig' in association with 'Ant dip'

Phase I: Behavioural stimulus

1 Discover covered terrestrial ants nest

Phase II: Acquisition of a tool material

2 Select and/or detach rigid stick material

3 *Pick up and transport stick material to the covered mound*

Phase III: Active tool-use

4 Grip stick tool

5 Dig and remove topsoil from the mound with the stick

Phase IV: Completion of sub-module

6 Upon removal of topsoil, discard stick

Phase V: Acquisition of a tool material

7 Select and/or detach nearby organic material, leaf, herb, or stem

8a *Modify the organic material by stripping its extraneous leaves*

8b *Remove excess bark*

8c *Adjust length by biting of distal tip*

Phase VI: Active tool-use

9a Grip the tool

9b Position self relative to the nest/trail to avoid the biting insects

10 Reach towards the nest/trail and insert the probe

11 Extract the probe and bring it to the mouth

Phase VII: Completion

12 Run the tool through the lips from its proximate to its distal end: consume ants attached

If the super-ordinate affordance is realised, END

If the super-ordinate affordance is still relevant, repeat from 9

If the super-ordinate affordance is still relevant, but the probe tool no longer affords use, repeat from 7

EC Effectivity of the chimpanzee individual

PA Properties of the ant nest:
Hidden under hard soil

PS Properties of the digging stick material:
Size and rigidity afford the functional mode 'dig'

ET

SA Super-ordinate affordance:
Excavation of mound entrance

ET_2 Effectivity of the chimpanzee individual and organic probe - causal function 'insert and probe'

SA_2 Super-ordinate affordance:
Extraction of ants from their nest

PA_2 Properties of the ant prey:
At the nest - higher density, aggressive.

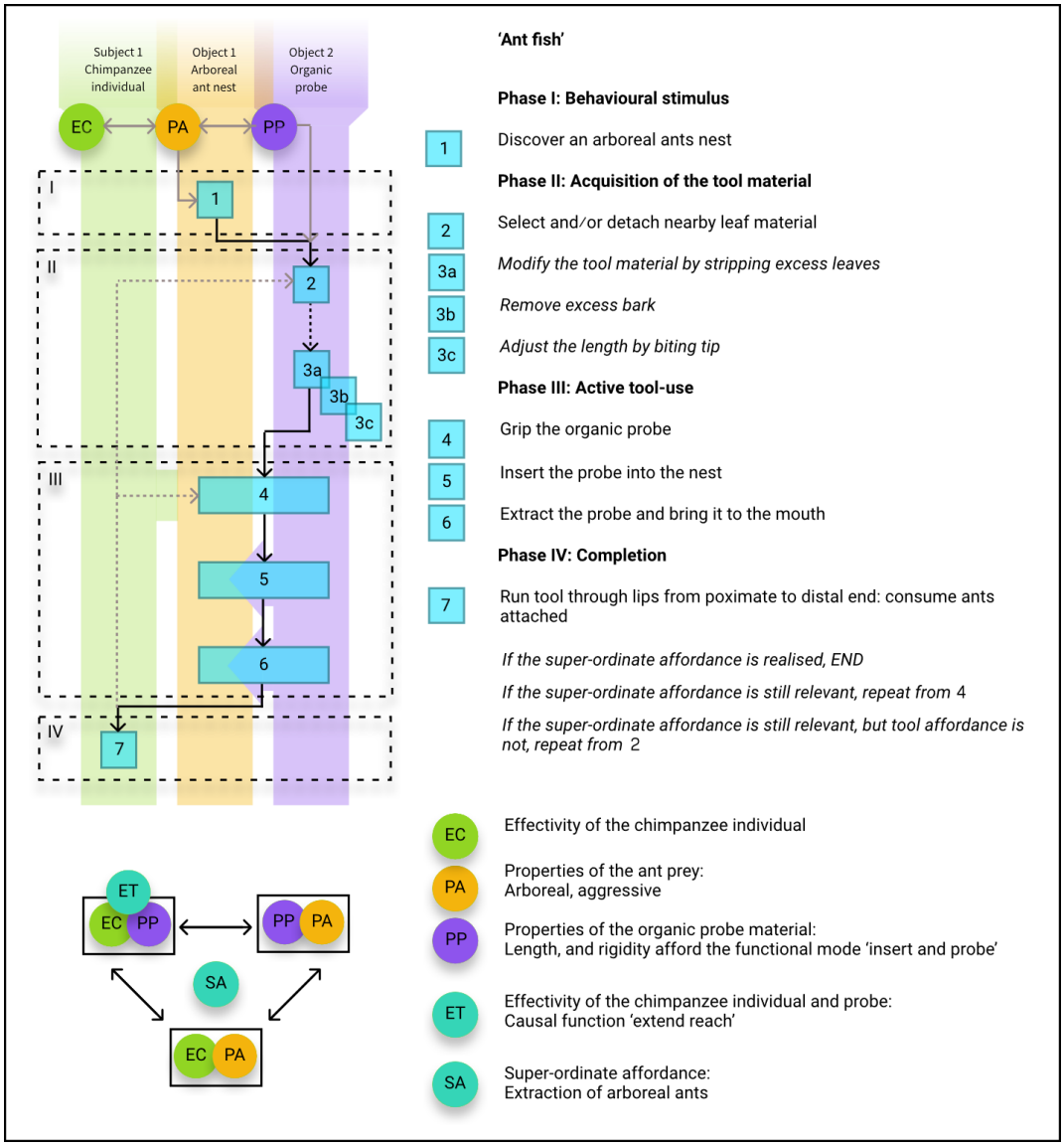
PP Properties of the organic probe material:
Long, rigid, affords the functional mode 'insert and probe'

coated in mud" (Sugiyama, 1995b, p. 197). Figure 3 (p. 93) shows digging behaviour as part of 'open and probe', a compound variant created by the sequential association of the perception-action modules 'dig', and 'ant-dip'.[24] The super-ordinate predation affordance is distributed across 4 constituent foci: the chimpanzee, covered ant-nest, a hard stout stick which forms the digging tool, and organic material which forms the subsequent probe tool. 3 spatial relationships were counted towards Object order, 1 static (between probe and hole entrance) and 2 dynamic (between hammer-stone and mound; probe and prey item). The combined operational sequence length ('dig' + 'ant dip') has a minimum of 11 critical actions (maximum = 15), in 6 phases. No modifications were reported for either of the putative digging tools, however, the 3 modifications made to the sequential probe tool (as part of 'ant-dip' – see previous paragraph), are included in the technical complexity of this variant.

Ant fish In 2008, Yamamoto et al. (2008, see also Yamamoto et al., 2011) reported the invention and modification of a novel tool behaviour, 'ant-fishing', which they observed performed by a single juvenile male. Ant-fishing is not unique to Bossou, having been observed at a number of other sites (McGrew, 1992; Nishida, 1973; Nishida & Hiraiwa, 1982; Nishie, 2011; O'Malley et al., 2012; Suzuki, 1966; Tutin & Fernandez, 1992; Wondra et al., 2016). The variant is behaviourally similar to ant-dipping in both tool form (slender probe) and mode of tool use (insert and probe), but differs in the primary insect species which is predated - i.e. wood-boring or carpenter ants (*Camponotus spp.*), rather than army ants (*Dorylus spp.*); and in the spatial context in which tool use takes place - i.e. the majority of episodes take place in an arboreal, rather than terrestrial context. Physicality of the context is likely to affect technical expression, with the one hand (i.e. the free-hand) often required

[24] As digging tool-use has not been reported outside the associative context of subsequent ant-dipping, its inclusion into the Bossou repertoire, and into all subsequent quantitative analysis, falls under the purview of the compound-variant 'dig and probe'. The module 'dig', which is recognized as an independent variant in later chapters, is not treated as such here.

Figure 4 Cognigram for the Bossou variant 'Ant fish'

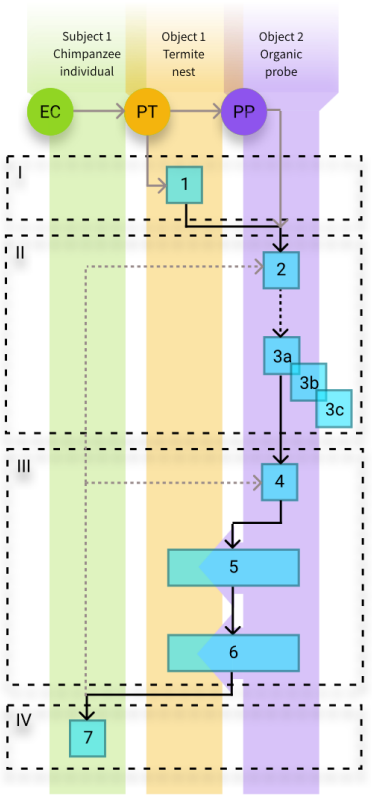


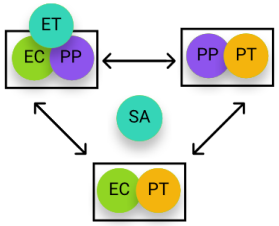
to provide postural support, and laterality a function of the spatial relationship between the tree-trunk entry holes of the ants' nest, and the nearest site suited to sitting, standing, or suspension (Marchant and McGrew, 2007, p. 24). At Bossou, Yamamoto et al. (2008, 2011) reported that ants were removed from fishing-probes by one-handed direct-mouthing only, with no occurrence of the two-handed pull-through technique.[25] Figure 4 (p. 95) describes ant-fishing as a single-perception action module in which the super-ordinate affordance (predation of carpenter ants) arises through the dynamic interplay of 3 foci: the chimpanzee, an organic material which forms the probe tool, and the carpenter ants in their arboreal nest. 2 spatial relationships were counted towards Object order, 1 static (between probe and nest entrance) and 1 dynamic (between probe and ant prey). Minimum number of critical actions is 6 (maximum = 9), in 4 phases, with up to 2 tool modifications, including: stripping of excess leaves, and adjustment of the tools length - each classed as reductive.

Insect pound Despite the common presence, and non-tool-assisted predation of termite mounds throughout the Bossou home range, tool-assisted foraging of *Macrotermes* (and *Pseudacanthotermes*) species is rare among the Bossou chimpanzee community (Humle, 1999, 2003; Sugiyama & Koman, 1979). An anecdotal report by Sugiyama & Koman (1979b) describes an episode in which two adult male chimpanzees were observed predating termites nesting in the hollows of tree: the chimpanzees modified small twigs by removing their side branches and leaves, then inserted the twigs into the hollow, beating and pounding the bottom of the hole several times. When the chimpanzees retrieved the twigs, termites could be seen attached to them, "broken and adherent" (Sugiyama and Koman, 1979b, p. 515), which the chimpanzees removed by 'direct-mouthing', licking them from the twig. 'Insect pounding' is shown in Figure 5 (p. 97) as a single perception-action module, distributed between 3 foci: the chimpanzee, organic material which

[25] This could alternatively, quite feasibly, be explained by the small sample-size; number of observations being 2, performed by the same individual (Yamamoto *et al.*, 2008).

Figure 5 Cognigram for the Bossou variant 'Insect pound'





'Insect pound'

Phase I: Behavioural stimulus

1 Discover a termite nest in the hollow of a dead branch/fallen tree

Phase II: Acquisition of the tool material

2 Select and/or detach nearby short stick

3a *Modify the tool material by stripping excess leaves*

3b *Remove excess bark*

3c *Adjust the length by biting tip*

Phase III: Active tool-use

4 Grip the organic probe

5 Insert the probe into the nest, pounding the bottom of the hollow

6 Extract the probe and bring it to the mouth

Phase IV: Completion

7 Pinch off the broken, adherent termites with the mouth

If the super-ordinate affordance is realised, END

If the super-ordinate affordance is still relevant, repeat from 4

If the super-ordinate affordance is still relevant, but tool affordance is not, repeat from 2

EC Effectivity of the chimpanzee individual

PT Properties of the insect (termite) prey:
Contained within the hollow, potentially aggressive

PP Properties of the organic probe material:
Length, and rigidity afford the functional mode 'insert and probe' and 'hammer or pound'

ET Effectivity of the chimpanzee individual and probe:
Causal functions 'extend reach' and 'amplify mechanical force'

SA Super-ordinate affordance:
Extraction of insects (termites)

forms probe/pounding tool, and the termites in the tree hollow. 2 spatial relationships were counted towards Object order, both dynamic (between probe and entrance hole; probe and prey). Minimum number of critical actions required to describe the behaviour is 6 (maximum = 9), in 4 phases. The total number of tool modifications has been taken as 3, and includes: adjustment of the tool's length, stripping of excess branches, and removal of excess leaves. All tool modifications were classed as reductive.

Termite fish A second anecdotal report by Humle (1999) details an episode of 'termite-fishing' performed by a chimpanzee mother, with her infant: the female chimpanzee was observed digging a hole into the topsoil of a termite mound with her thumb and index fingers, before inserting a short, flexible stalk, bitten off at the distal end, into the mound. Upon withdrawal of the stalk from the mound, termites were seen clinging to the tool. The chimpanzees were then observed using their lips to pinch off the termites directly from the stalk. Figure 6 (p. 99) gives 'termite-fishing' as a single perception-action module, with 3 foci: the chimpanzee, organic material which forms the probe tool, and the termites in the termite mound. 2 spatial relationships are counted towards Object order, 1 static (between probe and entrance hole) and 1 dynamic (between probe and termite prey). Minimal critical sequence is comprised of 6 critical actions (maximum = 9), in 4 phases. Besides detachment of the tool form, Humle (1999) reported 2 modifications to the tools form, including adjustment of the stalk length (by biting of the distal tip), and stripping of excess leaves - each classed as reductive.

Fluid dip Honey-gathering is common among chimpanzees, and ubiquitous to the central sub-species (*P.t.troglodytes*), whose "sophisticated" processing and extraction strategies involve complex tool 'kits' of sequentially used tool forms (Bermejo & Illera, 1999; Boesch et al., 2009; Fay & Carroll, 1994; Fowler & Sommer, 2007; Nishida & Hiraiwa, 1982; Sanz & Morgan, 2007, 2009; Stanford et al., 2000; Tutin et al., 1995). More common among all sub-species, and comparatively simple, 'Fluid dipping' of honey produced by stingless and carpenter bees (*Meliponini spp.* and *Xylocopa spp.*) is customary at Bossou (Humle 2011; Ohashi 2006). Ohashi (2006) provides a

Figure 6 Cognigram for the Bossou variant 'Termite fish'

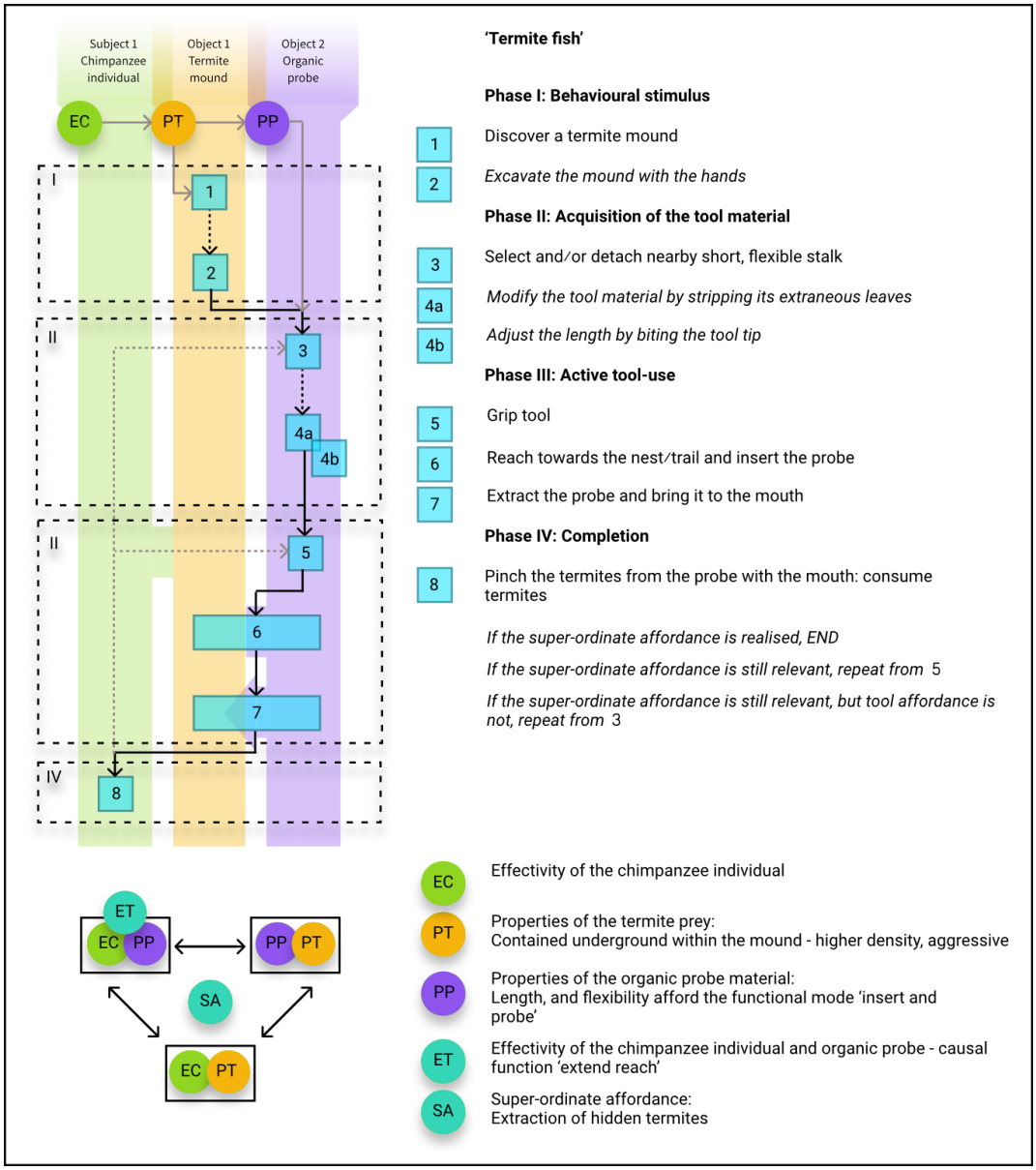
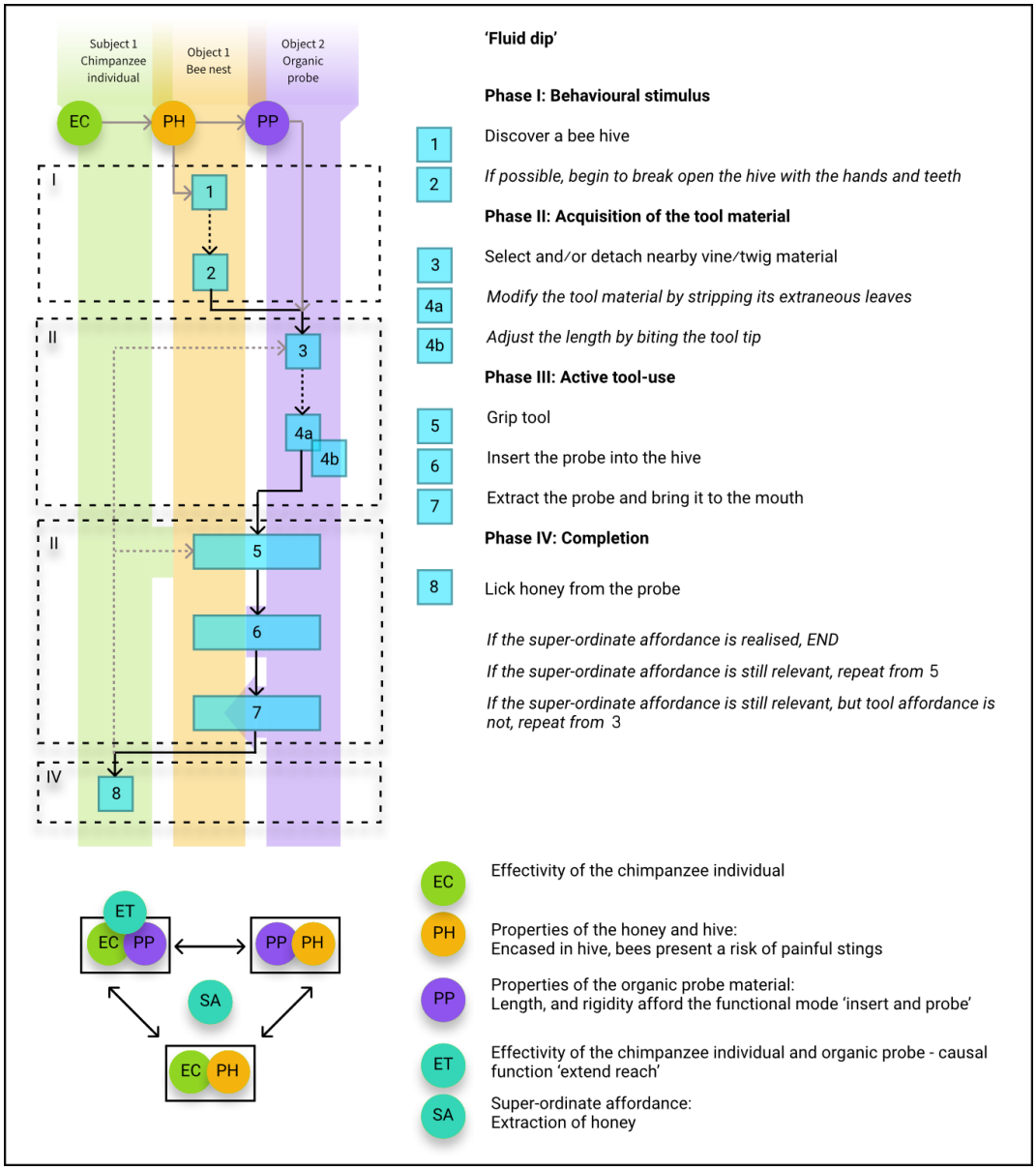


Figure 7 Cognigram for the Bossou variant 'Fluid dip'



description of two observed episodes of the behaviour; one in which a Bossou chimpanzee dipped for honey in a nest previously manually knocked down, broken apart, and some of the honey consumed by another conspecific; and another in which a chimpanzee dipped a detached vine into a bee nest made in the hollow between two trees. In the first episode, the chimpanzee was observed to uproot a stem, and "prepare" it, before inserting the modified probe tool into the beehive to extract the honey; after some time, the chimpanzee discarded the tool, and continued to process the beehive manually, only for another conspecific to pick up and re-use the discarded tool (Ohashi, 2006, p. 447). Figure 7 (p. 100) shows fluid-dipping as a single perception-action module. The super-ordinate affordance is distributed across 3 foci: the chimpanzee, organic vine or stick material which forms the probe tool, and the honey enclosed in the beehive matrix. 2 spatial relationships were counted towards Object order, 1 static (between probe and nest entrance) and 1 dynamic (between probe and honey) . The minimum operational length (i.e. dipping in a hollow, without manual breakdown of the nest or tool modification) comprised 6 critical actions (maximum = 9), in 4 phases. Since Ohashi (2006) did not specify what modifications were applied to the tool form, the modification phase of Figure 7 was derived from generic descriptions of fluid-dipping (Sanz & Morgan, 2007; Sanz & Morgan, 2009; Sugiyama & Koman, 1979b): A conservative maximum of 2 modifications to the tool form, adjustment of tool length, and stripping of excess leaves, were included – both considered reductive reshaping.

4.2.2 Causal cognition for subsistents used in the predation of insects/processing of insect products

In terms of technical cognition, each of the probing behaviours involves a high degree of manual coordination and dexterity with wand-dipping requiring precision grip and fine-level motor control (Humle, Snowdon, and Matsuzawa 2009; Sugiyama 1995b). Probe tools function to extend the reach of the user through peri-personal space, with proficient tool-using of this kind indicative of grade 3 'self-mind-reading' when tool-users can readily adapt their techniques to differing, or

ongoing, task parameters. Comparison of tool behaviours targeting social insects and their products (both within the Bossou repertoire, and more broadly, between sites) demonstrates proficient probe tool-users are able to respond flexibly to a number of micro-ecological conditions, adjusting tool material, length and technique to accommodate site context (i.e. arboreal nest, mound or trail), and lifestyle condition of the insect prey (i.e. termites, epigaeic or non-epigaeic ant species) (Humle, 2006, 2011; Humle & Matsuzawa, 2002; Koops et al., 2015; Möbius et al., 2008; Sanz et al., 2014; Schöning et al., 2008). At Bossou, ant-dipping probe length was dependent upon the characteristics of the prey species (average 72.3cm for epigaeic nests versus 53.7cm for intermediate species) and condition of the prey target, with chimpanzees using longer tools at nest sites than at trails; ants being more aggressive and at higher densities at nest sites (Humle and Matsuzawa 2002). Further, Humle & Matsuzawa (2002) found technique by which the Bossou chimpanzees removed ants from the dipping tool was a function of tool length, with the pull-through technique being exclusively associated with tools >50 in length. Whilst Yamokoshi and Myowa-Yamokoshi (2004) hypothesise the direct-mouthing technique is more efficient in terms of consumption rate, Humle & Matsuzawa (2002) argue the pull-through technique may be most efficient at minimising risk when higher numbers of ants are on the tool, crumpling the ants and preventing them from biting the chimpanzee before they can be eaten.

Longitudinal studies by Humle (2003), and Humle et al. (2009), found development of ant-dipping behaviour among the Bossou community tool place via a combination of individual and social learning mechanisms, with individuals' rate and likelihood of achieving technical proficiency strongly influenced by the context and frequency of opportunities for practical engagement with tool and task materials. Reaching the level of adult proficiency indicative of grade 3 causal cognition requires many years of practice, motivation for engagement increasing with age, in tandem with time spent engaged subsequent to the cessation of co-present adults' tool-using (Fragaszy et al., 2013; Humle, 2011, pp. 64–65). Mothers' tool-using appears necessary to the early education of attention, with Humle et al. (2009) finding that infants only engaged in ant-dipping tool behaviour

when their mother's where engaged in the same behaviour. Re-use of the mother's, and other co-present conspecifics', tools was also important to technical development, but reduced over-time with the accrual of experience, and as others' tolerance diminished: Fragaszy et al. (2013) found juveniles less than 5 years of age re-used tools previously constructed and used by others two-thirds of the time; those 5-10 years of age, one third; and adults, less than one fifth.

The variety and near-universal preponderance of customary and opportunistic organic probe tool techniques among chimpanzee communities (and among the central sub-species, in particular) is unsurprising, given the ready availability of suitable materials and abundance of suitable prey species which coincide in several diverse ecological contexts found throughout chimpanzee habitats. Yet tool-assisted strategies of insect predation and honey extraction exhibited by the Bossou chimpanzees appear comparatively simple in contrast to the more hierarchically complex techniques, some involving 'kits' of sequential tools, found among chimpanzee communities elsewhere (e.g. Boesch et al., 2009; Musgrave et al., 2020; Sanz & Morgan, 2009; Sanz & Morgan, 2007). While some aspects of inter-site difference, for instance, prey preference and lack of termite predation, are likely to reflect social custom indicative of grade 2 cued-dyadic causal cognition, it is worth considering how site formation and the nature of engagement with available insect resources maybe influencing the development of technical cognition at the site (Boesch & Boesch, 1990; Fowler & Sommer, 2007; Humle, 2006; Humle & Matsuzawa, 2002; Koops et al., 2015; McGrew, 1974, 1992; Möbius et al., 2008; Myowa-Yamakoshi & Yamakoshi, 2011; Sanz et al., 2014; Schöning et al., 2008). Describing the temporal durability of the ant-dipping context and opportunities for tool-reuse, Fragaszy et al. (2013) note ant-dipping at Bossou is perhaps more fleeting than appears at first glance: tools collected at the mound, though of perishable material, may last up to several days, and re-use (particularly among infants and juveniles) during the episode is abundant; however, significant disturbance of the entrance to the ant-mound, caused in the process of the foraging behaviour, frequently forces ant colonies to emigrate within 24 hours, leaving the mound empty, and tools un-reusable between bouts unless the site is quickly recolonised (Fragaszy et al., 2013, p.

5; Humle, 2010). At Bossou, ant-dipping behaviour also targets emigrant and foraging ant trails [in contrast to the majority of sites which feed exclusively at the mound (see Humle, 2011a, p. Figure.9.2, p. 100)] and that it is these trails which constitute the majority of the juvenile practice context – Humle et al. (2009) report that Bossou mothers with infants younger than 5 years of age dip more frequently at the trail, where ant-density is lower, and risk of incurring ant-bites, reduced. Given the transient nature of both mound and trail, it might be questioned whether significant build-up of materials can occur to scaffold attention toward the development of more hierarchically complex technical behaviours (following Fragaszy et al., 2013; Meulman et al., 2012; Musgrave et al., 2020; Sanz & Morgan, 2007).

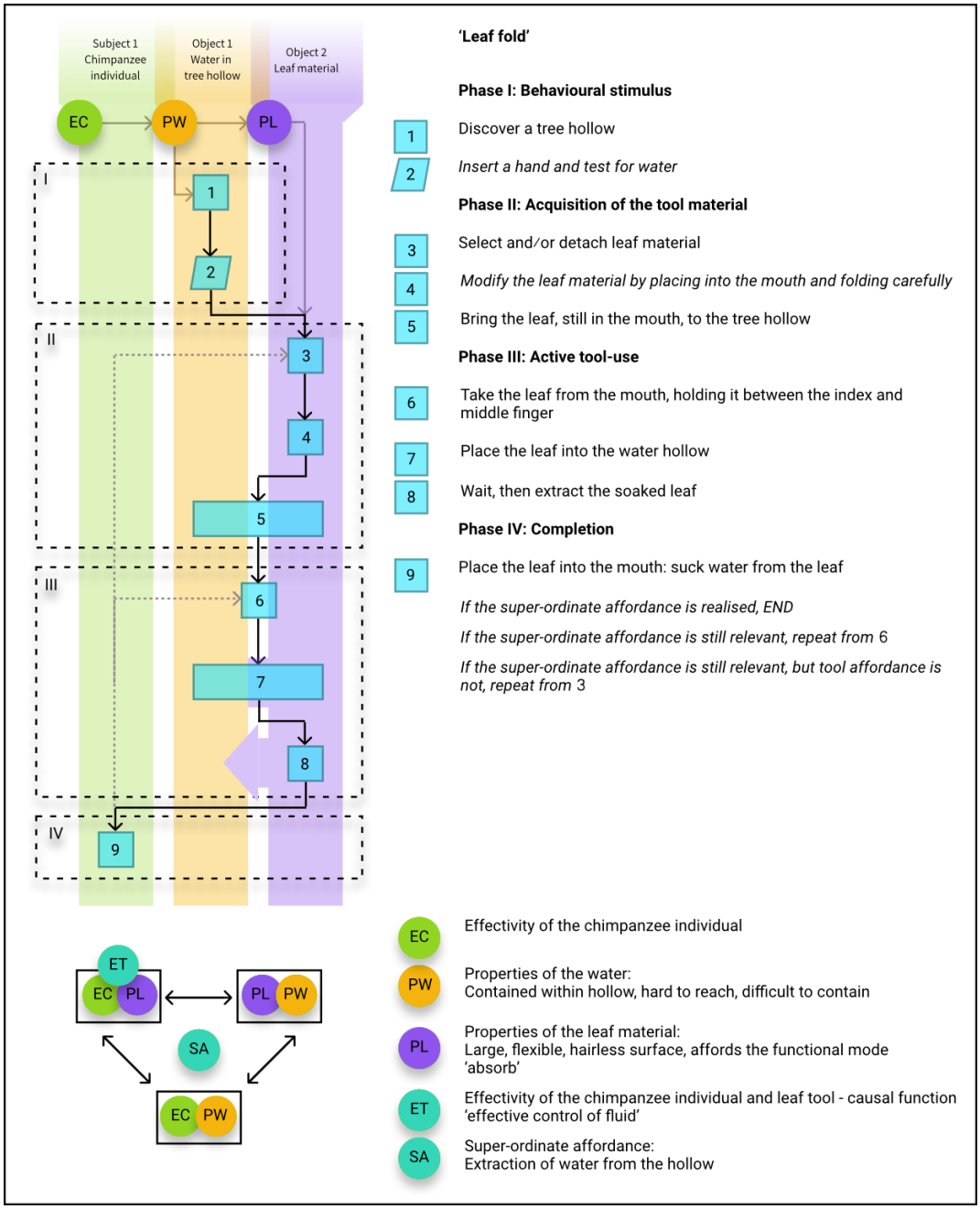
The same argument extends to development of more complex social cognition, including modes of active teaching: although tool re-use does occur at Bossou, it is not by active tool transfer (e.g. Musgrave et al., 2016), and though mothers may adapt their own tool-using strategies to accommodate their young (i.e. by preferentially targeting ant trails, rather than the nest site), this behaviour is more consistent with opportunity- rather than active- teaching (following Caro and Hauser, 1992; Hoppitt *et al.*, 2008). Using inter-site comparison between Gombe and Goualougo, Musgrave et al. (2020) argue that degree of teaching, including rates and probability of tool transfer, exhibited by adult chimpanzees during termite gathering increases with task complexity. Active tool transfer is energetically costly to the tool donor – detracting from their own tool-using and reducing feeding – and is predicted to occur only when it would be otherwise difficult for the donor recipient to independently acquire information and technical skill relating to the task context (Caro and Hauser, 1992; Hoppitt *et al.*, 2008; Boesch, 2013). At Goualougo, where termite fishing techniques involve a high degree of hierarchical complexity, Musgrave et al. (2016; see also Musgrave et al., 2020) found mothers used strategies which actively mitigated the cost of transfer, demonstrating an apparent sensitivity to, and anticipation of juveniles' learning needs, suggesting that grade 3 conspecific mind-reading (or at least behavioural evidence of grade 3) is an emergent product of a virtuous cycle between task and social-cognitive complexity.

For most of the behaviours detailed in the previous section, 'ant dip', 'termite dip', 'dig and probe', 'insect pound', and 'fluid dip', material cognition is considered minimally constitutive. Since chimpanzees are known to target army ant eggs by inserting their hand and arm directly into ants' nests (Humle 2011a), to consume termites directly from the mound (Ohashi, 2006), and to break down bees nests without the aid of tools, none of the above tool behaviours can be said to provide wholly novel function. However, at Bossou, carpenter and driver ants present significant biting risk, and tool-use functions to supplement and improve efficiency of ant consumption whilst circumventing this risk, with Yamakoshi (1998, see also Yamakoshi, 2001) reporting tool-use for one twelve-month period constituted 44.3% of total time spent foraging for insects. Likewise, in dipping for honey, bee species each present their own challenges: meliponine species are known to collectively attack intruders (Schorkopf, 2016), whilst carpenter bee nests maybe difficult to access, often being attached to substrate or between recesses in trees or canes. Although honey consumption can be achieved (and is observed to take place) without the aid of tool-use, probe tools efficiently function to overcome the structural and behavioural defences of bees and their nests, increasing efficiency by extending the reach of the user, in order to reduce the effective distance between honey and chimpanzee, whilst extending the distance between aggressive bees and chimpanzee, in order to avoid the risk of bites and/or stings. For each of the above variants, insect behaviour affords the form, and subsequently mode of tool-use; tools need to be selected for their appropriate material and modified to an appropriate length, in each of the above cases, primarily as a functional response to degree of risk. The chimpanzee must then coordinate itself relative to both tool and the insects, often (when dipping for ants at the nest), perching above whilst dipping to avoid being bitten, grasping a tree with one hand, the other extended out over the nest (Sugiyama, 1995b). By providing access to arboreal ant-species, ant fishing may provide a novel function for the Bossou chimpanzees, increasing breadth of diet and reducing feeding competition. However, since the behaviour is currently only exhibited by a single male, scope of the advantage gained relates solely to the individual.

4.2.3 Subsistents for the collection of water and marine resources

Leaf sponge Whiten *et al.* (Whiten *et al.*, 1999, 2001) categorise leaf-sponging as a universal feature of chimpanzee behavioural repertoires. Three techniques have been reported which use leaves to collect drinking water from tree hollows. These include “leaf spoon” (Goodall, 1968; McGrew, 1977; Sugiyama, 1995a), in which chimpanzees spoon water from the hollows with unfolded leaves; “leaf sponge” (Goodall, 1964, 1968; McGrew, 1977; Sugiyama, 1994), in which chimpanzees crumple the leaf in the mouth before soaking, then sucking water from the leaf; and “leaf fold” (Tonooka, 2001; Tonooka et al., 1994) in which chimpanzees fold the leaves in the mouth into origami-like structures, soak them, then suck or squeeze the water from them. All three techniques are present and habitual at Bossou (Humle, 2011; Sugiyama, 1995a; Tonooka, 2001; Tonooka et al., 1994). A typical episode, following Biro et al. (2006, p. 482), begins when a chimpanzee individual approaches a drinking source, usually a tree-hollow which has collected rain water, to which the chimpanzee reaches a hand in to test for the presence of water. If present, the chimpanzee individual then leaves the hollow to collect leaf material, which is carefully placed, laid parallel, into the mouth, where it is chewed or folded gently with the tongue, and transported, still in the mouth, to the hollow. At the hollow, the chimpanzee retrieves the leaf from the mouth, and held between the index and middle fingers, inserts it into the water(Biro, Sousa and Matsuzawa, 2006). Once enough time has passed for the leaf to have become soaked, the chimpanzee retrieves the tool and places it into the mouth, drinking the water collected from the leaf’s parallel folds, and sucking water from it. Leaves may be re-inserted multiple times, until they are finally dropped, usually at the end of the drinking bout. Figure 8 (p. 107) presents leaf spooning, sponging, and folding, as three technical variations of a single perception-action module, in which the shared super-ordinate affordance (i.e. collection of water) is distributed across three foci: the chimpanzee, organic leaf material which forms the tool, and the water in the waterhole or tree hollow. 2 spatial relationships were counted to Object order, 1 static (between sponge and hollow entrance) and 1

Figure 8 Cognigram for the Bossou variant 'Leaf fold/sponge'



dynamic (between sponge and water). Minimal behavioural complexity (describing 'leaf spoon') is described by 7 critical actions (maximum = 8), in 4 phases. The operational sequences for 'leaf sponge' and 'leaf fold' include an additional modification to the tool material: 'chew leaf' and 'fold leaf in mouth', respectively. Since the functional aspect of the leaves (absorbency) was increased without an overall reduction to the tool's mass, modification mode has been classed as replicative reshaping. Absorption capacity of the 'folded' form is increased through the repetition of folds, and of the 'sponge' form, through the increased surface area achieved by break down of the leaf material into multiple fibres. All three techniques typically involve multiple iterations of one or more phase, the same leaf being used throughout. When leaves are discarded and new leaves selected, the discarded leaves are often reused by others, bypassing the need to modify a new tool (Biro et al., 2006; Tonooka, 2001) .

Push-pull On one occasion at Bossou, during the course of a leaf-sponging episode, a juvenile female chimpanzee was observed to include a modified probe tool form, using the probe tool to push and pull the leaf sponging tool into, and from the tree-hollow (Matsuzawa, 1991a; Sugiyama, 1995a, 1997).While this behaviour does not appear to be customary at Bossou, it also does not appear to be unique, with similar compound tool behaviour linking probe and leaf tools for the collection of drinking water has been reported anecdotally at both Mahale and Taï (Whiten *et al.*, 2001; Matsusaka *et al.*, 2006). Figure 9 (p. 109) gives this behaviour, labelled 'push-pull', as a composite perception-action sequence built from the sequential association of the modules 'leaf-sponge' and 'push-pull'. The super-ordinate affordance (i.e. collection of water) is distributed across 4 foci: the chimpanzee, leaf material which forms the sponge tool, stick material which forms the probe tool, and the water contained in the tree hollow. A total of 4 spatial relationships were counted for Object order, 1 static (between leaf and hollow entrance), 3 dynamic (between probe and leaf, and leaf and water; probe and leaf). Total operational sequence length is described by a minimum of 10 critical actions (maximum = 11), in 6 phases. Since no modification of the probe tool was included in Sugiyama's (1995a) summary, no additional modification actions have been included

Figure 9 Cognigram for the Bossou variant 'Push-pull'

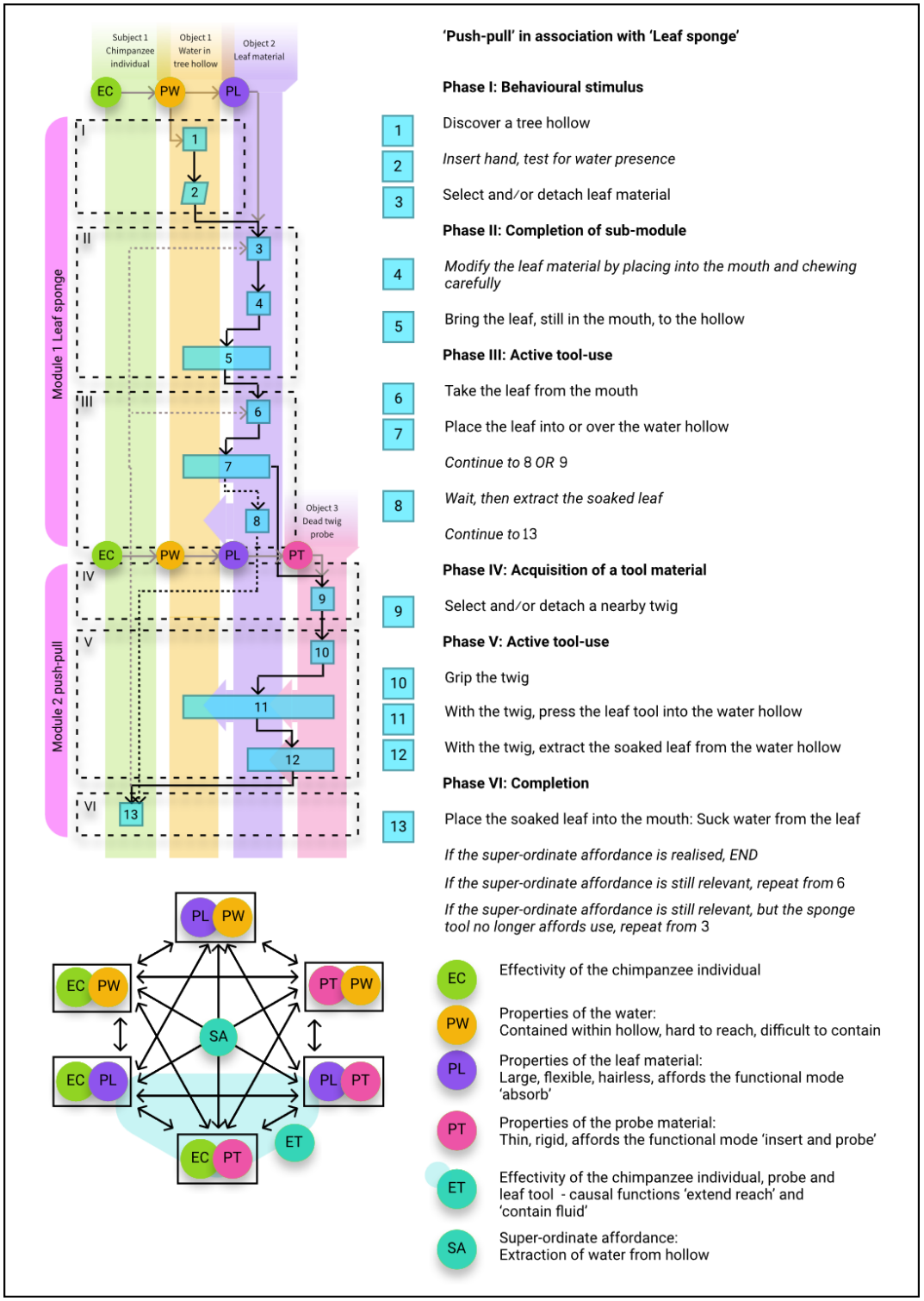
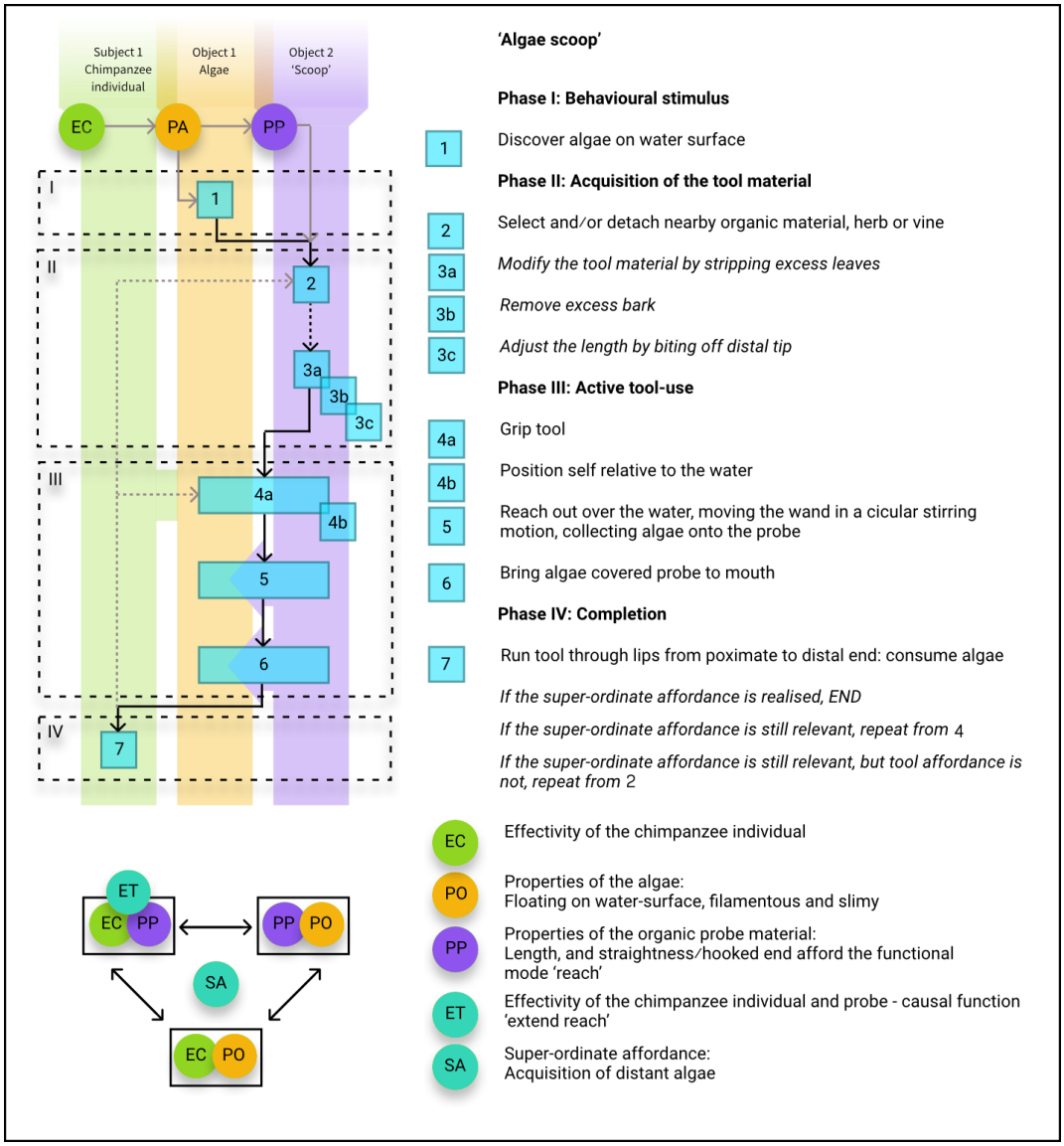


Figure 10 Cognigram for the Bossou variant 'Algae scoop'



besides the 1 already counted in the module 'leaf sponge'. Tool manufacture was classed as replicative reshaping (from the chewing of the leaf sponge) and linkage, with the two functional aspects of the tool, leaf and twig, remaining physically discrete.

Algae scoop In comparison with leaf tools used in water-collection, exploitation of marine resources is unusual in primates, including chimpanzees (Kempf, 2009; Russon *et al.*, 2014); and, although algae consumption has been observed at a number of chimpanzee sites, use of tools as aids to algae consumption is rare (Boesch et al., 2016; Devos et al., 2002; Matsuzawa et al., 1996; Sakamaki, 1998).[26] Adult chimpanzees at Bossou customarily perform 'algae scooping', using long slender stems or leafless plant stalks to 'fish' algae (*Spirogyra sp.*) from ponds (Humle et al., 2011; Matsuzawa, 2019; Matsuzawa et al., 1996; Ohashi, 2006). Humle et al. (2011) give the general pattern of behaviour, initially reported by Matsuzawa et al. (1996), as follows: A chimpanzee uproots a grass stem from nearby vegetation by hand and shapes the stem into a wand, adjusting the length by chewing off the end, and stripping the leaves with either an upwards sweeping motion of the hand, or by mouth. Reaching out over the water, the wand is then inserted into the pond and algae is scooped from the surface in a careful whisking motion. Once the stem is covered in algae, the tool is brought to the mouth and the algae removed by pulling the wand so that it moves from proximal to distal end through the lips, comparable with the 'direct-mouthing' technique of removing ants from dipping probes (Section 4.2.1). Figure 10 (p. 110) describes algae scooping as a single perception-action module in which the single super-ordinate affordance (consumption of water/algae) is distributed between 3 foci: the chimpanzee, organic stick material which forms the probe tool, and the algae floating on the surface of a pond, or other body of water. 2 spatial relationships were counted towards Object order, both dynamic [between wand and algae (collection); wand and algae (retrieval)]. Algae scooping includes a minimum of 7 critical actions (maximum = 9), in 4 phases. Tool modification is classed as reductive and involved a maximum 3 operational steps, including adjustment of length, stripping of leaves, and removal of bark

[26] With the notable exception of *M.f.aurea* (Gumert & Malaivijitnond, 2012)

(following Matsuzawa et al., 1996), with the number of modifications dependent upon the material type selected for the tool.

4.2.4 Causal cognition in Bossou drinking tools

While the universal use of leaves for water collection and drinking by chimpanzees could be indicative of a genetic predisposition (Whiten et al., 2001), inter-group variations in technique and material preference suggest affordance perception is influenced by observations of conspecific behaviour, and by access to discarded tool materials (Tonooka, Inoue and Matsuzawa, 1994; Hobaiter *et al.*, 2014; Gruber *et al.*, 2015). Chimpanzees at Gombe, for instance, exhibit no clear preference in the materials selected to perform 'leaf-spoon' (Goodall, 1968; McGrew, 1977), while those at Bossou, Taï, and Budongo do: Chimpanzees at Taï dip using 'wadges' formed from chewed fruit pulp (Boesch, 1991a), while those among the Sonso community select tool material on the basis of absorption efficiency and knowledge (Lamon *et al.*, 2018).[27] Tonooka (2001; see also Sugiyama, 1995) found Bossou chimpanzees were highly selective in their choice of tool material, sometimes searching beyond the immediate area of the target resource for preferred leaves when availability was low or depleted by previous use.[28] Although the relative efficiency of the preferred leaf material is untested (against other leaf materials available at Bossou), Tonooka (2001) and Sugiyama (1995a) do note that the majority of leaves selected belong to two species – *H.brauniunum* and *Carpara procera* – both large, hairless, and flexible.[29] Strong preference and shared properties of the two leaf species could suggest a perception of affordance relevance relative to the task context (i.e. perception that these particular properties afford absorbency, relevant to the efficient control of liquids), indicative of grade 3 causal cognition. If so, longitudinal studies by Sousa et al. (2009) and Biro et al. (2006) suggest this perceptual capacity is almost certainly an emergent function of

[27] Lamon et al. (2018) found that moss sponges were more efficient in terms of absorption rate and time required to manufacture. Chimpanzees which had previously expressed both moss-sponging and leaf-sponging behaviours, preferentially selected moss over leaf materials.
[28] 70.3% of the leaf tools in Tonooka's (2001) study belonged to the same species – *H.braunianum*.
[29] Sousa (2011) found a significant correlation between leaf-tool weight and quantity of water held – larger tools were concluded to carry more water.

practical experience, scaffolded by access to others discarded tool materials. Use of leaf tools for drinking water is established among Bossou chimpanzees as young as 1.5 years of age, however, despite sometimes attempting to constructing leaf tools themselves, infants younger than 3.5 years exclusively use tools discarded by, or begged from, other individuals – usually the mother (Biro, Sousa and Matsuzawa, 2006; Sousa, Biro and Matsuzawa, 2009). Tools constructed by juveniles in this period are generally unusable, with failures attributed to the use of inappropriate raw materials - leaves which are too small resulting in tools which fall apart, and leaves collected from the ground are often too dry and so crumble. That adult tools were found to be larger and more efficient (carrying a greater volume of water per submersion) than those of younger chimpanzees, and that juvenile chimpanzees over the age of 3.5 continued to reuse discarded tools after successfully learning to shape their own, suggests access to discarded tools serves as a "large, 'supernormal' stimuli" (Sousa et al., 2009, p122) – scaffolding the acquisition of tool-manufacturing and tool-behavioural skills by enabling younger, unskilled individuals to obtain a greater amount of water than they might otherwise. Tonooka (2001) observes that, once established, manufacturing techniques varied with age; 'leaf sponging' was most often, if not exclusively, performed by juveniles – adults chimpanzees did not chew leaves prior to use, only folded them – indicating a possible transient tool-use stage between inexpert ('leaf spoon') and more experienced ('leaf fold') techniques. Though by no means definitive, a transient stage between leaf spooning and leaf folding supports the hypothesis that individual material engagement, and the past engagement of others, is key to the development of expert cognition for this skill, as it is only through practical interaction that chimpanzees appear to discover the alternative technical affordances of the leaf material - in this case the enhanced absorbent property afforded by effective tool-modification.

Noting the transition between juvenile and proficient techniques of leaf-tool-use at Gombe, McGrew (1977) writes of one infant's bout: "playful characteristics in the behavioural sequence are manifest. Dipping is exaggerated to splashing, and this is repeated throughout the bout. The infant interrupts the sequence with irrelevant activity… Although most of the elements are singly present,

the complete sequence of leaf sponging is never performed… it is impossible to say whether the infant is playfully sponging or spongily playing" (McGrew, 1977, p. 277). Rather than trial-and-error progress towards a preconceived technical function, the transition to proficient technique is characterised as an emergent singular purposivity arising through the gradual refinement of playful, or explorative, engagements. For McGrew (1977), the development of leaf-sponging technique is also a process of socialisation: as with many other chimpanzee tool behaviours, use of leaves to drink water is often performed in a social context, where opportunities to observe skilled performance of the behaviour, by mothers or by other adult conspecifics, are abundant. By drawing attention to particular aspects of their own practice, adult behavioural models inadvertently contribute to the normative shaping of juveniles' landscape of affordances (following Rietveld and Kiverstein, 2014). In exploring the diffusion pattern of recently innovated 'moss-sponging', among the Sonso community, Hobaiter et al. (2014) found uptake was significantly influenced by social learning (though the specific mechanism was not identified), with the pattern of behavioural transmission matching patterns of association within the social network. Notably, Hobaiter et al. (2014) report that leaf-sponge re-use at Sonso typically only occurred as an interruption to, or shortly following, the original tool-makers tool using, and rarely in their absence [as Sousa et al. (2009) report sometimes occurs at Bossou], suggesting that the perceived salience of the leaf-sponge tools is perhaps either limited to, or at the least strongly enhanced by, direct observation of their use. Conversely, at Bossou, Tonooka (2001) notes juveniles increased their observation of others' tooling behaviour in the period prior to their own successful manifestation of the behaviour – suggesting that information from others behaviour became more perceptually relevant as individual familiarity of tool function increased. Consequently, it is argued that, although causal cognition in leaf-sponging is generally more adequately descriptive of grade 2 cued dyadic-causal understanding, at Bossou, increasing familiarity of tool function may lead to an emergent recognition of the shared purposivity embodied in others' tooling actions (i.e. grade 3, conspecific mind-reading). Though independent learning may be a large component of the learning and

refinement process for manufacturing technique, social learning via grade 2 cued-dyadic cognition is likely to play a significant role in directing attention towards the critical affordances of the tool and tool-using task.

With regard to higher grades of causal cognition, some researchers, notably Sugiyama (1995a), have argued that Bossou chimpanzees ability to arrive at drinking sites with leaves already in their mouths is evidence of 'planned' tool-use, lending support the assumption that chimpanzees possess a level of causal understanding of the self in future scenarios and the ability to forward mental time travel (grade 3 self-mind-reading). However, even adapted to fit the non-representational framework of this thesis, such an assumption should remain tentative at best since there is no way of determining (without further information) that discovery of the leaf material does not simply afford as much impetus to search for water as the discovery of a water hole solicits the search for leaf material. Flexibility in the order of the operational sequence could suggest a level of embodied causal reasoning in which the principles of object combination may be perceived independently of any precisely ordered action sequence required to bring that combination about. Flexibility is also found in the contexts and resources in and to which leaf tools are applied: leaf-sponging has been alternatively reported at Bossou to target the collection of fermented sap produced by humans tapping oil-palm trees (Hockings *et al.*, 2015), as sequential tool-using, when performed as part of 'palm sap collect' (see Section 4.2.5), and as compound tool-use, when used in conjunction with a probe tool in 'push-pull' (Sugiyama and Koman, 1979b; Sugiyama, 1995a). Transfer into alternative contexts and the ability to combine functional behaviours suggests a flexible underlying embodied causal understanding of the physics of the leaf/moss tool in isolation of any particular task context (a precursor to grades 5-7 causal cognition). As previously argued in the Chapter 3 (Section 3.6.1.7), sequential tool-use could be seen as an indicator of, or potential precursor to, grade 7 causal network understanding, since it brings together domain specific knowledge to produce shared function. Here, it is argued that the behaviour 'push-pull' is more likely indicative of the latter, since the super-ordinate affordance ultimately produces is not

creatively novel – i.e. it simply combines the two separate causal functions of the tool aspects (i.e. extension of reach and containment of liquids), whereas to qualify as grade 7, they must combine to produce a novel, shared causal function (e.g. combination of the ability to apply torque with the ability to apply friction, producing the ability to apply heat with fire). A better candidate for grade 7 is 'moss-sponging' among the Sonso community, which Hobaiter *et al.* (2014; see also Lamon *et al.*, 2018) argue represents a cumulative adaptation of 'leaf-sponging' behaviour, exchanging one material for another, more effective one. Cumulative culture has previously been considered an exclusive characteristic of human material repertoires, however, the flexibility and entanglement of chimpanzee tools to collect water challenges this assumption (though see Dean *et al.*, 2014).

Turning to algae-scooping, use of scooping wands to extend the reach of the body suggests partial grade 3 causal understanding of the self and of the tools' causal function as an extension of the self through peri-personal space, and group-wide spread/inter-site differences do suggest grade 2 causal cognition is present. Ontogeny is unknown, though lack of tool performances among individuals aged 2 years or less does indicate a minimum age for behavioural uptake. It is also difficult to extrapolate the degree of sensitivity to epistemic feedback produced through pragmatic tool action from the behavioural descriptions available, mature tool users do appear to select and shape their scooping-wands to match changes in task context, and in particular, to match the location and relative abundance of algae floating at the pond surface – switching tools during a bout to maximise efficiency (Matsuzawa, Yamakoshi and Humle, 1996; Humle, Yamakoshi and Matsuzawa, 2011; Matsuzawa, 2019). Algae wands are broadly categorised into two forms, flexible hooked wands (often made of fern, for its' natural hooked ends), and longer, sturdier, smooth wands (Matsuzawa, Yamakoshi and Humle, 1996; Matsuzawa, 2019). Hooked wands are thought to function better for fine-scooping, close to the water's edge, and smooth wands, for collecting algae from farther away (Humle, Yamakoshi and Matsuzawa, 2011). A bout may often involve use of shorter hooked tools before longer smooth tools, suggesting an ability to flexibly respond to changes in the affordances of the diminishing algae (i.e. grade 3). Evidence for grade 3 self-mind reading is

also represented by the substantial differences in tool lengths and predominant shapes of tools used at different sites, which further support the argument that algae-scooping chimpanzee individuals perceive and are solicited by the affordances relevant to the specific challenges presented by the same task in their local ecological contexts. Shorter hooked tools are predominant at Bossou, where algae is removed from the surface, while longer, smooth tools are predominant at Bakoun, where chimpanzees need to reach the bottom of deep water (Boesch *et al.*, 2016).

In terms of degree of material constitution, leaf tools meet the criteria for minimal constitution only. Though their use does not provide a novel function, chimpanzees often collecting water by hand, it does supplement pre-existing behaviour by increasing scope and effectivity, enabling access to harder to reach water sources – namely water collected in the hollows of trees (Sugiyama, 1995a; Biro, Sousa and Matsuzawa, 2006). Although there is no strict seasonality to leaf tool-use at Bossou, and techniques are practiced year round, Sugiyama (1995a) found frequency of sponging/folding behaviour was increased during the dry season when water was low in the area. Variance in technique means some individuals are able to 'outperform' others; but, by enabling access to water trapped in tree hollows, leaf tool-use thus provides a population-level adaptive advantage by maximising access to water resources in times of drought as well as year-round. Depending upon the historical climate, it may be the case, particularly given the universality of leaf-tools used in water collection, that this form of tool-use has, in the past, been maximally constitutive to cognition (to the extent perceptual relevance has become genetically predisposed) – at drier sites, tool-use still provides an important source of access to water in higher-up parts of the habitat where water does not pool (e.g. McGrew, 1977). In contrast, algae-scooping is considered strongly (though still not maximally) constitutive to Bossou chimpanzee technical cognition: use does not provide a wholly novel function, chimpanzees having been observed collecting algae by hand (Devos *et al.*, 2002; Sakamati, 1998), but does increase scope of consumption at the site. Yamakoshi (1998) found tool-assisted feeding constituted 100% of algae-consumption over a one year period. Humle *et al.* (2011, p. 120) note that algae are "very filamentous and slimy" such that collection by hand appears

less efficient than by tools. Increased efficiency in algae consumption could provide adaptational advantage by providing unprecedented levels of access to a highly nutritious food resource in an area otherwise low in water and other food resources. Opportunistic exploitation of algae increases dietary breadth, potentially decreasing in-group feeding competition. Consumption rates at Bakoun imply algae is a preferred resource, exploited when opportuned rather than as a necessity (Boesch *et al.*, 2016). Since algae distribution is densest in areas of deep water, Boesch *et al.* (*ibid*) argue the exploitation of tools may increase the efficiency of algae collection by enabling access without prolonged immersion into water, reducing the risk of injury associated with traversing slippery stones in the riverbed. Bakoun "algae fishing" differs from "algae scooping" at Bossou, in that chimpanzees at Bakoun scrape the bottom of the riverbed rather than simply collecting the algae floating on the water surface.[30] The risks associated with immersion in deep water are therefore much greater at Bakoun than at Bossou; however, given the presumed hydrophobic nature of chimpanzees (Goodall, 1986), it is possible algae-scooping at Bossou still functions as an innovation designed to maximize exploitation of a preferred, and advantageous, resource whilst minimizing the water 'hazard' (though see Nishida, 1980).

4.2.5 Subsistents for the processing of oil palm-products

Oil palms and their products play a role in the nesting and feeding behaviour of chimpanzees at the majority of study-sites where they are available (Mahale being the exception), though the significance of this role, and the number of palm parts consumed varies site-by-site.[31] Chimpanzees at Bossou rely heavily on palm resources, especially in times of scarcity (Humle & Matsuzawa, 2004; Yamakoshi, 1998, 2001). Palm products consumed include leaf petiole, palm heart, resin, pith, mesocarp fruit, inflorescences, nuts, and even the palm wine produced by humans (Hockings et al.,

[30] It is likely the differences in technique reflect different target species of algae rather than culturally distinct patterns.
[31] McGrew (1985) notes that oil palm were either absent, or beyond the shorter reach of chimpanzee ranges, at Mount Assirik, Senegal, and Budongo, Uganda; explaining why oil palm products are not processed (or rarely processed) at these sites.

2015; Humle & Matsuzawa, 2004; Sugiyama & Koman, 1979; Yamakoshi, 1998; Yamakoshi & Sugiyama, 1995). 4 technical variants in the Bossou repertoire aid in the acquisition and processing of palm products: these are, 'nut-crack', 'anvil prop', 'pestle-pound', and 'palm-sap collect'.

Nut-crack 'Nut cracking' is considered one of the most complex tool variants performed by non-human primates (Boesch et al., 2017; Matsuzawa, 1996; Sanz & Morgan, 2010; Visalberghi & Fragaszy, 2012), and the only NHP variant besides aimed throwing in which non-organic materials are customarily selected for use as tools. With the behaviour functioning to remove the hard outer shell of nuts whilst leaving their kernel intact, successful extraction of the kernel is reliant upon the efficient hierarchical spatial and temporal coordination of its three external aspects: nut, hammer-stone, and anvil - the latter two considered a 'composite' tool-set (following Carvalho et al., 2008; Sugiyama, 1997). Nut-cracking appears endemic to western chimpanzee groups (Sugiyama and Koman, 1979b; Boesch and Boesch, 1981; Anderson, Williamson and Carter, 1983; Whitesides, 1985; Kortlandt and Holzhaus, 1987; Yamakoshi and Matsuzawa, 1993), but is surprisingly absent in eastern and central populations despite suitable ecological conditions (Boesch et al., 1994; McGrew, 1992; McGrew et al., 1997; Sanz & Morgan, 2007; Whiten et al., 2001). This has led previous authors to speculate nut-cracking maybe limited to the sub-species *P.t.verus*, and bounded by the geographical barrier of the Nzo-Sassandra river (Boesch *et al.*, 1994); though more recent reports of nut-cracking in Cameroon have since challenged this hypothesis (Morgan and Abwe, 2006). At Bossou, cracking of oil palm nuts (*Eliaeis guineensis*) is the most frequently observed tool variant, performed customarily, and year-round (Humle, 2003; Humle, 2011; Sugiyama & Koman, 1979; Yamakoshi, 1998). To perform the behaviour, chimpanzees first gather and, where necessary, transport a hammer and anvil stone to the cracking site – usually at the base of a nut-producing oil palm (Carvalho, 2011; Sakura & Matsuzawa, 1991). Crouching next to the anvil, the chimpanzee selects a nut and places it in a stable position in the cavity formed by the anvil surface. The hammer-stone is then gripped in one hand and used to repeatedly strike the nut upon the anvil, with the chimpanzee pausing occasionally to check the status of the nut-shell. When the shell is split, the

chimpanzee removes the kernel with their fingers and consumes it. The process is often repeated, and when a nut-supply is exhausted, the chimpanzee often transports the hammer and anvil to another site to continue (Biro, Sousa and Matsuzawa, 2006, p. 484). Figure 11 (p. 121) gives nut-cracking as a single perception-action module in which the super-ordinate affordance (extraction of palm kernels) is distributed between 4 foci: the chimpanzee, two discrete non-organic materials which form the hammer and anvil, and the oil palm nuts. 3 spatial relationships were counted to Object order, 1 static (between nut and anvil) and 2 dynamic (between hammer-stone and nut; nut and anvil). The minimum behavioural sequence is described by 10 critical actions (maximum = 12), in 5 phases. Tool modification was classed as linkage, with the functionality of the tool-set dependent upon the composite juxta-positioning of the hammer and anvil as two distinct objects.

Anvil prop Matsuzawa (1991b; see also Biro et al., 2006; Susana Carvalho et al., 2008) reported that in some instances, during the nut-cracking process), chimpanzees positioned a small stone under one end of the anvil, effectively stabilising the striking surface by keeping it level. The behaviour is unique to the Bossou repertoire, where it is classed as habitual (Humle, 2011; Whiten et al., 1999, 2001), and is considered a form of meta-tool-use (see Section 3.5.4.1) – the function of the tool being to supplement the efficacy of another tool (i.e. the hammer and anvil composite set used in nut-cracking), rather than to provide a novel function of itself. For this reason, the variant 'anvil prop' has been classed as belonging to the functional context 'other', rather than as an independent subsistent. Figure 12 (p. 122) & 13 (p. 123) gives use of an anvil prop as an optional iterative loop integrated within the perception-action module 'nut-crack' (see Figure 11, p. 121). The super-ordinate affordance in this case arises through the interplay of 5 focal aspects: the chimpanzee, an inorganic material which forms the anvil prop, two separate objects which when used together form

Figure 11 Cognigram for the Bossou variant 'Nut crack'

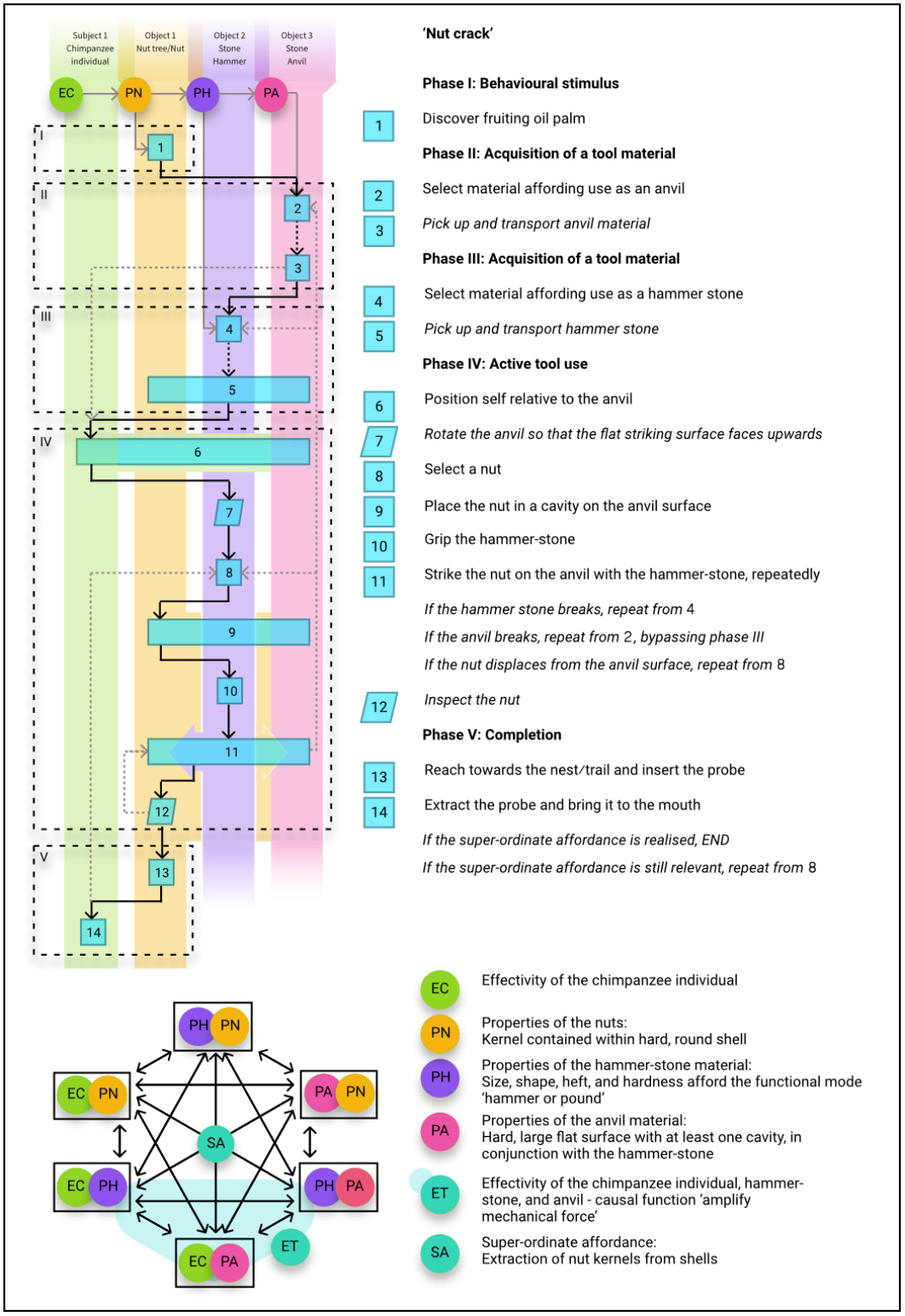
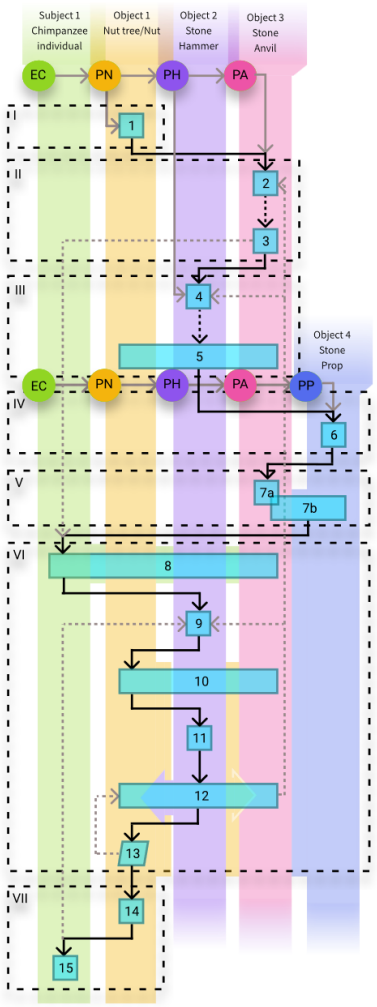


Figure 12 Cognigram for the Bossou variant 'Anvil prop'



'Anvil prop' in association with 'Nut crack'

Phase I: Behavioural stimulus

1 Discover fruiting oil palm

Phase II: Acquisition of a tool material

2 Select material affording use as an anvil

3 *Pick up and transport anvil stone*

Phase III: Acquisition of a tool material

4 Select material affording use as a hamer stone

5 *Pick up and transport hammer stone*

Phase IV: Acquisition of the meta-tool material

6 Select material affording use as anvil prop

Phase V: Active meta-tool-use

7a Rotate and lift the anvil

7b Apply the prop underneath the anvil, bringing the anvil surface level and steady

Phase VI: Active tool-use

8 Position self relative to the anvil

9 Select/pick up a palm nut

10 Place the nut in a cavity on the anvil surface

11 Grip the hammer stone

12 Strike the nut on the anvil with the hammer stone, repeatedly

If the hammer stone breaks, repeat from 2*, bypassing phase III*

If the anvil breaks, repeat from 4

If the nut displaces from the anvil surface, repeat from 7

13 *Inspect the nut, bite the shell*

Phase VII: Completion

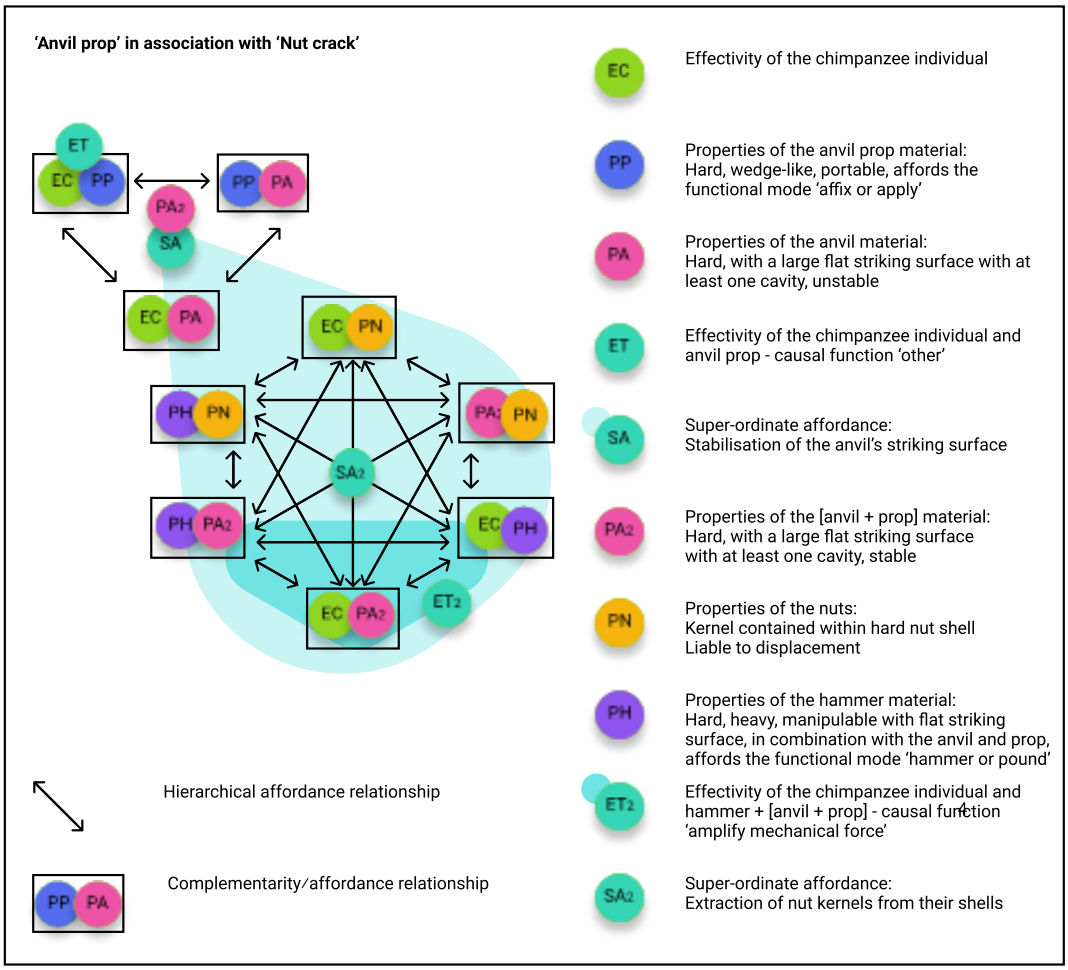
14 Place the hammer stone to one side

15 Extract the kernel from its shell with the fingers, and consume

If the super-ordinate affordance is realised, END

If the super-ordinate affordance is still relevant, repeat from 9

Figure 13 Affordance relationships making up the Bossou variant 'Anvil prop'



the hammer and anvil composite tool-set, and the nut kernels encased within their shells. 4 spatial relationships were counted for Object order, 2 static (between prop and anvil; nut and anvil) and 2 dynamic (hammer-stone and nut; nut and anvil). The combined minimum operational sequence is described by 13 critical actions (maximum = 15), in 7 phases, with no modificatory actions besides curation. Manufacture mode is classed as linkage, and involves association of the anvil prop with the anvil, and of the anvil with the hammer.

Pestle-pound Unlike nut-cracking, 'pestle-pounding' is behaviourally unique to Bossou, where it is habitual amongst the adult chimpanzee community (Humle & Matsuzawa, 2004; Sugiyama, 1994; Yamakoshi, 2011; Yamakoshi & Sugiyama, 1995). Following the description provided by Yamakoshi (2011, p. 108), pestle-pounding can be broken down into two distinct, sequentially performed feeding behaviours: non-tool assisted processing and consumption of palm leaf petioles; followed by use of the detached petioles to excavate the palm heart, enabling access to, and consumption of the palm pith. The first behaviour, petiole feeding, typically begins when a chimpanzee enters the crown of an oil-palm tree; the chimpanzee fans out the mature leaves with their hands and feet, pressing them down to expose the younger palm stems. These are then grasped in a bunch and uprooted, giving access to the soft white base of the petioles, which the chimpanzees chews and eats. Yamakoshi and Sugiyama (1995; see also Yamakoshi, 2011) noted in their observations that extraction of the leaf stems appears very difficult, and that chimpanzees often tried multiple times without success, resting between attempts. Successful uprooting of the stems creates a vertical hole (or holes) in the palm crown, and it is these holes which the chimpanzee then exploit in order to access the palm heart by pestle-pounding. To perform the second behaviour, pestle-pounding, the chimpanzees stands upright on the crown, and, gripping a discarded leaf still resting on the radiating leaves at the crown in both hands, uses it as a 'pestle' to repeatedly pound and deepen the hole in the meristem. The tool is then extracted, and after licking the petiole for any pith attached, it is put aside. The chimpanzee then inserts an arm into the hole to extract and eat the pulped fibres.

Figure 14 Cognigram for the Bossou variant 'Pestle-pound'

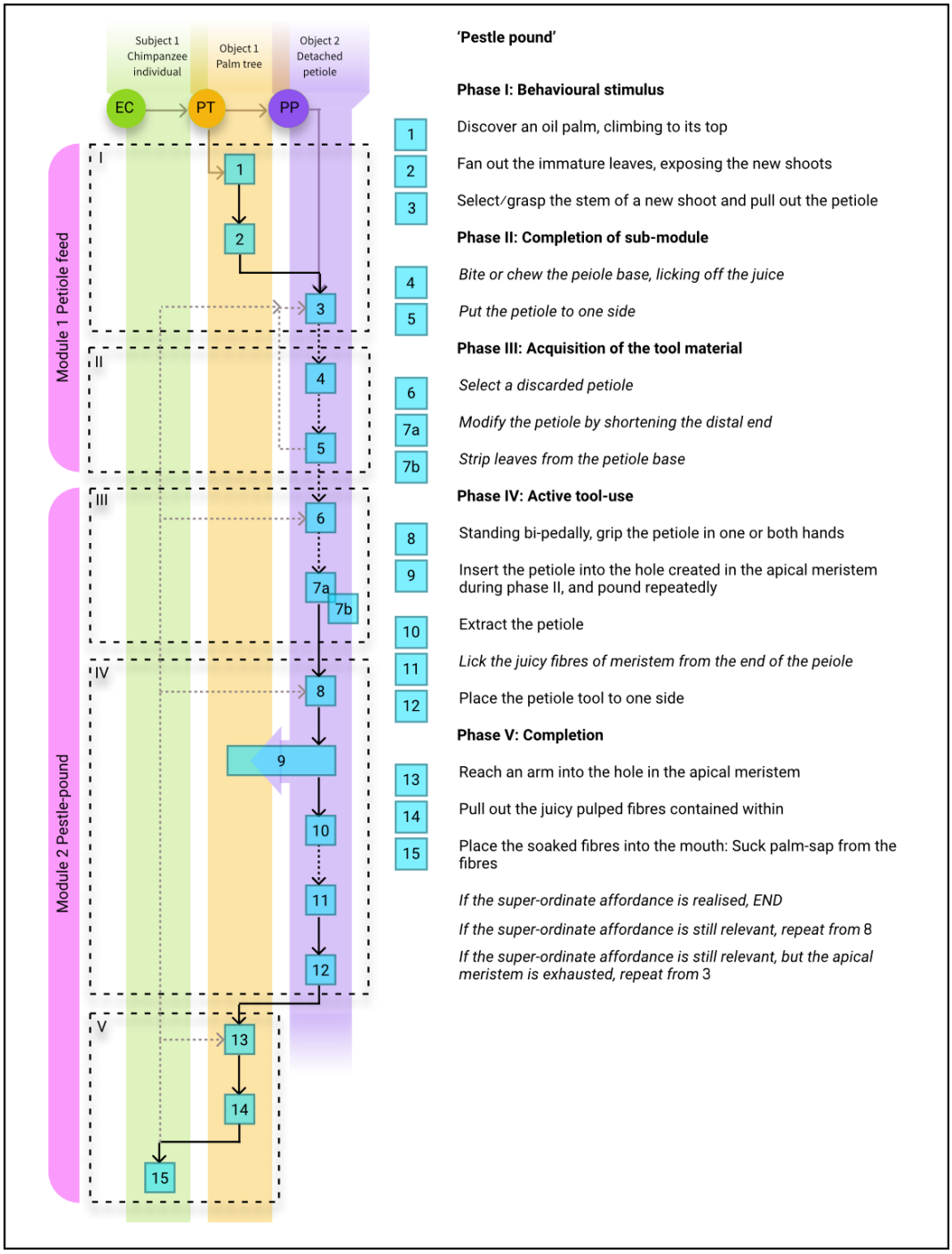


Figure 15 Affordance relationships making up the Bossou variant 'Pestle-pound'

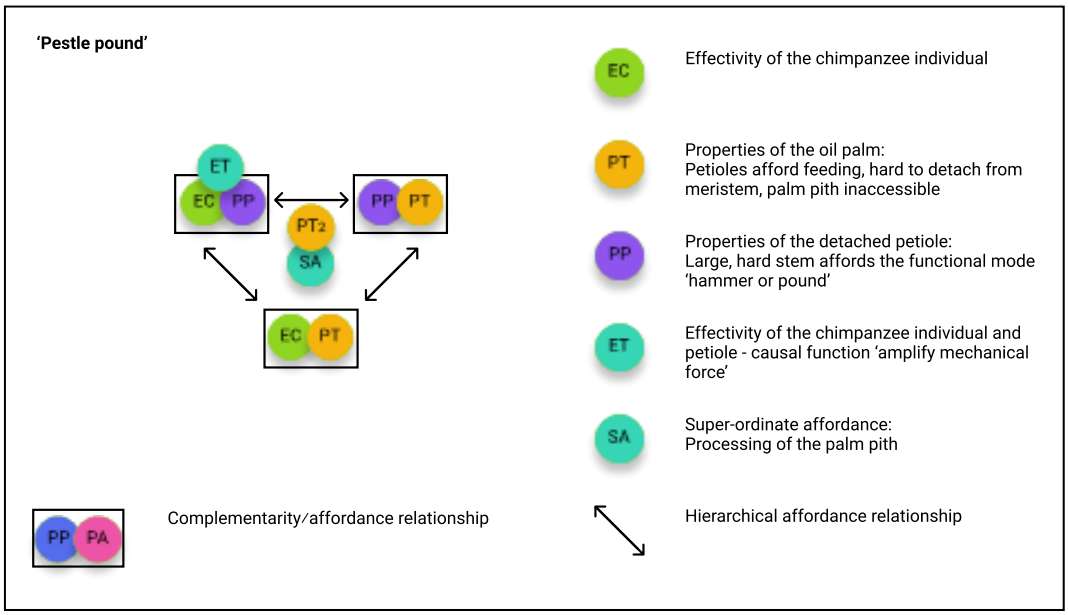
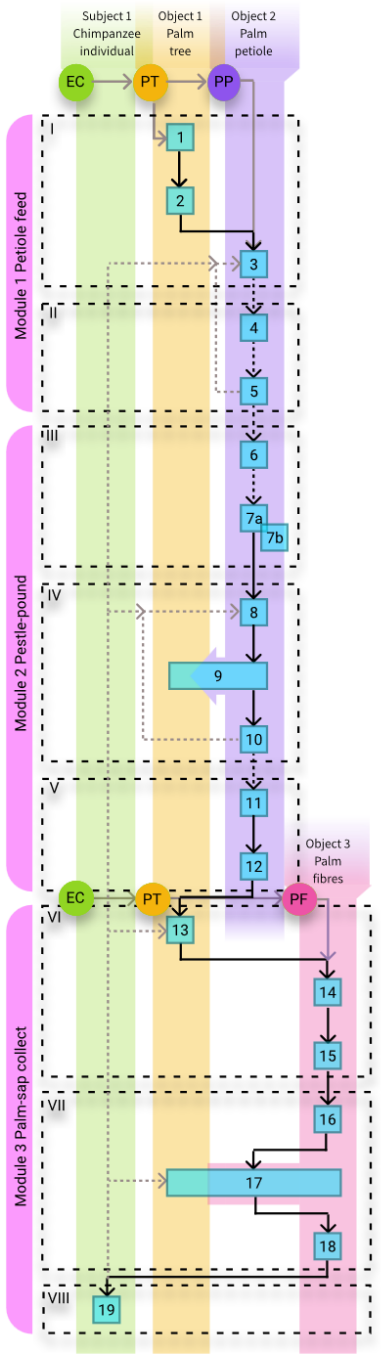


Figure 14 (p. 125) & 15 (p. 126) present pestle-pounding as a compound perception-action sequence formed by the sequential association of the modules 'petiole feed' and 'pestle-pound'. The super-ordinate affordance of the behaviour arises through the dynamic interplay of 3 foci: the chimpanzee, leaf petiole which is first partially consumed, and then used as a tool, and the pith contained in the apical meristem of the oil palm plant. 1 dynamic relationship (between pestle and palm-crown) was counted for Object order. Minimal operational sequence length is comprised of 10 critical actions (maximum = 16), in 6 phases. 2 modifications have been counted towards technical complexity for the behaviour, including shortening of the distal end of the petiole tool, and stripping of leaves near the petiole base (following Humle & Matsuzawa, 2004, p. 560) – each classed as reductive reshaping.

Palm-sap collect Chimpanzees at Bossou have also been observed to combine pestle-pounding with leaf-sponging, in a feeding behaviour Sugiyama (1994) termed 'fibre-sponge sucking', since referred to as 'palm-sap collection' (Humle, 2003, 2011). According to Humle's (2003, 2011) reporting of the Bossou technical repertoire, palm-sap collection is not customary among the adult population, and given that the behaviour is reliant upon exposure of the apical meristem afforded by pestle-pounding, it can be assumed that the behaviour is an opportunistic innovation, idiosyncratic to the site.[32] Sugiyama (1994) reported an anecdotal observation in which, following pestle-pounding, a female chimpanzee reached her arm into the excavated hole and pulled out some of the pulped fibres, which she chewed and sucked "as she would a sponge" (*ibid*, p. 327). She then dropped the chewed fibre-sponge back into the hole, before bringing it back up, and sucking sap from it again. Figure 16 (p. 128) & 17 (p. 129) give palm-sap collection as a compound action-perception sequence formed by the sequential association of the modules 'petiole feed', 'pestle-pound', and 'fibre-sponge' (a variation of the technique, 'leaf-sponge'). The super-ordinate affordance of the technical variant is distributed between 4 foci: the chimpanzee, the leaf petiole

[32] The variant is not referenced independently in the cross-site repertoire comparisons by Whiten et al. (1999, 2001), nor by Sanz & Morgan (2007) – most likely it has been treated as a variety of leaf sponging, as for moss sponging.

Figure 16 Cognigram for the Bossou variant 'Palm-sap collect'



'Palm sap collect' in association with 'Pestle pound'

Phase I: Behavioural stimulus

1 Discover an oil palm, climbing to its top

2 Fan out the immature leaves, exposing the new shoots

3 Select/grasp the stem of a new shoot and pull out the petiole

Phase II: Completion of sub-module

4 *Bite or chew the peiole base, licking off the juice*

5 *Put the petiole to one side*

Phase III: Acquisition of the tool material

6 *Select a discarded petiole*

7a *Modify the petiole by shortening the distal end*

7b *Strip leaves from the petiole base*

Phase IV: Active tool-use

8 Standing bi-pedally, grip the petiole in one or both hands

9

10 Extract the petiole

Phase V: Completion of sub-module

11 *Lick the juicy fibres of meristem from the end of the peiole*

12 Place the petiole tool to one side

Phase VI: Acquisition of a tool material

13 Reach an arm into the hole in the apical meristem

14 Pull out the juicy pulped fibres contained within

15 Modify the fibrous material by placing into the mouth and chewing carefully

Phase VII: Active tool-use

16 Take the fibres from the mouth

17 Place the fibres into the hole in the apical meristem, and soak in the palm sap

18 Extract the soaked fibres

Phase VIII: Completion

19 Extract the kernel from its shell with the fingers, and consume

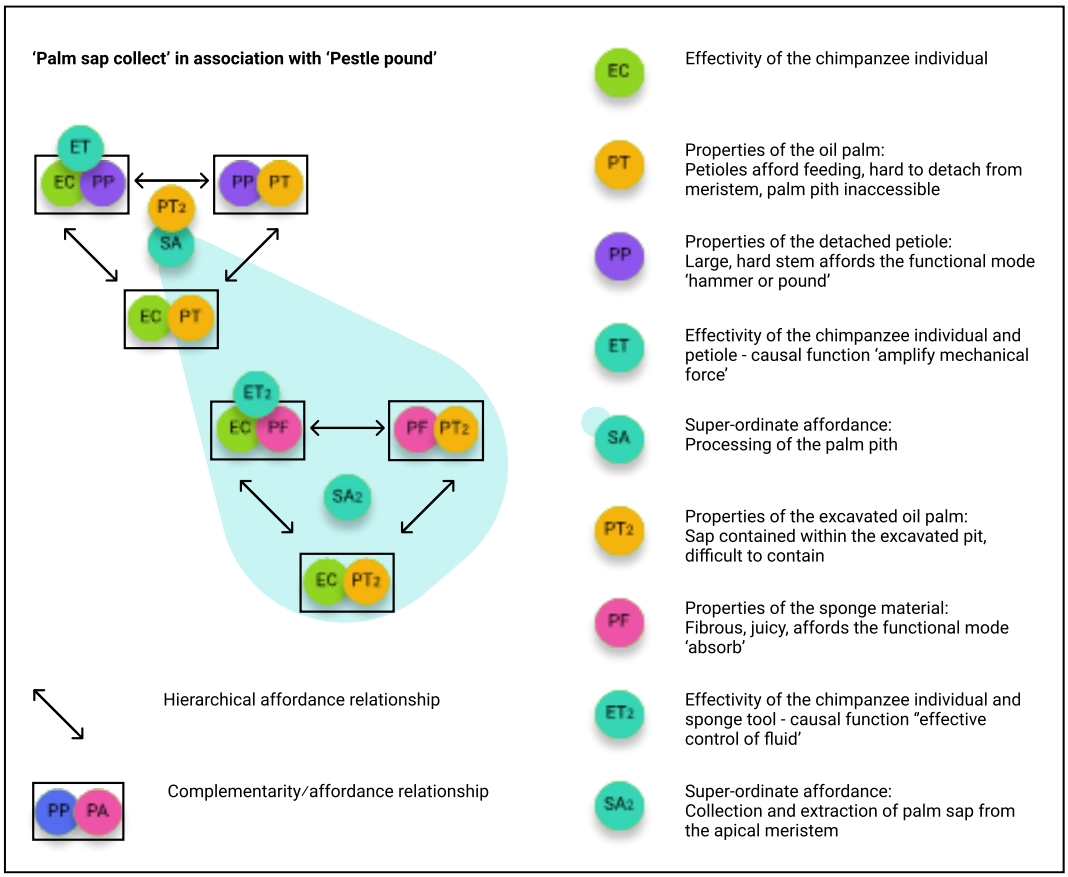
If the super-ordinate affordance is realised, END

If the super-ordinate affordance is still relevant, repeat from 16

If the super-ordinate affordance is still relevant, but the sponge tool no longer affords use, repeat from 13

If the super-ordinate affordance is still relevant, but the apical meristem is exhausted, repeat from 3

Figure 17 Affordance relationships making up the Bossou variant 'Palm-sap collect'



which is first partially consumed, and then used as a tool, the pith contained in the apical meristem of the oil palm which is first partially consumed, and then used as a tool, and the sap contained within the excavated hole in the palm crown. 2 spatial relationships were counted towards Object order, 1 static (between fibre sponge and hole in the apical meristem) and 1 dynamic (between sponge and palm-sap). The minimal sequence length is described by 14 critical actions (maximum = 20), in 8 phases. 3 modifications have been counted towards the technical complexity of this variant, including the 2 entailed in 'pestle-pound', shortening of the distal end of the petiole tool, and stripping of leaves near the petiole base; and an additional 1 for the module 'fibre-sponge', chewing of the pith fibres. Primary mode of modification has been taken as replicative reshaping, as per the variant 'leaf sponge' (see Section 4.2.3).

4.2.6 Causal cognition in tool-assisted oil palm processing

Studies on the kinematics of nut-cracking show successful tool-use is dependent upon the efficient management of force transfer through the hammer-stone, which, in conjunction with the anvil acts to amplify the mechanical force of their user. To crush the shell casing without effecting damage, or displacing the nut kernel requires an elastic blow in which total kinetic energy is preserved (Bril et al., 2009, 2011; 2012; Fushimi et al., 1991): in practical terms, proficient tool-use not only requires chimpanzees select tools based on their functional affordance, but also that they adjust their striking actions according to the functional properties of the tools selected (i.e. grade 3 causal cognition in the form of self-mind-reading). Preliminary experiments among captive chimpanzees, and evidence from Bossou and Taï suggests that this is the case: Bril *et al.* (see also Foucart *et al.*, 2005; 2009; 2011) found more experienced adult chimpanzees successfully adjusted their strike force and amplitude with the weight of the tool in order to conserve overall kinetic energy, whilst also adapting the amplitude, angle of incidence, and regularity of strikes to immobilise nuts on smoother surfaces. Experiments at Taï found chimpanzees lifted tools to different amplitudes according to the resistance of the nut species processed (Gunther and Boesch, 1993; see

also Visalberghi *et al.*, 2015), while an in depth study by Sirianni et al. (2018) found the Taï chimpanzees modulated strike amplitude according anticipated tool weight, and again retrospectively, to experienced tool weight. While artificially hollowed-out hammers were initially lifted with a higher acceleration, overshooting typical strike amplitude, in subsequent use this effect was gradually mitigated as the chimpanzees 'tuned down' lifting acceleration (Sirianni *et al.*, 2018). At Bossou, material selectivity in tool choice demonstrates recognition of the functional affordances of both hammer and anvil tools, with shape appearing as a significant factor in tool choice, including flatness of the striking surface as a selection criterion for both hammer and anvil (Sugiyama and Koman, 1979b; Fushimi *et al.*, 1991; Biro, Sousa and Matsuzawa, 2006). Sugiyama and Koman (1979b) describe deliberate placement of nuts within the cavities on the anvil surface, caused by previous tool-use, which functioned to further stabilise the nut and prevent fly-off, while Fushimi et al. (Fushimi *et al.*, 1991) observe that Bossou chimpanzees often rotated anvils in order bring the striking surface into a horizontal position. Chimpanzees may also use anvil props to stabilise the anvil (hypothetically representative of grade 6 or 7 causal cognition if treated as secondary tool-use), however, the purposiveness of this behaviour hard to establish. Biro *et al.* (2006; see also Biro *et al.* 2010), for example, discuss the possibility of accidental meta-tool-use, suggesting the placement of the wedge stone maybe an incidental result of the chimpanzee rolling the anvil into a suitable position, prior to cracking, the anvil so happening to fall on top of a wedge-like stone, as opposed to deliberate placement as a response to the functional affordances of anvil and wedge. Besides shape, the functional assignment of used stones is also reflected in their weight and size: Bossou hammer-stones were found to be significantly smaller and lighter than anvils, with only a small degree of overlap (Sakura and Matsuzawa, 1991; Biro, Sousa and Matsuzawa, 2006). Interestingly, Biro *et al.* (2006) found smaller hammer-stones approaching the lower weight limit (0.5kg) which were frequently used were those with compact shape and one or more flat surfaces, suggesting a perceptive trade-off between optimum weight and optimum shape for grip and striking angle.

Many of the above mentioned studies stress this kind of technical cognition as a function of direct practical engagement and experience with tool materials (e.g. Biro et al., 2006; Bril et al., 2011; Foucart et al., 2005; Fushimi et al., 1991), a pattern confirmed in the longitudinal data detailing ontogeny of nut-cracking behaviour at Bossou.[33] Studies by Inoue-Nakamura and Matsuzawa (1997) and Biro et al. (2006) show frequency of nut-cracking-related object manipulation increases at the site with age, with the nature of manipulations developing through four recognisable, progressively complex, stages, beginning with single object manipulation of nuts and stones at age 1.5 years; transitioning into object association, placing nuts on anvils and hitting nuts with the hands or feet; followed by successive combinatory manipulations, placing a nut on an anvil and striking it with a hand; and finishing, with the emergence of successive combinatory manipulations, co-ordinated in the appropriate sequence to perform nut-cracking behaviour, at around age 3.5 years (see also Hayashi & Inoue-Nakamura, 2011). Studies of efficiency show a gradual honing of bodily technique through practice, resulting in a greater number of nuts cracked per minute, and fewer strikes required to access the kernels (Humle, 2003; Biro, Sousa and Matsuzawa, 2006). Whereas adult chimpanzees displayed high levels of tool-fidelity and "stereotyped" bodily technique, consistent from one bout to the next, Biro et al. (2006, p. 492) observed juveniles frequently changed preferred hand and tools during bouts, consistent with Bril et al.'s (2011) observation that captive chimpanzees often switched tool when nuts responded "rebelliously" to the hammer or anvil, as though tuning their perception of appropriate tool form. Throughout the formative process, infants and juveniles display persistent interest in the tools, tool-related materials, and tool activities of others; besides scrounging of nuts and shells from anvils, infants have also been observed to touch their mother's tools, even holding their mother's hand or arm during her tool-use (Inoue-Nakamura and Matsuzawa, 1997; Matsuzawa *et al.*, 2001; Biro, Sousa and Matsuzawa, 2006; Hayashi and Inoue-Nakamura, 2011). Exploring the scaffolding effect of

[33] Fushimi (1991) reports that whereas adult males chose heavier tools, and modulated strike force, reducing total number of strikes necessary to crack the nuts, less experienced juvenile and adolescent tool-users often selected hammers too light for the task.

others' tool materials at Bossou, Fragaszy et al. (2013) found nut-cracking tools previously curated and used by others comprised 40% of unweaned juveniles' (i.e. <5 years of age) tool selections and use, their re-use maintaining the same previous hammer and anvil components, and typically occurring at the same previous site of use. As individuals became more experienced, and their opportunities for re-use more competitively constrained, re-use was found to diminish, juveniles between 5 and 10 years of age re-using tool materials in only 20% of observed occasions – a similar level to that observed among proficient adults (Fragaszy, Biro, *et al.*, 2013). Increased chasing away of more experienced juveniles is likely to bring about the end of the critical sensitive period for development of the nut-cracking skill, with individuals who had not acquired the behaviour by age 7, never doing so (Inoue-Nakamura and Matsuzawa, 1997; Matsuzawa *et al.*, 2001; Biro, Sousa and Matsuzawa, 2006; Hayashi and Inoue-Nakamura, 2011; Fragaszy, Biro, *et al.*, 2013).

As Fragaszy et al. (2013) point out, increasing competitive constraints do not prohibit the re-use of tools between use episodes, such that the early education of attention necessary for technical enskilment seems reliant upon the stimulus enhancement afforded by concurrent tool-use (grade 2 cued-dyadic causal cognition). That said, the more durable aspects of past tool-use provide local enhancement which is clearly influential to affordance perception, and constitutive to the technical cognition of nut-cracking tool-users. At both Taï and Bossou, for instance, tool-users have been observed to preferentially place nuts in the hollow depressions on the anvil surface which are formed through sustained past practice, and which afford immobilisation of the nut (Sugiyama and Koman, 1979b; Boesch and Boesch, 1983); Foucart et al. (2005) write, "if after a long period of use, the cavity is too large or covered with shell fragments that might impede its movements, the chimpanzee will move the nut to another place on the anvil or to another anvil". Meanwhile, spatial distribution and redistribution of tool-related resources around the landscape directly shapes their future movement: At Taï, for example, Sirianni et al. (2010) found material selection was influenced by tool mass and transport distance relative to the anvil, as well as by the nature of the anvil site, with preferred tool weight increasing as transport distance decreased, and lighter hammers

preferred when cracking on a tree as opposed to an embedded stone substrate. Tool transport also occurs at Bossou (though to a lesser extent, and over smaller distances than at Taï), and uniquely among chimpanzee sites, includes transport of portable anvil stones, enabling independent re-use of each functional component by other conspecifics at the same or another location – all other sites making use of embedded anvils only (Fragaszy et al., 2013). Suitable hammer-stone and anvil materials are available throughout the Bossou forest (Sakura and Matsuzawa, 1991). Although Sugiyama (1981) originally found Bossou chimps only cracked at trees where stones were readily available, further research by Carvalho (2011) found chimpanzees often transported hammer and anvil stones, and occasionally nuts, to cracking sites, creating cumulative palimpsests of suitable tool materials around nut-producing trees – oil-palm-trees, as opposed to anvils, forming the geographic determinant, or focus, of the tool-site and cracking activity. Transportation and engagement in the context of nut-cracking directs attention in both the immediate and longitudinal sense, scaffolding future engagement by curating the ecological and associative contexts in which these tool-related materials are encountered. Biro et al. (2006) report that, upon approaching the nut-cracking site, chimpanzees collected stones and transported them to nut piles, moving the same tools from pile to pile scattered around the clearing as they exhausted each resource.

Strong localisation of tool-activity as well as delayed re-use of anvil pits could be considered foundational to grade 4 causal cognition, emergent in the establishment of community specific canonical affordances (following Borgo *et al.*, 2013). Limited behavioural evidence does exist which could support such the presence of canonical affordances, including the preferential re-use of previously combined pairings of hammer-stone and anvil components (Carvalho *et al.*, 2009), which in combination with low levels of tool multi-functionality, could indicate the perception of strict artefact roles and criteria. At Taï, neighbouring chimpanzee groups exhibit 'local' nut-cracking strategies which cannot be explained solely with regard to ecological conditions, each group making preferential selection of differing materials (Luncz, Mundry and Boesch, 2012). Luncz and Boesch (Luncz and Boesch, 2014) found an immigrant female adhered to local 'norms' of technical

behaviour, adapting her tool-using behaviour and material preferences to match those of the new group, despite similar ecological opportunity and an overall reduction in energetic efficiency. Discerning symptom from cause is difficult, however, since adjusting behaviour is arguably important both in the sense of achieving informational and normative conformity (Cladiere and Whiten, 2012), especially when faced with the new ecological and social challenges that come with female-immigration. Though ecology is likely to remain broadly similar, incoming females are still challenged with foraging in a new territory, comprised of differing resource distribution and availability – learning from others how to find and process local food resources is an effective by-pass to the effort a single individual would otherwise need to dedicate to independent discovery. Adopting the local behaviour of a new group may also function to reduce aggression directed towards incoming females, managing others perception in order to hasten social integration (Kahlenberg et al., 2008; Lydia V. Luncz & Boesch, 2014).

In contrast to nut-cracking, little is known about the ontogeny or origin of pestle-pounding; however, since the behaviour is present among almost all tool-using individuals of the Bossou community and not at any other site (even where ecological conditions might support uptake), it is most often assumed to be an individual innovation, likely derived from the established petiole-feeding tradition already present at the site, and since socially transmitted beyond its initial innovator (Yamakoshi, 2011). Social context and the availability of behavioural models to facilitate transmission marks another point of difference between the two behaviours – whereas nut-cracking takes place terrestrially, and is a highly conspicuous activity, pestle-pounding takes place in the socially isolated context atop the narrow palm-crown. Acquisition of pestle-pounding, in common with nut-cracking, is fostered by the opportunities for practical engagement afforded by past tool-use, with petiole feeding and past tool-use scaffolding future tool-use through the provisioning of readily available tools (i.e. the discarded leaf petioles), and visible exposure of the apical meristem (Yamakoshi and Sugiyama, 1995). Several authors have postulated that environmental scaffolding, by-passing the need for tricky tool acquisition and manufacture, is critical for uptake of the

behaviour in juveniles and others for whom the removal of usable palm-fronds is too difficult or requires too much strength; Yamakoshi (2011), for example, observes that though juveniles practice pestle pounding from the age of 4, no individual of this age is able to yet engage in petiole feeding. Investigating the effect of scaffolding, Fragaszy et al. (2013) found Bossou chimpanzees could pull out fronds at a mean age of 6.9 years, and that younger juveniles were dependent upon re-use of recently abandoned sites at which tools were still present – usually those previously utilised by the chimpanzee mother. Motivation to engage with the tool context appears independent of food rewards, and practice occurred even in instances in which the holes in the apical meristem had been made too deep for the juvenile to reach and extract pith fibres. As with other behaviours at the site, the proportion of episodes involving re-use of others' tools was found to decline with age (Fragaszy, Biro, *et al.*, 2013). Investigating experience-related levels of technical proficiency, Humle (2003) found no significant differences between adult and sub-adult tool-using efficiency; however, trends were identified which suggested a potential gap between the ages in terms of total pith harvested, including a higher pounding rate, and increased time spent extracting per extraction, among adults. Humle (2003) notes the possibility that, even once able to extract palm-fronds, sub-adult individuals may lack the strength to pestle-pound as effectively, suggesting a period of skill-honing through practice is required subsequent to successful manifestation of the tool-method; further, since extraction often requires insertion of the arm up to the shoulder, it is possible body-size constrains ability.

In terms of degree of material constitution, both nut-cracking and pestle-pounding behaviours can be considered maximally constitutive to Bossou chimpanzees' technical cognition. Each provides a novel function - the oil-palm's apical meristem and nut kernels being otherwise inaccessible; [34] and both are likely provide an adaptive benefit - through the provisioning of access to highly nutritious, additional palm-resources - with the added import that these and other palm

[34] Although Boesch and Boesch (1982) found oil-palm nuts are likely soft enough to open without the aid of stone tools, they also suggest the process of opening nuts with the teeth may cause long-term damage such that it is not worth the effort, especially considering the high volumes of nuts consumed (up to 200 in a day).

resources are utilised as fall-back foods by the chimpanzees at the site (Yamakoshi and Sugiyama, 1995; Yamakoshi, 1998). Across a twelve-month period, Yamakoshi (1998) reported cracking tools accounted for 91.3% of total time spent feeding on seeds, whilst petiole feeding comprised 43% of time spent feeding on pith. Inter-site behavioural variation in performance (or lack thereof) for both behaviours, particularly between neighbouring communities lends support to the hypothesis that broad patterns of material engagement (i.e. beyond the tool activity itself), across time, are constitutive to local tradition and technical cognition. Comparing the neighbouring sites of Bossou, Yeale, and Seringbara, Humle & Matsuzawa (2004) found relative frequency of pestle-pounding and petiole feeding at each site correlated with the degree of spatial clustering of palm-trees distributed throughout the local habitat, raising the proposition that encounter rate determined by habitat use, as opposed to sheer ecological opportunity, is vital to engagement. This may account for absence of petiole feeding and pestle-pounding at sites such as Seringbara, where ecological conditions are suitable, but the chimpanzee community do not exploit any part of the oil-palm. At Bossou, in contrast, pressure to exploit oil-palm resources as fall-back foods likely increases the rate of engagement with the palms' potential tool contexts. Exploitation of oil-palm nut kernels, mesocarp, and occasionally the fibre of dead trees (Yamakoshi and Sugiyama, 1995; Yamakoshi, 1998), increases interaction with the oil-palm resource, and thus promotes likelihood of behavioural innovation. Interestingly, Humle (2003) notes pestle-pounding behaviour frequently occurred prior to nesting in oil-palms, with the additional observation that 52.1% of direct observations of nesting followed Bossou chimpanzees processing and consumption of some part of the palm. In the same study, Humle & Matsuzawa (2004) hypothesise a similar potential scenario could explain geographic distribution of nut-cracking, and in particular, absence of such behaviour among communities east of the Nzo-Sassandra river. The authors argue that though crack-able nuts and suitable materials are available, the introduction of oil-palm in west-central Africa is, in fact, far more recent than in West Africa, having taken place during in the early Holocene (Adebidi Sowunmi, 1999; also cited by Humle & Matsuzawa, 2004), and that exploitation of oil-palm products by eastern communities is therefore

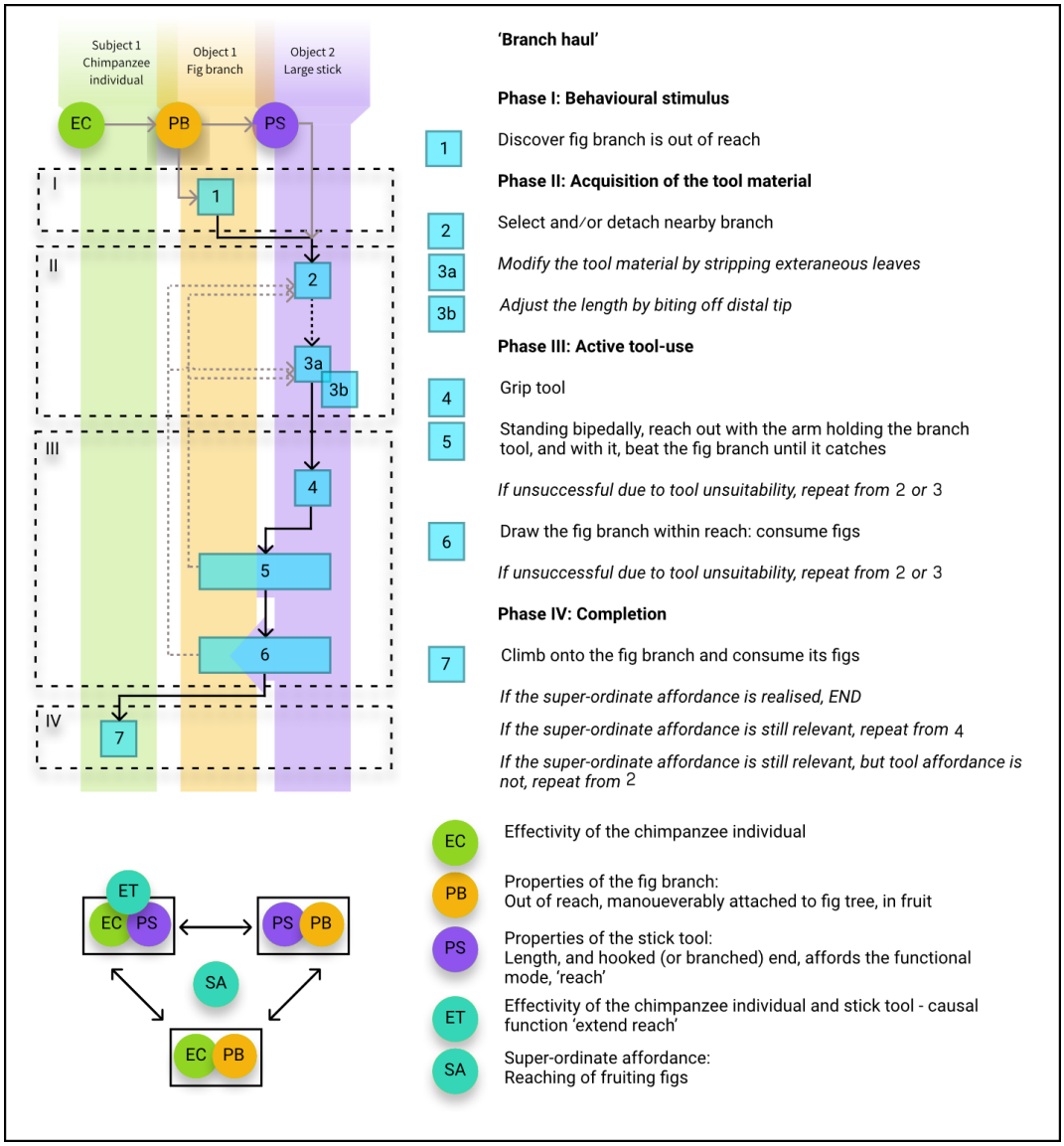
likely to be a much more recent innovation. With this being the case, we can hypothesise that it is through the long-term association, and through the engagement of successive generations accumulating multiple sites which increase opportunity, focus the attention and afford new behavioural possibilities, that complex tool innovation occurs and is maintained. Considering the centrality of the oil-palm to daily chimpanzee life at Bossou, and to the movement of materials around the Bossou landscape, it seems unsurprising that it is also the focus point associating several forms of tool-use, and that these variants also become entangled to produce novel, sequential forms of more 'complex' tool-use such as 'palm-sap collection' and 'anvil prop' (see section 4.2.5).

4.2.7 Other subsistents

3 subsistents have been reported at Bossou which function outside the three major contexts (insect predation, water collection, and processing of palm-products) covered by the previous sections: these are 'branch haul', 'expel', and 'resin pound'. The variants listed in this section are less frequently observed, with only 'expel' classed as customary, and appear of a more *ad hoc* nature than the majority of those listed in other sections; consequently, reporting of all three variants is largely anecdotal.

Branch haul First observed at Bossou in 1977 by Sugiyama and Koman (1979b), the variant 'branch haul' (see also 'branch hook', Whiten et al., 1999, 2001) is unique to Bossou, and involves use of a long branch to hook and pull another branch closer. Sugiyama and Koman (1979b) reported an episode in which adult male chimpanzees at Bossou were observed using long sticks as hooks to bring a fruit-bearing branch within reach, and emphasise the tool-use as a spontaneous act of

Figure 18 Cognigram for the Bossou variant 'Branch haul'



innovation responding to a specific circumstance. The male chimpanzees, unable to reach a branch covered in figs, broke off small branches with twigs from a nearby tree, and removed their bark and side branches with the teeth producing hook-style sticks. The chimpanzees grasped the sticks and attempted to reach the fig branch, standing bipedally, and extending the hook tool towards the branch. Once a stick was caught in the branch, the successful chimpanzee brought the branch down with its weight, until it was able to climb up onto the now-in-reach fig branch. Figure 18 (p. 139) shows this behaviour as a single perception-action module, in which the super-ordinate affordance of fig acquisition and consumption is constituted by three foci: the male chimpanzee, the branch which forms the reaching-stick-tool, and the fruiting fig branch. 2 spatial relationships were counted to Object order, 1 static (between hooked branch and fig branch) and 1 dynamic (between hooked branch and fig branch). The minimal operational sequence is comprised of 6 critical actions (maximum = 8), in 4 phases. 2 modifications by reductive reshaping have been counted towards the technical complexity of this variant: adjustment of tool length by biting of the distal tip, and stripping of excess twigs/side-branches.

Expel Though use of larger sticks and branches for reaching maybe rare outside of captivity, use of 'expelling' or prising stick tools in the rousing and/or hunting of vertebrate and invertebrate prey has been observed at a number of wild chimpanzee field-sites (Huffman & Kalunde, 1993; Nakamura & Itoh, 2008; Nishida, 1973; Pruetz et al., 2015; Pruetz & Bertolani, 2007; Whiten et al., 1999, 2001). Few reports exist in the published literature concerning hunting of vertebrates at Bossou, though rare non-tool-assisted predation is known to take place (Carvalho et al., 2010; Sugiyama, 1981, 1989; Sugiyama & Koman, 1987). Humle (2003, 2011) reported tool-assisted expelling of vertebrates as customary at Bossou, describing in particular, an episode in which prising tools were used to expel a tree pangolin from its nesting hole: upon discovery of the nesting hole, Humle (2003) observed that a chimpanzee detached a long thin branch, removed its protruding leaves, adjusted the tool length

Figure 19 Cognigram for the Bossou variant 'Expel'

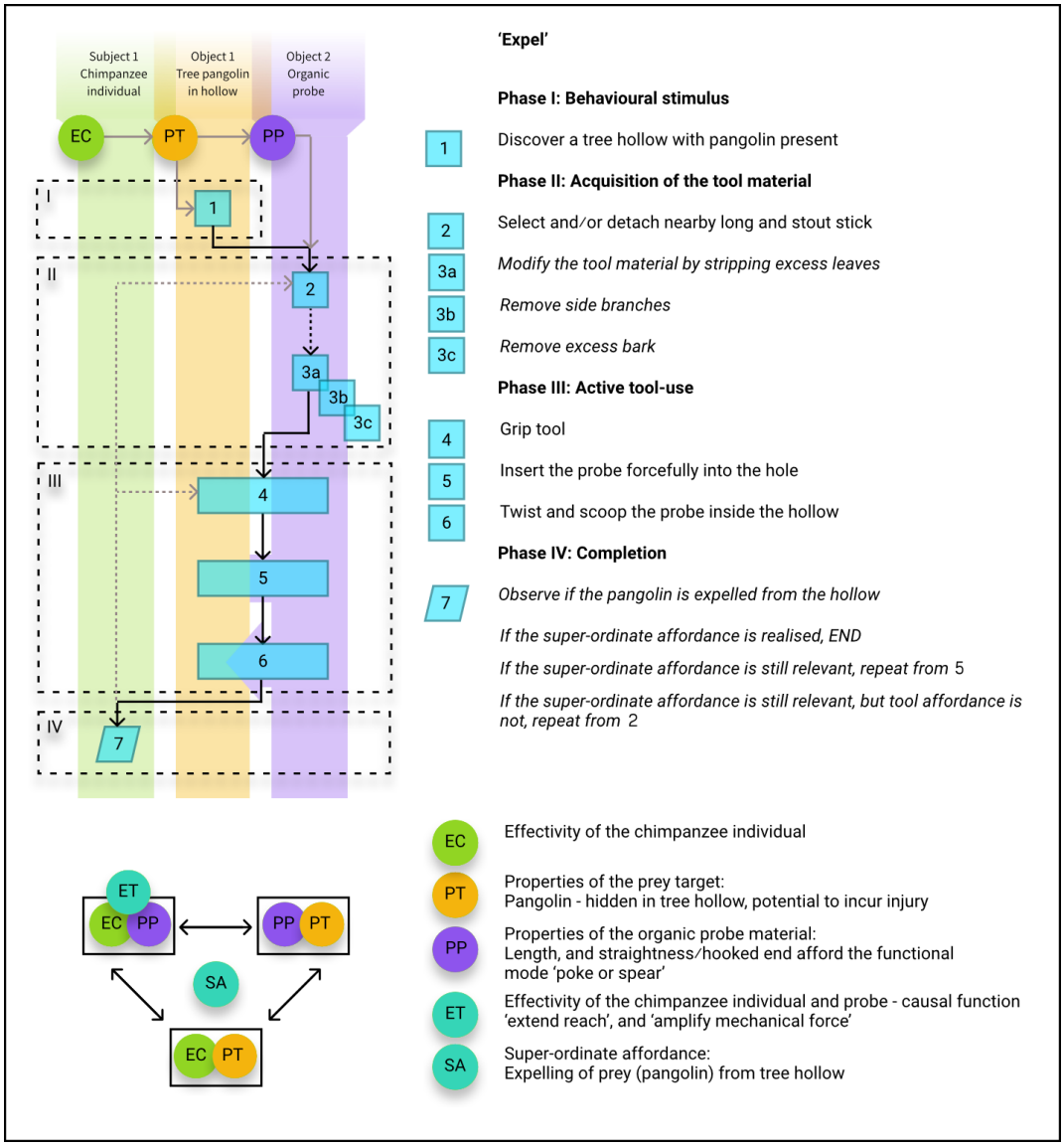
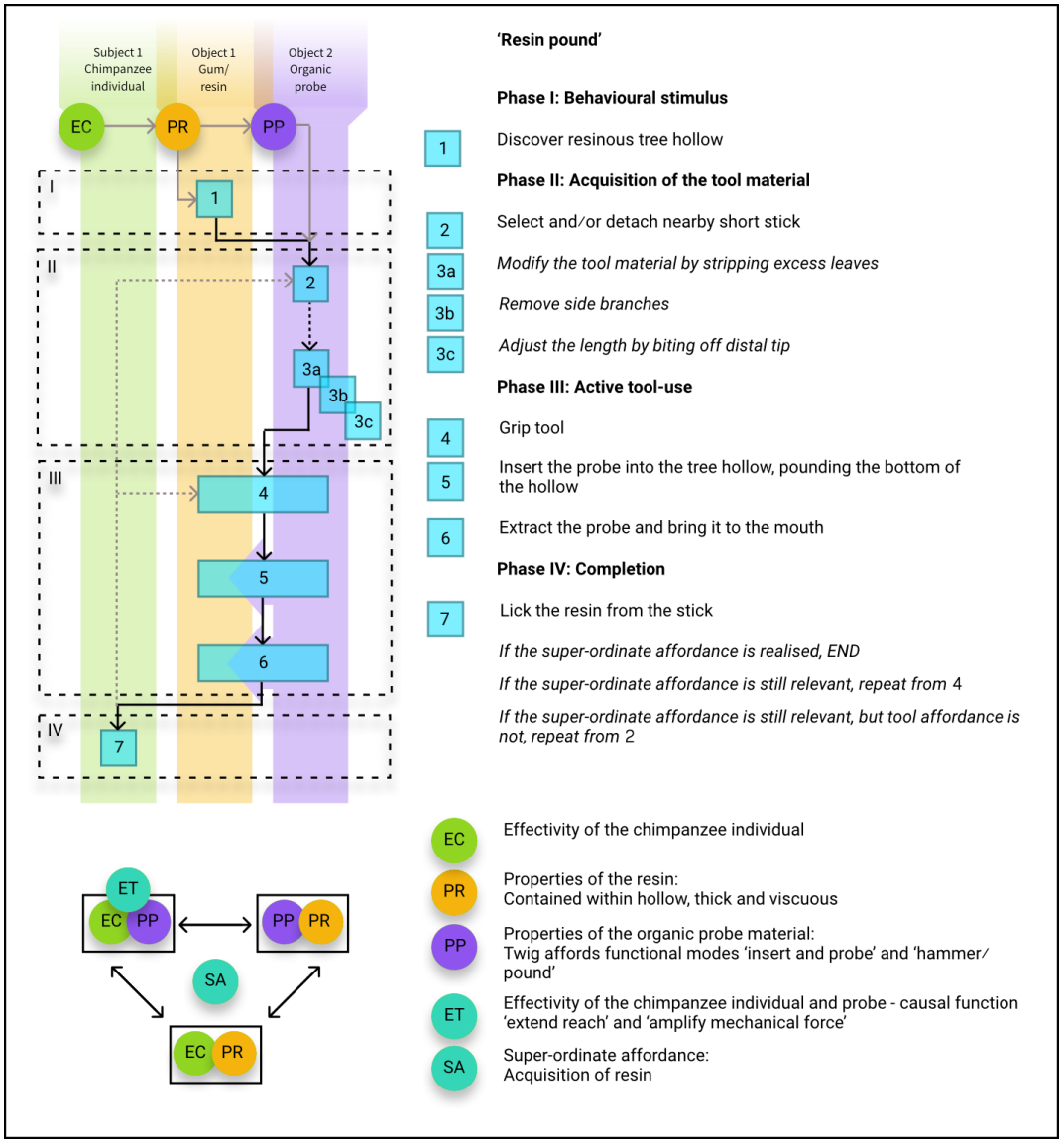


Figure 20 Cognigram for the Bossou variant 'Resin pound'



by biting, and thinned the end by stripping the bark with its teeth. The branch tool was then inserted forcefully into the hole in a 'jabbing' or 'spearing' motion, followed with a sharp twisting and scooping motion of the tool. Figure 19 (p. 141) depicts expelling behaviour as a single perception-action module, in which the super-ordinate affordance of the tool is seen to arise through the dynamic interplay of 3 foci: the chimpanzee, the stiff organic material which forms the probe/spear, and the vertebrate prey hidden and protected within its nesting hole. 2 spatial relationships were counted for Object order, 1 static (between expelling tool and hollow entrance) and 1 dynamic (between expelling tool and hidden allospecific). The minimum operational sequence length includes 6 critical actions (maximum = 9), in 4 phases. Humle (2003) reported modifications to the tool both prior to, and during use, and included 3 total possible actions: stripping of excess leaves, adjustment of length, and thinning of the bark at the tip.

Resin pound Sugiyama and Koman (1979b) reported five adolescent and juvenile Bossou chimpanzees' performance of 'resin pounding', a variant behaviourally similar to insect pounding (Section 4.2.1); in the episode described, probes fashioned from organic stick materials were observed inserted into tree hollows (always *Carapa procera*), and used to pound, mix and stir the resin inside. The broken down resin was seen to adhere to the probe ["conglutinated stickily onto it" (Sugiyama and Koman, 1979b, p. 515)] so that when extracted, the resin could be drawn from the hole. The chimpanzees then licked the resin from the stick and repeated the process, presumably re-using the same tool throughout the episode. In order to manufacture the probe tools, Sugiyama and Koman (1979b) reported that the chimpanzees detached sticks and removed their side branches and excess leaves with their teeth. Figure 20 (p. 142) presents resin pounding as a single perception-action sequence in which the super-ordinate affordance of the tool-using task is comprised by 3 foci: the juvenile or adolescent chimpanzee, the stick material which forms the probe tool, and the resin encased inside the *Carapa* tree hollow. 2 Spatial relationships were counted for object, both dynamic [between probe and resin (pounding); probe and resin (extraction)] The minimal operational sequence is described by 6 critical actions (maximum = 9), in 4 phases. The 3

modifications of the probe tool include adjustment of length, stripping of excess leaves, and removal of side branches – each classed as reductive reshaping.

4.2.8 Causal cognition in other subsistents

Branch haul, expel, and resin dip, each represent spontaneous cases of tool-use in which probe tools function to extend the reach of the user, with transfer of force direct from subject to tool, and agential perception extended through the peri-personal space of the probe tool (grades 1 & 3). Only prising tools used in the expelling of vertebrate prey are customary, however, both resin dipping and branch hook were performed by more than one individual, concurrently and/or immediately sequentially, suggesting at least grade 2 cued-dyadic causal-reasoning is also present and that others perceive the causality and super-ordinate affordance of other tool-users material interaction, if not its causal function - much of the spontaneous tool-use was reported as ineffective and/or unsuccessful (Sugiyama and Koman, 1979b; Humle, 2003). That said, in each case, chimpanzees were observed to adapt their tools to the parameters of the tool task: Sugiyama & Koman (1979, p515) note the resin-pounding probe tools that they observed used were longer than those used for insect pounding, the sturdiness and control afforded by a shorter stick more perceptually relevant than the affordance of a longer tool to avoid insect bites. Expelling and prising behaviours, as well as the behaviour 'branch haul' were each reported to exhibit high levels of reflexivity during the bout, or bouts, including re-posturing, tool re-shaping, and tool replacement (though this was also a factor of the arboreal context – tools which were dropped, were lost).

Notably, for branch-hauling, the arboreal context is unlikely to support the same kinds of tool-reuse, which for other chimpanzee behaviours contributes to the virtuous cycle of re-emergent opportunity scaffolding the enskilment process; in the episode of observed by Sugiyama & Koman (1979b), for instance, the authors describe at least nine tools being used by three chimpanzees in the course of one bout. Tool re-use did not occur, apart from when the same tool form was modified

to a smaller length, and the chimpanzees never retrieved used sticks from the ground (Sugiyama and Koman, 1979b, p. 520). Expelling and prising behaviours which share an arboreal context - and for which re-use is similarly diminished - are more likely to have achieved customary status among the Bossou community due to their similarity and degree of behavioural overlap with other technical behaviours already present in the tool repertoire: e.g. other inserting and probing tools such as 'ant dip', 'investigatory probe', etc. Expelling behaviour is less complex (and less delicate) than many other chimpanzee probe-tool foraging behaviours, as is clear from the opportunistic criteria by which chimpanzees appear to select their prising tools: Humle (2003) reports prising tools were made of a single tree species, which was clearly the nearest material to hand. Vines were available but ignored, suggesting that although chimpanzees affordance perception does reflect the functional needs of the task, perceptual relevance is strongly influenced by time-pressure.

All variants described in the previous section have been scored as minimally constitutive to cognition, none providing a novel function, but each to some degree increasing the scope and effectivity of pre-existing abilities. While for branch haul and resin pound, this means enabling access to otherwise inaccessible food resources; for expel, tool-benefits are muddied by unknown tool function. As mentioned in the behavioural description given in the previous section, vertebrate predation, and hunting of vertebrates for predation, particularly, is rare among the Bossou community, as is ecological opportunity (Carvalho et al., 2010; Sugiyama, 1989; Sugiyama & Koman, 1987). Of the anecdotal reports which were found, most detail chance discovery of a vertebrate prey species, without any active pursuit, and with captures attracting little interest among conspecific adults (Carvalho et al., 2010; Sugiyama, 1981, 1989). In several accounts, the captured animals were 'toyed' with, and not eventually consumed (Carvalho et al., 2010; Hirata et al., 2001). Expelling behaviours may thus be more explorative than necessarily predatory, and the benefit to the user is, at the very least, facilitation of access to potentially difficult to reach areas whilst minimising risk of injury inflicted by the disturbed animal.

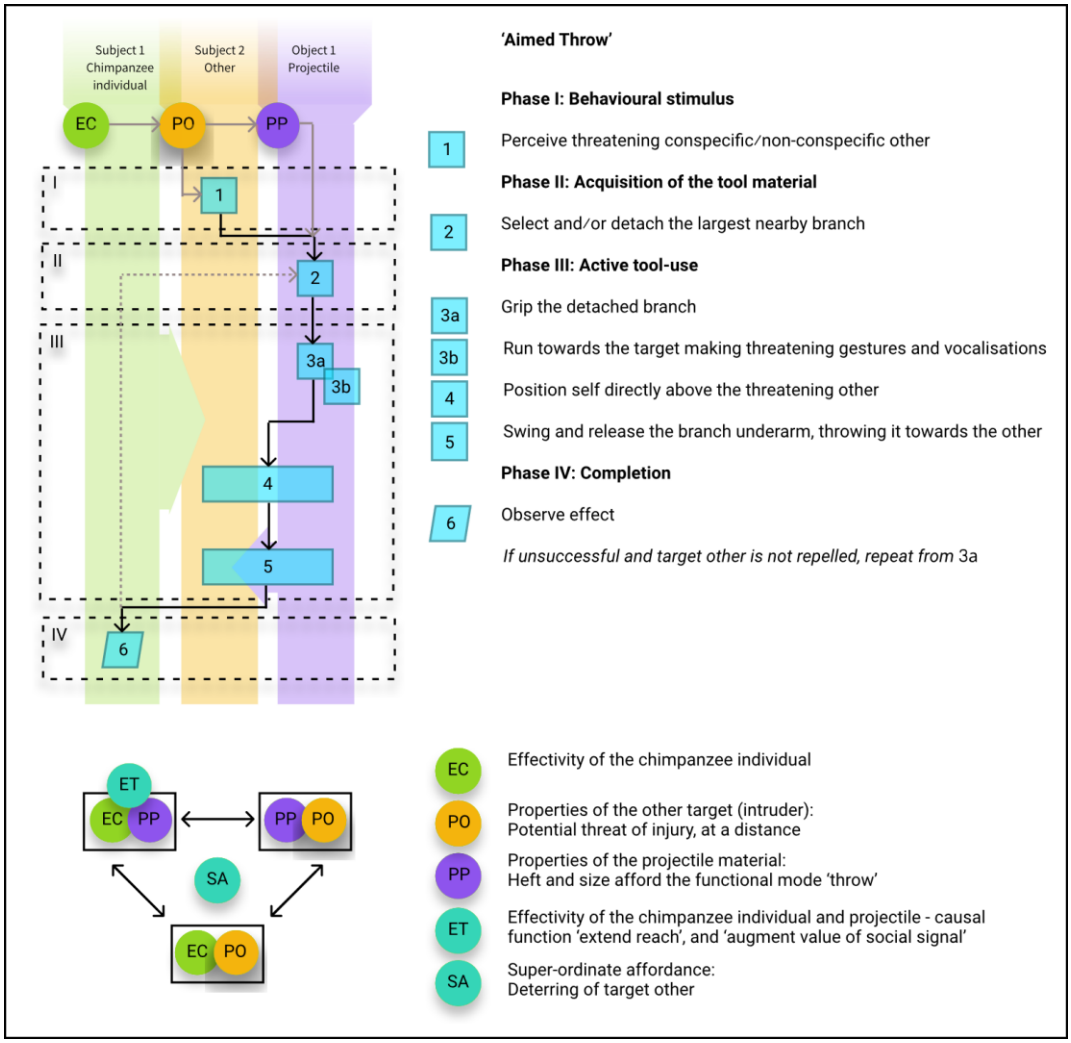
4.2.9 Social tool-use variants

4 Bossou variants function in a social context, as part of social display, or to solicit attention or a behavioural response from another, including: 'Aimed throw', 'branch drag', 'flail or club', and 'leaf clip'.

Aimed throw Chimpanzees at Bossou, as well as those at other chimpanzee sites, have been observed to throw stones and branches in agonistic displays directed towards both conspecific and non-conspecific others (Albrecht & Dunnett, 1971; Boesch & Boesch, 1989, 1990; Goodall, 1964, 1968; Matsuzawa, 1999; McGrew et al., 2003; Nishida et al., 2009; Sugiyama & Koman, 1979). The behaviour is classed as customary by Humle (2003, 2011; see also Whiten et al., 2001),[35] and is most often performed by adults, most especially males, though juveniles and adolescents have also been observed to incorporate object throwing into their play behaviours (Sugiyama and Koman, 1979b; Myowa-Yamakoshi and Yamakoshi, 2011; Koops, Furuichi, *et al.*, 2015). Sugiyama and Koman (1979b, p. 515) describe a typical case as follows: responding to the intruder, the chimpanzee (in this case the dominant and third male) breaks off the largest branch nearest to hand, and grips the branch, carrying it as they run toward the target, all the while making exaggerated threatening gestures and vocalisations. Stopping almost directly above the target, the chimpanzee swings the branch underarm to throw it. In many cases the intruder was deterred. Figure 21 (p. 147) shows the variant, 'aimed throw' as a single perception-action module, in which the single problem of repelling another (conspecific or otherwise) is resolved through dynamic interplay of three foci: the chimpanzee, the organic or inorganic material which forms the tool/projectile (e.g. a branch or stone missile), and the recipient conspecific/non-conspecific other. 1 dynamic relationship (between

[35] Matsuzawa (1999) has aimed throwing classed as habitual only.

Figure 21 Cognigram for the Bossou variant 'Aimed throw'



projectile and threatening other) was counted to Object order. Minimal critical actions required to describe the behaviour are 7 (maximum = 7), in 4 phases. No modifications are counted besides, in some cases, the detachment of organic missile materials from their tree substrates. Reuse is not recorded for the behaviour since use was effectively exhaustive.

Branch drag According to Whiten et al.'s (Whiten *et al.*, 1999, 2001) cross-site comparison of tool repertoires, 'branch dragging' is a universal chimpanzee behaviour, typically performed by males as part of their social displays (see also Albrecht & Dunnett, 1971; Boesch & Boesch, 1990; Matsuzawa, 1999; Teleki, 1973). At Bossou, the behaviour is habitual, rather than customary (Humle, 2003, 2011). Since no detailed behavioural description could be found from the published literature from Bossou, Nishida et al.'s (1999) generic ethographic description was used to construct the cognigram for this behaviour.[36] Nishida et al. (1999) describe branch dragging as follows: A male chimpanzee detaches or takes the end of an already detached branch, and, grasping it with one hand, drags the branch, charging towards another conspecific or other non-conspecific. Branch dragging is often accompanied by panting and/or hooting, which draws the attention of any observers. Figure 22 (p. 149) shows branch dragging as a single perception-action module, distributed between 3 foci: the male chimpanzee, the branch tool, and the recipient/s of the display. 1 dynamic spatial relationship (between branch and social target) was counted for Object order. The minimum number of critical actions required to describe the behaviour is 6 (maximum = 6), in 4 phases. No modifications to the branch tool have been included (besides detachment).

Flailing stick or club Behaviourally similar to branch-dragging, chimpanzees at Bossou have been observed to customarily flail a stick or branch, sometimes striking an inanimate object, the ground,

[36] From other publications' citations, it seems likely the description has been reported, in Japanese by Sugiyama (1998). As I was unable to obtain a copy of this, and since Sugiyama's report is cited by Nishida et al. (1999) as an example of branch dragging which matches their own behavioural ethogram, this more general description has been used instead. An alternative, Matsuzawa's (1997) anecdotal report of an episode of analogous 'dragging' behaviour, in which an alpha-male chimpanzee from Bossou charged, dragging the carcass of a dead infant, was felt to be too contextually specific and not coherent with the general pattern of 'branch-dragging' behaviour.

Figure 22 Cognigram for the Bossou variant 'Branch drag'

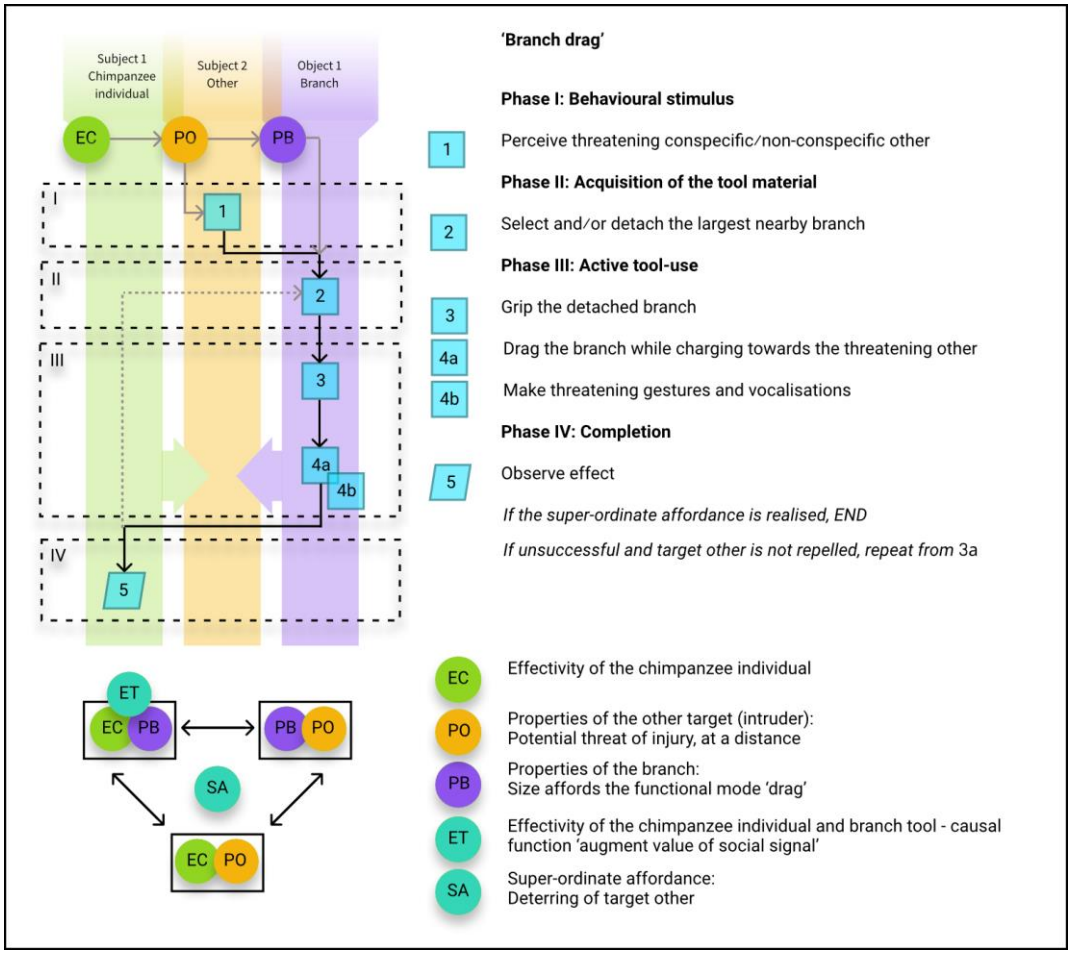
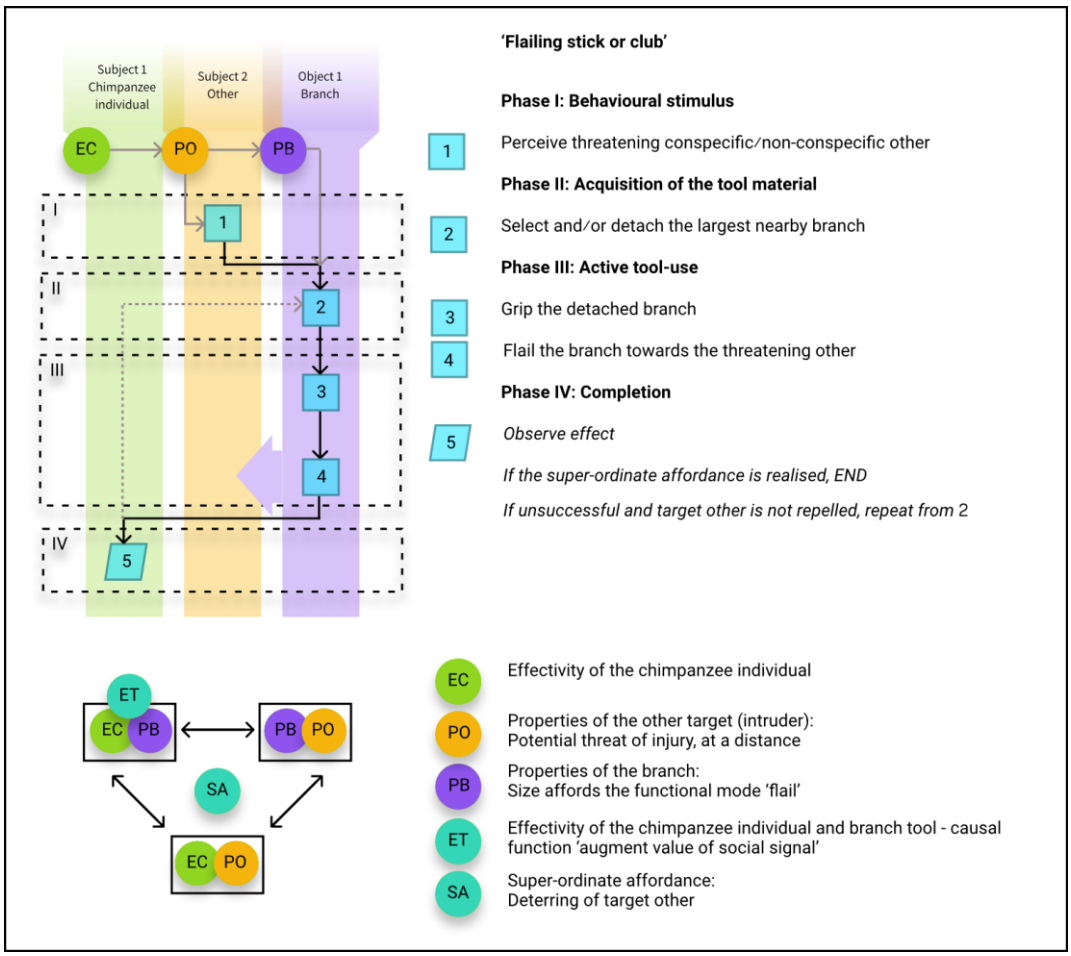


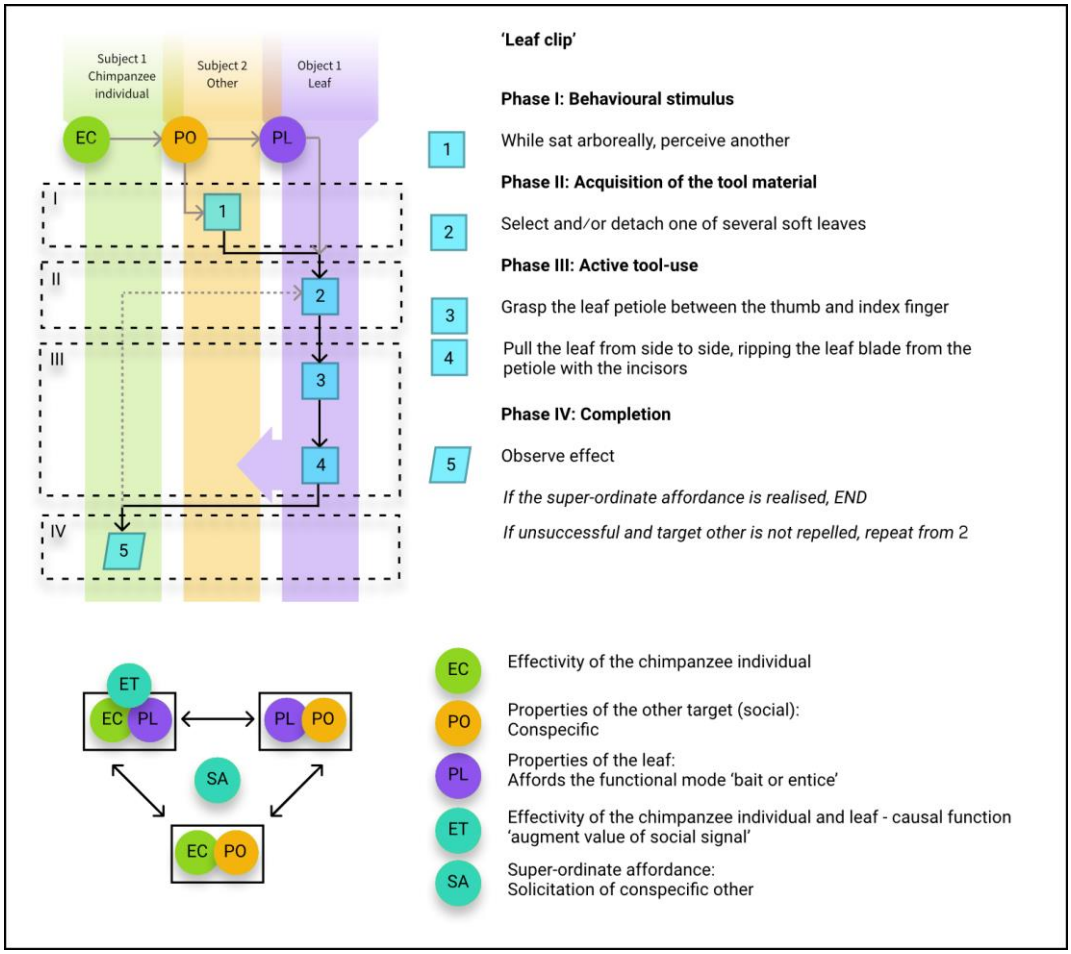
Figure 23 Cognigram for the Bossou variant 'Flail or club'



or a conspecific/non-conspecific other (Humle, 2003, 2011). Again, since no detailed behavioural description specific to Bossou could be found in the literature, a general description derived from other sites' reporting has been used (cf. Albrecht & Dunnett, 1971; Boesch & Boesch, 1990; Goodall, 1986; Nishida et al., 1999). Figure 23 (p. 150) expresses the flailing or clubbing display as a single perception-action module, in which the super-ordinate affordance (solicitation of attention and/or a behavioural response from another) arises through the transactional relationship between 3 foci: the chimpanzee 'signaller', the branch tool, and an observing conspecific/non-conspecific other, or struck object. 1 dynamic spatial relationship (between club and social target) is counted to Object order. The minimal operational sequence can be described by 5 critical actions (maximum = 5), in 4 phases, with no modifications counted towards the technical complexity of this behaviour.

Leaf-clip **'**Leaf clipping' is present at many chimpanzee study-sites, though the form, function (i.e. the response elicited, and/or context of the performance), and frequency of the social signal varies from site to site (Boesch, 1995; Hobaiter & Byrne, 2014; Nishida, 1980; Sugiyama, 1981; Watts, 2008). At Mahale and Ngogo leaf-clipping occurs as part of sexual display, and less frequently as an expression of social frustration or anxiety (Nishida, 1980b; Nishida et al., 1999; Watts, 2008); at Taï, the behaviour primarily functions in the context of social frustration, drawing attention prior to a secondary display such as pant-hooting or buttress drumming (Boesch, 1995; Kalan and Boesch, 2018). At Bossou, leaf-clipping is customary (Humle, 2003, 2011), and has a variety of performative contexts, including play, frustration, aggression, and solicitation of copulation (Matsuzawa, 1999; Sugiyama, 1981). Sugiyama (1981) describes a typical episode as occurring arboreally ["chimpanzees on the ground never clip leaves" (*ibid.,* p441)], with the signalling chimpanzee sat conspicuously in a tree facing its target audience. The chimpanzee selects and detaches one or several soft leaves and, grasping a leaf petiole between thumb and index finger, pulls it from side-to-side, repeatedly ripping the leaf blade from the petiole with its incisors, which produces a loud and distinctive sound. When the leaf blade has been almost entirely removed, the stem is discarded, and another leaf detached and clipped. Figure 24 (p. 152) gives 'leaf-clipping' as a single perception-action module, with 3 foci:

Figure 24 Cognigram for the Bossou variant 'Leaf clip'



the chimpanzee 'signaller', leaf material, and the conspecific observer/s. 1 dynamic spatial relationship (between leaf tool and social target) was counted towards Object order. The minimal operational sequence is comprised of 5 critical actions (maximum = 5), in 4 phases. No modifications have been included towards the technical complexity of this variant.

4.2.10 Cognition in social tools

Chimpanzees have an extensive repertoire of communicative gestures - of which aimed throwing, branch dragging, clubbing, and leaf-clipping are only a few - and are able to choose the appropriate mode of gesture given the affordances of a social situation featuring conspecifics. For example, chimpanzees are more likely to use tactile gestures when the target does not have their attention towards them, and silent visual gesture when a target is already looking at them (Hobaiter and Byrne, 2011) - indicating a degree of familiarity with conspecific response akin to that expected of grade 3 causal cognition (or conspecific mindreading). Social tool behaviours at Bossou, however, do not always target conspecifics, and the escalation from non-tool assisted, to tool-assisted display, rather than demonstrating familiarity, may be indicative of lack of familiarity – the exaggerated and cross-modal nature of 'aimed throwing', and 'branch dragging', an effective one-size-fits-all. Relative to other social forms of tool-use, aimed throwing is considered more causally, and neurologically complex, with throw accuracy reliant upon coordinating the timing between applied acceleration and release of a missile, with relation to the perceived velocity and distance of the target (Hopkins, Russell and Schaeffer, 2012). For Gärdenfors and Lombard (2018), aimed throwing is indicative of lower level grade 6 causal reasoning, complexity arising from the spatial detachment of cause and effect: In chimpanzee aimed throwing, tool-users extend their own causality into extra-personal space *through* the causality of the missile, whose causal function is to augmenting the value of the social signal by extending both the threat gesture, and reach of the user, in order to distancing the target. Evidence among humans demonstrates that skilful perception of these kind of tool affordances requires engagement with tool materials in the task context, and is emergent only

through prolonged practice. Bingham et al. (1989), for example, showed skilled human throwers were able to select optimal missile weight by hefting, which produced sufficient epistemic feedback even when visual cues (i.e. size differences) were removed. Another study by Zhu and Bingham (2010) found this same ability was not present among un-skilled throwers, for whom improvement came only with practice, and the visual epistemic feedback this produced. In comparison to human aimed throwing, Chimpanzee throwing is not renowned for its precision (Westergaard *et al.*, 2000), and in the wild, the intentional 'aimed' aspect is more often inferred by the researcher by the individual's orientation towards the target whilst throwing, rather than their actually hitting it (e.g. Sanz & Morgan, 2007). That said, neurological evidence does demonstrate that throwing by chimpanzees does exert a metaplastic effect: Cantalupo and Hopkins (2010) found chimpanzees with reliable throwing accuracy had significantly larger cerebella than those without, while Hopkins et al. (2012) have shown the process of learning to throw increased connectivity between chimpanzees' cortical regions, specifically between premotor and primary motor cortex. The increase in connectivity, interestingly, also correlates with increased communicative ability, throwers performing better in communicative tasks than non-throwers (Hopkins, Russell and Schaeffer, 2012). In leaf-clipping, sustained, and repetitive engagement is necessary both for the honing of physical skill, and the development of the signal values (which vary significantly between sites), and Sugiyama (1980) reports infants often take time to produce the distinctive sound.

Scope for transmission of social tool use is increased by the inherently attention directing nature of the task context, but limited by tool and context durability. Tool reuse is limited by the predominant arboreal context, in which the majority of social tool-use takes place, and by the exhaustive nature of social tool-using – techniques which entail dropping, throwing, and ripping up of tools, effectively preventing re-use. Likewise, motivations to engage with social tool materials, and rewards for unskilled tool-users, are likely to differ from those associated with other functional contexts. Without access to scrounging opportunities, and others tool materials, rewards are most likely self-affective, and not necessarily tied with successful solicitation of a reliable response: for

example, among juveniles, leaf-clipping behaviour begins as play, and is sometimes performed as a form of 'self-soothing' (Sugiyama, 1981; Myowa-Yamakoshi and Yamakoshi, 2011). At Mahale, Nishida (1980b) hypothesised that leaf-clipping may have arisen during the making of a leaf mid-rib ant-fishing tool (Nishida, 1980), the affordance once discovered, having escalated to a purposive gesture of its own. A similar scenario is impossible at Bossou, since observation of leaf-clipping at Bossou significantly predates observation of ant-fishing (which, when observed, was only performed by a single juvenile male), and is unlikely more generally, given the widespread nature of the behaviour at the sites. Leaf-clipping is, however, resonant of chimpanzee non-tool related feeding behaviour, including peeling and processing of fleshy fruits, and other aspects of tool manufacture, such as stripping of excess leaves from other kinds of probe tool. Given the abundant opportunity to engage with leaf materials, and chimpanzees natural foraging dispositions, it seems plausible that the behaviour could simply fall well within a zone of latent solutions (Tennie, Call and Tomasello, 2009; Tennie *et al.*, 2020), easily re-innovated at multiple sites, but with local 'meanings' constantly, and flexibly, re-co-constituted through shared material practice, via the socially and temporally distributed process of social negotiation (Wittgenstein, 1953; Plooij, 1978; Frohlich, Wittig and Pika, 2016; Pika and Frolich, 2019); and, depending upon adaptive value, phylogenetic ritualisation (Hobaiter and Byrne, 2014; Byrne *et al.*, 2017) – i.e. tool-use transforming grade 2 social cognition into emergent grade 3.

Degree of material constitution for all social behaviours is considered minimally constitutive to technical cognition, on the basis that, since all operate across largely similar physical distances, and target the same set of sensory-modalities as non-tool assisted social behaviours, none provides a wholly novel function. That said, social tools do work to supplement and exaggerate communicative gesture, improving the ability to (a) reinforce affiliative bonds, (b) effectively control others behaviour, and (c) to avoid risk of physical conflict/risk of injury by effectively managing the space between self and others. Given the postulated link between social complexity and

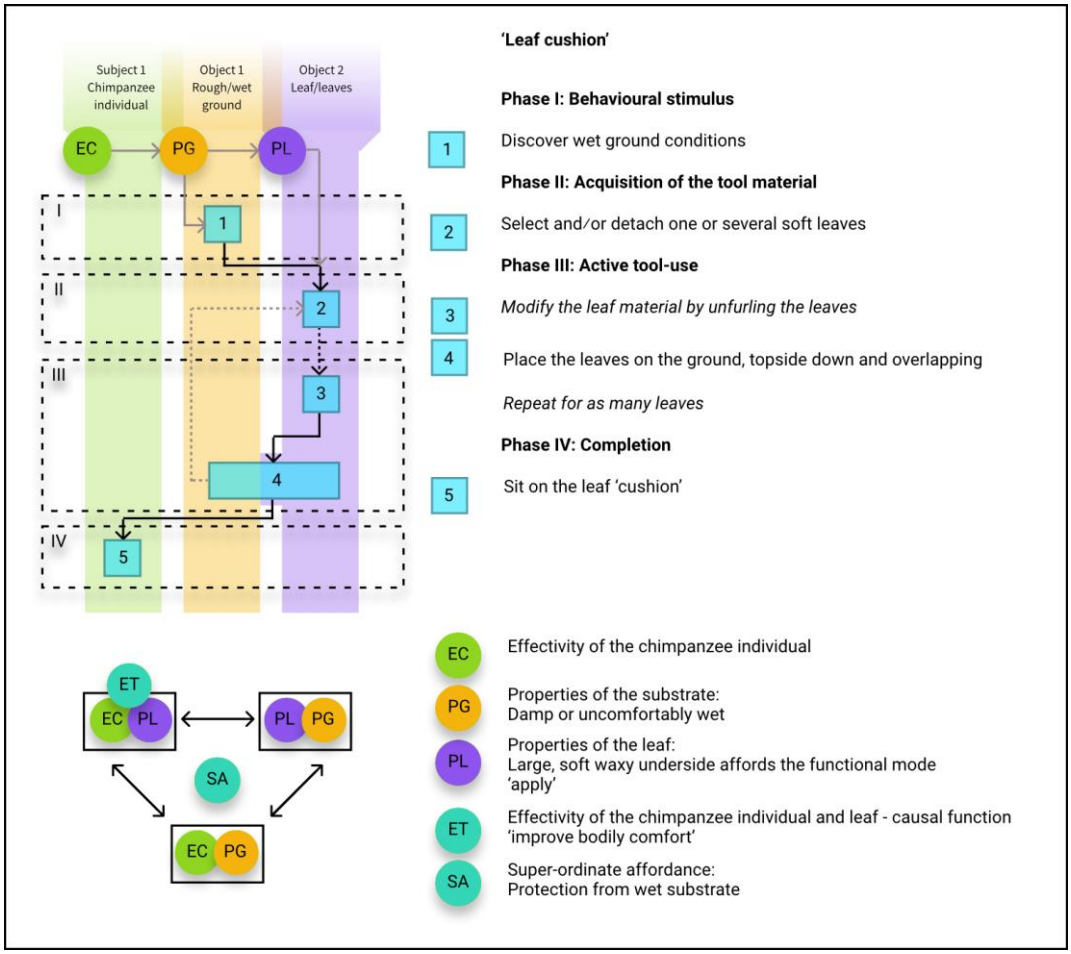
encephalisation (Dunbar, 1998; Dunbar and Shultz, 2007; Perez-Barberia, Shultz and Dunbar, 2007), tools which alter the nature of social interaction, may *de facto* alter cognitive development.

4.2.11 Hygiene or bodily comfort variants and their cognition

Leaf cushion Hirata et al. (1998) reported two occasions on which chimpanzees at Bossou used sets of leaves to sit on wet ground, the leaves acting as a protective barrier between the chimpanzees and the damp earth. In both instances, tool-use was inferred after-the-fact, from hairs on and around the deposited leaf materials, or from observation of use (i.e. sitting on the leaves) without direct observation of tool-handling (i.e. laying of the leaves) (Hirata, Myowa and Matsuzawa, 1998). In total, four leaf sets were recovered, three compound-leaves likely taken from the same parasol tree, and one set of five leaves from a carapa tree (*Carapa procera*); some of the leaves showed signs of having been detached, and some of having been folded, and were placed overlapping one another in an orderly manner, covering an area sufficient for a chimpanzee to sit. Termed 'Leaf cushion' [see also 'seat-vegetation' (Whiten *et al.*, 1999, 2001)], the behaviour is the only variant in the Bossou chimpanzee tool-repertoire categorised as for the purpose of bodily comfort and/or improving hygiene. Figure 25 (p. 157) shows the variant 'leaf cushion' as a single perception-action module, in which the super-ordinate affordance (i.e. sitting on the ground without getting wet) is distributed between 3 foci: the chimpanzee, leaf materials, and the damp ground. 1 static spatial relationship (between leaf cushion and damp ground) has been counted to Object order. The operational sequence is simple, and is described by 4 critical actions (maximum = 5), in 4 phases. No modification phase was described in either of the incidents reported by Hirata et al. (1998), though the authors do assert reuse was likely, the leaves at one site having been left in three sets.

Material cognition is minimally constitutive since the causal function of the tool does nothing to alter the effectivities of the user, instead functioning to alter the properties of the

Figure 25 Cognigram for the Bossou variant 'Leaf cushion'

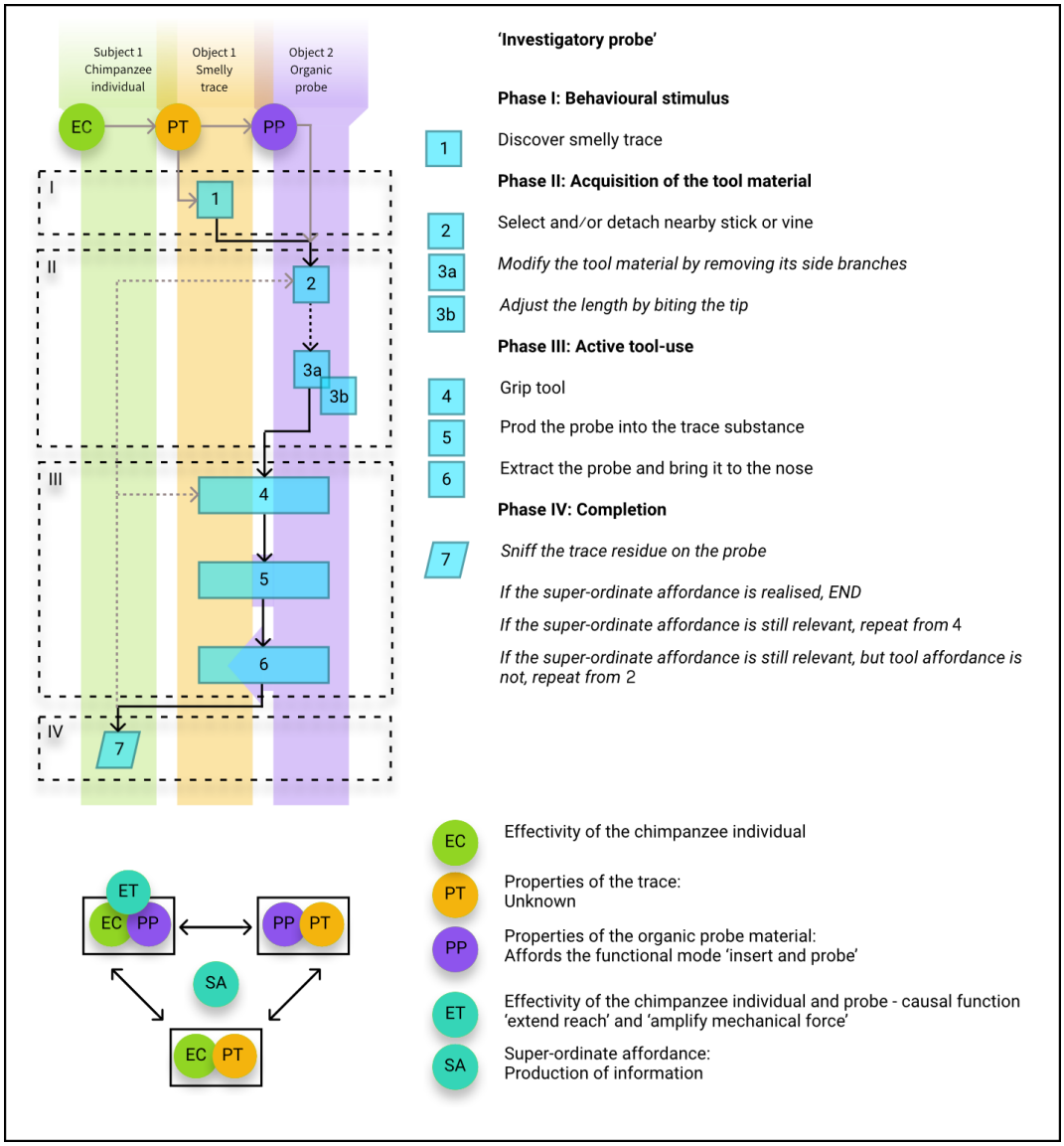


environment; leaves may make the wet ground more inviting to sit upon but are not necessary for sitting. Further, if the sole function of leaf cushions are to avoid the discomfort of sitting on wet ground, it is unlikely they provide significant adaptive advantage. There is no evidence to infer causal cognition above level 2 cued-dyadic causal reasoning (more than chimpanzee having been observed to engage in the behaviour).

4.2.12 Other tools and their cognition

Investigatory probe **'**Investigatory probing' is a considered a universal form of chimpanzee tool-use, customary in all wild study-site groups (Sanz & Morgan, 2007; Whiten et al., 1999, 2001); this includes Bossou, where chimpanzees manufacture and use sticks or vines to probe animal or human traces (Humle, 2003, 2011; Matsuzawa, 1999; Ohashi, 2006). According to Ohashi (2006, p449), chimpanzees at Bossou will sometimes break off a stick or vine in order to probe something smelly on the ground, stripping off excess leaves, inserting the probe, and then sniffing it; Matsuzawa (1999) reported that chimpanzees have been observed to pick up a stick in one hand, push the probe into a tree-hole, retrieve the tool, and sniff its tip – the apparent function of this behaviour possibly to explore otherwise inaccessible "crooks and crevices" (Matsuzawa, 1999, p. 653). Sugiyama & Humle (Sugiyama and Humle, 2011) reported that some Bossou chimpanzees used probe-like tools to explore and/or deactivate snares (see also Ohashi, 2006). Figure 26 (p. 159) gives investigatory probing behaviour as a single perception-action module, in which the impetus for tool use arises from the dynamic interplay of 3 foci: the chimpanzee, the organic material which forms the probe tool, and the object of interest (a snare, smelly substance on the ground, or visually obscured hollow). 2 spatial relationships, 1 static (between probe and trace) and 1 dynamic (between probe and trace). The minimum operational sequence required to describe the behaviour involves 6 critical actions (maximum = 8), in 4 phases. Ohashi (2006) described 'fashioning' of the investigatory probe, but did not specify particular manufacturing modes or actions. From generic descriptions of

Figure 26 Cognigram for the Bossou variant 'Investigatory probe'



analogous behaviour at other sites, and the manufacturing modes of similar tool forms used at Bossou, a conservative estimate of 2 modifications has been counted towards the technical complexity of this variant: modificatory actions included are adjustment of tool length, and stripping of excess leaves.

Of all NHP tool behaviours, chimpanzee investigatory probing combines epistemic with pragmatic action in the most literal sense, as individuals use the tool to 'probe' their environments. As with other probe tool-use outlined in this chapter, investigatory probes extend the causal reach of the user, in some contexts, putting an effective distance between the user and the item they are exploring, mitigating chance of experiencing harm or discomfort. Goodall (1968), Sanz & Morgan (2009), Estienne et al. (2019), and others (see Motes-Rodrigo *et al.*, 2019), describe perforating and probing tools as functionally explorative, as though investigatory probing had integrated into skilled tool-use as part of the pragmatic function. That chimpanzees frequently withdraw their probes and sniff their ends, prior to and throughout tooling bouts, suggests epistemic feedback from the behaviour reinforces the perceived relevance of tool affordances by confirming presence of a prey species. Since investigatory probing is part and parcel of young chimpanzees early probe behaviour (juveniles learning to manipulate probe tools through reuse, and prior to successful tool-use in ant-dipping and other insect predation contexts). Investigatory probing is thus also likely to foster skill acquisition, confirmation of a smelly prey target encouraging further exploration with the tool. Meanwhile, solicitation of the probe affordance in the context of trap de-activation does not require prior-perception of stored forces in the trap mechanism (grade 6 causal cognition), since the affordance is clearly already relevant in the context of novel situations in which engaging with unfamiliar objects or others poses risk (eg. van Lawick-Goodall, 1968, p. 206): continued de-activation, by means of probe tool-use, however, demonstrates perceptual learning through

engagement.[37] Taking into account the reinforcing effect investigatory probing is likely to exert in the education of juvenile attention, degree of material constitution is considered strong, but not maximal: Both investigation and trap de-activation by other means are possible (see Ohashi & Matsuzawa, 2010), however, probe tools physically distance the user from their source of investigation, mitigating chances of harm or discomfort.

4.3 Summary

A review of the Bossou tool-set demonstrates the embodied, extended, and distributed nature of chimpanzee tool-use. At the micro-level, tool variants are grounded by real time and environmental contexts, with chimpanzees able to navigate the spatial relationships between themselves, their tools, and targets, through the extended perceptive capabilities afforded by tools' causal functions. At the macro-level, techniques are the cumulative effort of multiple generations of chimpanzees and their materials, with tool use innovated, maintained or lost as a result of the inter-related, distributed processes of social learning and opportunistic material engagement. Although the majority of Bossou tool use is minimally constitutive to cognition, and functions to broaden the scope and effectivity of pre-existing behaviours, as opposed to providing novel functions, long periods of learning through exposure to and interaction with other tools demonstrate material engagement is nevertheless key to the development of technique and solving of more complex technical problems. Matsuzawa *et al.* (2001) describes the ontogeny of Bossou tool-use as an education by "master-apprentice". 'Education', Matsuzawa et al. note, is derived from the latin word 'to extract' (Matsuzawa *et al.*, 2001, p. 573), and though chimpanzee education is perhaps not always intentional in the sense observed by Boesch (1991b) at Taï, it nevertheless results in a "drawing forth of potential abilities" (Matsuzawa, 2012, p295); in the Bossou case, as a result of the

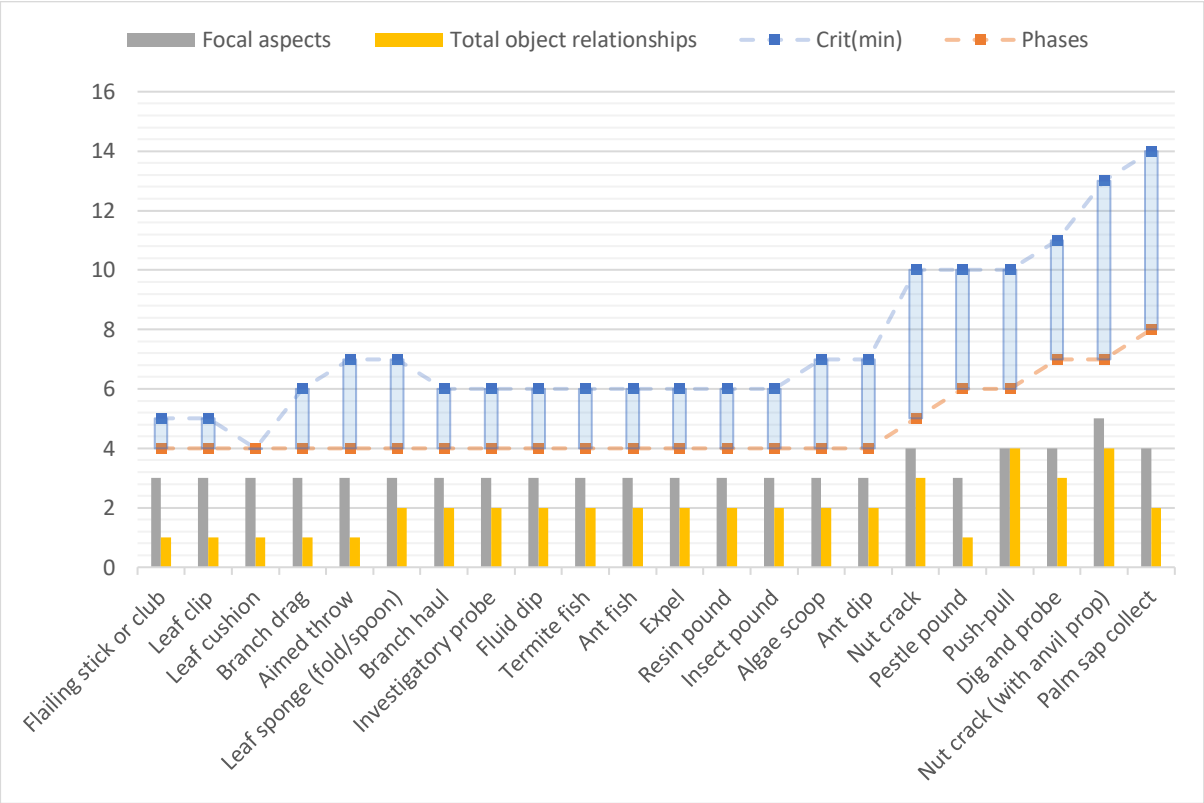
[37] It is likely trap deactivation is not a customary function of investigatory probing since the use of tools for this purpose is far less efficient than manual deactivation. Sugiyama & Humle (2011) therefore suggest trap deactivation maybe a separate innovation which simply failed to be maintained.

dynamic and distributed process of learning through material interaction and observation of the material interactions of particular others.

Physical cognition is visible in the number and flexibility of alternative techniques, and in the appropriate mapping of tool morphology to ecological context. Whilst social cognition is visible in the selective observation of other conspecifics, social tool-use, and cultural variations exhibited between groups. Causal cognition of individual variants appears limited to grades 1, 2 and 3, though some anecdotal evidence indicates an ability through past engagement to perceive the causality of stored forces in inanimate objects, and to perceive causality of objects as extensions of the agential self even when spatially detached from the person. On a more holistic level, it is interesting to note the number of broadly similar behaviours for which a given function or technique has been transferred to other contexts. Flexibility in this sense is indicative of the ability to be solicited by the causal functional affordances of certain types of tools independent of a specific environmental context. It would appear chimpanzees at Bossou, for example, would be capable of solving almost any problem for which the solution requires only the extension of the users reach by means of a stick or branch probe provided the relevance of the problem was significant enough to solicit attention. It is likely this ability arises from prolonged interaction with a tool form, present in a variety of environmental contexts; materials suitable for constructing probe tool are widely available throughout the Bossou home range, and in a variety of contexts, providing opportunity and means for broadening of tool function. In contrast, stone tools though available, are concentrated by use, and cannot be readily modified, making them unsuitable for transfer to other cracking functions. On the flip side, specialisation of nut-cracking may contribute towards the development of conceptual tool categorisation. In an experimental setting at Bossou, hammer and anvil pairs were selected more often than could be accounted for by chance, with choice part individual preference and part awareness of functional suitability (recognition that this hammer works well with that anvil), suggesting nut-cracking tools are perceived as a composite unit rather than as two separate parts (Carvalho *et al.*, 2008). Although speculative, this could be indicative of the beginning of a shift in

perceptive capability, from thinking through tools, to thinking about them (e.g. Overmann & Wynn, 2019a, 2019b).

Figure 27 The relationship between problem solution distances and focal complexity/number of object relationships for technical variants at Bossou



Several levels of hierarchical object relationship are represented in the Bossou repertoire. Although most tool-use involves the relation of two objects, 'level two' and 'level three' (sensu Matsuzawa, 1996) tool using is also present, with a maximum of four objects (focal complexity = 5) successfully managed. Learning times indicate difficulty of skill acquisition increases with number of focal aspects and the more complementarity/hierarchical affordance relationships which need to be balanced (Inoue-Nakamura and Matsuzawa, 1997; Biro, Sousa and Matsuzawa, 2006). It is likely that modularisation of the tool-using sequence facilitates skill acquisition of more focally complex tool-use by reducing both behavioural complexity and the number of affordance relationships it is necessary to manage at a given time. This can be seen first in the ontogenetic process, for example in nut-cracking, where chimpanzees learn each object combination before combining nut, hammer,

Table 10 Tool forms, targets and materials of Bossou variants

Tool form	Variant	Target	Tool material	Selectivity	Re-use	Modification
Flexible probe	Algae scoop	Algae (*Spirogyra sp.*), water	Herb mid-stem	Yes	Yes	Reduction
	Ant-dip (single/wipe)	Invertebrates	Herb mid-stem, tree, vine	No	Yes	Reduction
	Ant fish	Invertebrates	Tree leaf mid-rib	-	No	Reduction
	Fluid (honey) dip	Honey, water	Tree stick, vine	-	Yes	Reduction
	Insect pound	Invertebrates	Tree stick	-	-	Reduction
	Resin pound	Resin, gum	Tree stick	-	-	Reduction
	Termite fish	Invertebrates	Herb stalk	-	Yes	Reduction
	Investigatory probe	Misc.	Shrub stick	-	-	Reduction
Stout stick/branch	Branch hook	Fruit	Tree branch	No	No	Reduction
	Dig	Invertebrates	Tree branch	-	No	Reduction
	Expel	Invertebrates/vertebrates	Tree stick	-	No	Reduction
	Pestle pound	Palm pith	Leaf petiole	-	Yes	Reduction
	Branch drag	Social	Tree branch, carcass	-	-	
	Club	Social	Branch	-	-	
Leaf form	Leaf sponge (fold/spoon)	Water, plum wine	Leaf lamina	Yes	Yes	Replication
	Palm sap collect	Palm sap	Palm fibre	-	No	Replication

Table 10 Cont. Tool forms, targets and materials of Bossou variants

Tool form	Variant	**Target**	**Tool material**	- **Selectivity**	- **Re-use**	**Modification**
Leaf form cont.	Sponge push-pull	Water	Tree stick, leaf lamina	-	-	Linkage
	Leaf clip	Social	Leaf blade	-	No	
	Leaf cushion	Hygiene	Tree leaves	-	-	
Lithic pounder/	Nut hammer	Palm nut kernel	Stone, tree trunk	Yes	Yes	Linkage
Misc.	Anvil prop	Palm nut kernel	Stone	-		Linkage
	Aimed throw	Social	Tree branch, stone	-	No	Reduction

and anvil; and also in expert sequential tool-use, such as palm-sap collection, where three modules are performed one after the other. On the one hand, modularisation can be seen as a strategy to reduce cognitive load, but on the other, it is also possible to see how tool-use facilitates the increased behavioural complexity of cumulative sequential variants, by directing focus and guiding action as the situational affordances of a task change through time.

Material constrains and enables tool cognition in numerous ways. The functional properties of tools guide action, with chimpanzees adjusting their behaviour both to prey and tool. Boesch and Boesch (1990) hypothesise that chimpanzee tool re-use is most likely to occur when a tool requires modification, or when material choice is a limiting factor; but also that as ease of modification decreases for a given material, so will tendency to modify, suggesting a trade-off between easily modifiable, but non-preferred, and difficult to modify but highly preferred materials. Sanz & Morgan (2007) found modification and reuse patterns at Goualougo corroborated the former hypothesis, with organic probe tools more likely to be reused than non-modified variants. Bossou chimpanzees exploit a wide range of organic and inorganic materials including leaves, leaf petioles, mid-stems, stalks, branches, twigs, and stones. Prey and target items include vertebrates, invertebrates, fruit, various palm-products, honey, resin, algae, and water (Table 10, pp.164-165). Proximity was described as the main factor in material selection for the majority of non-habitual tool variants though functional suitability was also a factor, available materials which did not afford the relevant function "ignored" (Humle, 2003, p. 249). Manufacture prior to, or modification during, tool-use was described for almost all perishable tools, even when selectivity was low, with the exception of tools used in social contexts, and presumably under greater time pressure. Modification phases most frequently included adjustment of tool length by means of the teeth and/or hands, and stripping of extraneous material such as leaves and bark. Material selectivity was high for the four most common subsistents, most especially nut-cracking, for which modification was also complex (including transport and linkage). Bossou variants also support Boesch & Boesch's (1990) assertion; all three

variants in which material factored into tool choice, and three of four tools with complex modification modes (linkage and/or replication), also had a high level of tool re-use.

This correlation could both explain or be explained by the mode of chimpanzee tool transmission. It is notable that many of the social tool variants, branch-haul, and ant-fish, for which reuse is not the norm, occur in an arboreal context, or result in loss of the tool whereas ant-dipping, nut-cracking, pestle-pounding, and algae scooping all take place at a focal site: the ant nest, oil palm, or tree hollow. Tool-use at these sites creates palimpsests, or tool caches, and where tools are non-perishable or sites visited frequently, reuse is not only likely but highly relevant. Recent evidence from a semi-wild experimental setting suggests likelihood of chimpanzee tool-use is significantly related to amount of time spent travelling to the tool-use site (Gruber, Zuberbühler and Neumann, 2016), lending support to the relative profitability hypothesis (Rutz and St Clair, 2012). Bossou has one of the largest chimpanzee repertoires, with tool-use an important part of feeding ecology at the site. Where time budget and energy expenditure are high, tool-use functions to increase likelihood of foraging success, and return on energetic investment, increasing range of available ecological niches, and access to nutrient rich encased resources (Yamakoshi, 1998, 2001). Cache-ing and reuse of tools no doubt further reduces energetic cost by subverting the need to search or manufacture new ones, increasing the relative profitability of otherwise complex tool behaviours. In turn, cache-ing also creates suitable learning sites which focus juvenile behaviour, shortening the distance between problem and reward, and reinforcing behavioural transmission. More complex modification procedures are associated with longer periods of skill acquisition. Since reuse is fundamental to learning, longer periods of learning mean extended periods of reliance on re-use of others tools.

Tool selection and modification are thus effective acts of ensignification, by moving materials around the landscape and altering their relevance, material choice becomes an enactive sign of value, with future generations more likely to use the same materials as those they observe and whose tools they reuse. Long-term study of termite fishing in several adjoining communities

suggests the visible effects of past tool-use, and not just accumulation of tools, may influence material selectivity and behavioural propagation. Pascal-Garrido (2018) found significant differences in the archaeological visibility of different tool materials. Stripping of bark was found to produce a tree scar which was still visible up to three years later, whilst twig and herb removal left scars which healed much faster, some within weeks, and perishable vine tools were invisible within a number of days (*ibid*). Three neighbouring sites with different material responses to the same ecological problem, each showed a transition towards increasing prefence for bark tools, with Issa exclusively selecting bark to manufacture termite probes (Almeida-Warren *et al.*, 2017; Pascual-Garrido, 2018); Mahale, having previously used twig, vine, grass, and leaf tools (McGrew and Collins, 1985) now using predominantly bark tools; and Kasekala increasing from 21% to 48.6% bark and 44% tools (Pascual-Garrido, 2018). Whilst these changes could reflect environmental change, it is also possible their visibility acts as a material sign, scaffolding tool-use and material selection by drawing visual attention to a given affordance. Notably, tool preference at Bossou in ant-dipping and other probe tool-use is lacking, but includes more grass, herb and leaf, than tree bark (seebTable 10, p164-165). Termite and ant fishing are unlikely to be behavioural innovations but behaviours belonging to a neighbouring group's repertoire, brought to the site by an immigrant female and her infant son. Behavioural transmission is yet to be confirmed, but it is possible the affordance simply isn't perceptible enough for transfer to occur.

Since copying is socially biased (Coussi-Korbel & Fragaszy, 1995; Fragaszy & Visalberghi, 2004; Hoppitt & Laland, 2013; Kendal et al., 2009; Van De Waal et al., 2013), preferential towards more dominant, successful tool-users (eg. Horner et al., 2010), or heavily influenced by matrilineal relationships and female dyads (Wrangham *et al.*, 2016; eg. Lamon *et al.*, 2017), techniques and their tool materials become active ingredients in the construction of self within the wider network of others and the group technological matrix (Mosley and Haslam, 2015). Chimpanzees' perception of affordance relevance thus reflect an element of social 'normativity' (sensu Rietveld and Kiverstein, 2014) besides that arising from socially biased transmission.

Case Study 2: 'Material engagement, tool-use and technical cognition amongst bearded capuchins (Sapajus libidinosus) at Serra da Capivara, Brazil.

5.1 The Case Study Site of Serra da Capivara

Serra da Capivara National Park (7.80'S, 41.30'W) is situated in the north-east of Brazil, in the drought state of Píauí. Habitat is classed as *caatinga*, typified by high seasonality, and low average annual rainfall. Climate at Serra da Capivara (hereafter SDC) has two seasons, dry from May to mid-October, and rainy from November to April. Rainfall is variable throughout and from year to year; the average annual rainfall recorded over 50 years was 644mm (measurement recorded at São Raimundo Nonato, (Moura, 2004)). At least four wild groups of bearded capuchins (*Sapajus libidinosus*) inhabit the limits of the study-site, in the south-east of the park, with populations ranging from 12 to 52 individuals (Mannu and Ottoni, 2009), groups often fusing for several days at a time before diverging again. Since published reports from the SDC often combine data from several groups, here all variants present at the site are presented, and inter-group behavioural variation discussed where relevant. Much like Bossou, the SDC site overlaps with human settlement, the main study-area situated approximately 20km from the city of São Raimundo Nonato, and humans having lived in and farmed areas of the park prior to its establishment as a world heritage site in 1991 (Moura, 2004). The site is also semi-provisioned, with food and water distributed towards the end of the dry season (Falótico, 2011). Tool-use has been observed at the site since early 2000 (Moura & Lee, 2004).

5.1.1 The Serra da Capivara repertoire and its place amongst the wider capuchin technical repertoire

Capuchin tool-use is characterised by stone-tool use, in particular the use of hammer and anvil sets to crack open seeds and nuts (Ottoni and Izar, 2008; Mannu and Ottoni, 2009; Visalberghi and Fragaszy, 2013; Falótico and Ottoni, 2016). Although several wild populations have been found

to use tools (Waga *et al.*, 2006; Ottoni and Izar, 2008; Ferreira, Emidio and Jerusalinsky, 2010; Mendes *et al.*, 2015), the majority of research has focused on tool-using behaviours at two long-term semi-wild study-sites, SDC and Fazenda Boa Vista (hereafter FBV), which despite being only 320km apart, display distinct technical repertoires. At Fazenda Boa Vista, tool-use is virtually entirely subsistent based, and predominantly comprises the use of stone tools to pound open various palm and cashew nuts, and *Manihot* seeds (Fragaszy *et al.*, 2004; Visalberghi *et al.*, 2008, 2016; Spagnoletti *et al.*, 2011).[38] Tool-use at SDC is comparatively broad with stone tools used in the solving of extractive foraging problems, similar to and overlapping with those present at FBV, but with a variety of additional functional modes and contexts (Moura, 2004; Mannu and Ottoni, 2009; Falótico, 2011; Falótico and Ottoni, 2013, 2016). Further, SDC has a number of unique variants, not exhibited at any other wild capuchin site, including habitual social tool-use and the customary crafting and use of vegetative probe tools (Moura and Lee, 2004; Mannu and Ottoni, 2009; Falótico and Ottoni, 2014; Haslam and Falótico, 2015; Falótico, Siqueira and Ottoni, 2017).

13 behaviours are reported for the SDC site, 8 of which are customary or habitual (61.5%), and 5 idiosyncratic or anecdotal (38.5%). 7 tool variants function in an extractive foraging context (53.8%); 3 hygiene (23.1%), 2 in a social context (15.4%), and 1 in another, unknown context (7.7%). The full repertoire of tool variants at SDC is listed in Table 11, below (p. 171). SDC Repertoire richness, heterogeneity, and evenness of variant distribution were calculated for both variant functional mode ($S_{fm} = 6$, $H_{fm} = 1.54$, $E_{fm} = 0.78$) and variant causal function (figure 3, $S_{cf} = 4$, $H_{cf} = 0.91$, $E_{cf} = 0.62$) following Shott (2010).

[38] One other variant is currently reported at the site – 'aimed throw'. However, this social variant is classed only as present, as opposed to nut-cracking which is habitual (Visalberghi *et al.*, 2017).

Table 11 Technical variants observed at Serra da Capivara since 2000

Functional Context	Variant	Population Distribution	Key Source/s
Subsistence	**Nut crack* (pound/hatchet)**	Customary	(Moura, 2004; Mannu and Ottoni, 2009; Falótico and Ottoni, 2016)
	Dig (dig/hoe)	Customary	(Moura, 2004; Mannu and Ottoni, 2009; Falótico and Ottoni, 2016; Falótico, Siqueira and Ottoni, 2017)
	Pound open	Customary	(Mannu and Ottoni, 2009; Falótico and Ottoni, 2016)
	Expel	Customary	(Mannu and Ottoni, 2009; Falótico, 2011; Falótico and Ottoni, 2014)
	Open and probe	Present	(Mannu and Ottoni, 2009; Falótico and Ottoni, 2014)
	Fluid dip	Customary	(Mannu and Ottoni, 2009; Falótico and Ottoni, 2014)
Social	Aimed throw	Customary	(Falótico and Ottoni, 2013)
	Poking stick (spear)	Present	(Mannu and Ottoni, 2009; Falótico and Ottoni, 2014)
Hygiene	Nasal probe	Present	(Haslam and Falótico, 2015)
	Toothpick	Present	(Haslam and Falótico, 2015)
	Self-poke	Present	(Falótico and Ottoni, 2014)
Other	*Rock pound*	Habitual	(Moura, 2006; Falótico and Ottoni, 2016; Proffitt *et al.*, 2016)

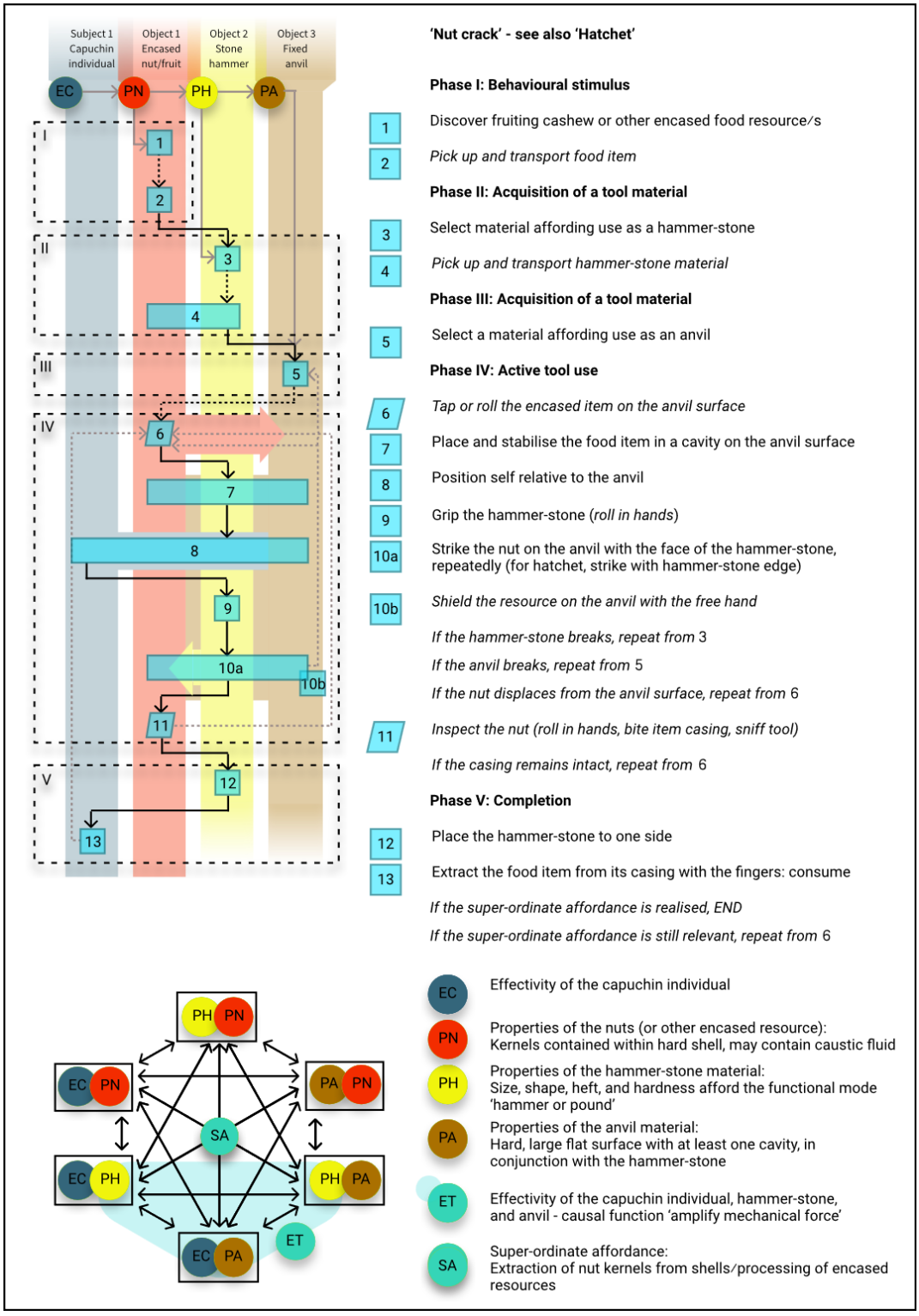
- **Bold font denotes a variant involving complex and/or sequential tool use**
  '*' Behaviours for which differing techniques (e.g. dig/hoe) are counted as independent variants

5.2. Cognigrams and thick descriptions

5.2.1 Subsistents with the primary causal function 'Amplify mechanical force'

Nut crack (Pound/hatchet) Stone pounding behaviour using hammer and anvil 'tool-kits' to crack open nuts, seeds, and fruits, remains the most prevalent and best archaeologically evidenced form of tool-using observed amongst wild *S.libidinosus* populations (Waga *et al.*, 2006; Ottoni and Izar, 2008; Ferreira, Emidio and Jerusalinsky, 2010; Visalberghi *et al.*, 2013; Mendes *et al.*, 2015). At SDC, the behaviour is customary amongst all capuchin groups, though the relative frequencies of the resources targeted differs between groups according to their ecological availability (Moura and Lee, 2004; Mannu and Ottoni, 2009; Falótico and Ottoni, 2016). As with chimpanzee nut-cracking (see section 4.2.2), successful tool-use requires effective spatial coordination of the two functional elements, the hammer and anvil, with regard to the target item, be it fruit, seed, or nut. The behavioural sequence used to describe the behaviour is therefore similar between species. However, unlike chimpanzee nut-cracking, the majority of 'anvils' used in capuchin nut-cracking are either not readily portable or remain fixed to the substrate (Ottoni and Mannu, 2001; Visalberghi *et al.*, 2007; Falótico and Ottoni, 2016); and according to Falótico (2011), capuchins were observed either to transport their target items and pounding tools to particular anvils, or to crack them in situ. Figure 28 (p. 173) gives nut-cracking as a single perception-action module in which the super-ordinate affordance of tool-use is distributed across 4 foci: capuchin, the material which forms the hammer-stone, the material which forms the anvil, and the target resource (e.g. a nut or other hard, encased food item). A total of 3 spatial relationships, 1 static (between nut and anvil) and 2 dynamic (between hammer-stone and nut; nut and anvil), were recorded for Object order. The minimum operational sequence length includes 9 critical actions (maximum = 12), in 5 phases. Besides optional transport of the tool materials, no modifications are included. Tool manufacture is classed as

Figure 28 Cognigram for the SDC variants 'Nut crack' and 'Hatchet'



linkage, with the functionality of the tool-set dependent upon the composite juxta-positioning of the hammer and anvil as two distinct objects.

Dig (dig/hoe) Capuchins at SDC are observed to customarily use 'hammer' stones to loosen and remove soil when foraging for the underground storage organs of plants (hereafter USOs) and for underground insect nests (Moura, 2004; Mannu and Ottoni, 2009; Falótico, 2011; Falótico and Ottoni, 2016; Falótico, Coutinho, *et al.*, 2018). Mannu & Ottoni (2009) describe two distinct, often sequentially combined, techniques: 'pestle' and 'hoe' (observed in the Jurubeba, Pedra Furada, and Bacão groups).[39] The former technique, 'pestle-ing' is typified by rapid and repeated pounding of the stone, either held in one or both hands, vertically against the soil, followed by dropping of the stone and removal the soil by hand; or held in one hand, while removing the soil with the other (Moura and Lee, 2004; Mannu and Ottoni, 2009, p. 246). 'Hoe-ing', in contrast, involves dragging of the stone horizontally to remove loosened dirt from the hole immediately following pestle-ing, or in order to remove leaf cover (Mannu and Ottoni, 2009, p. 245). Falótico *et al.* (2018) found Pedra Furada and Bacão groups most frequently used digging tools to excavate *farinha-seca* USOs, followed by *Louro* roots (*Otocea spp.*), and trapdoor spiders (*Actinopus spp.*), discovered while foraging on the ground. Figure 29 (p. 175) visualises digging behaviour as a single perception-action module. The super-ordinate affordance of the module is constituted by 3 foci: the capuchin, the stone material which makes up the digging tool, and the underground resource target. 1 dynamic spatial relationship (between hammer-stone and earth) was counted for Object order. The minimum operational chain to describe the behaviour was 8 critical actions (maximum = 10), in 4 phases. Besides optional transport, no modifications have been counted to the behaviour.

[39] 'Hoe' is here classed as a sub-category of the variant 'dig' on the basis of Falótico *et al.'s* (2018) report.

Figure 29 Cognigram for the SDC variant 'Dig'/'Hoe'

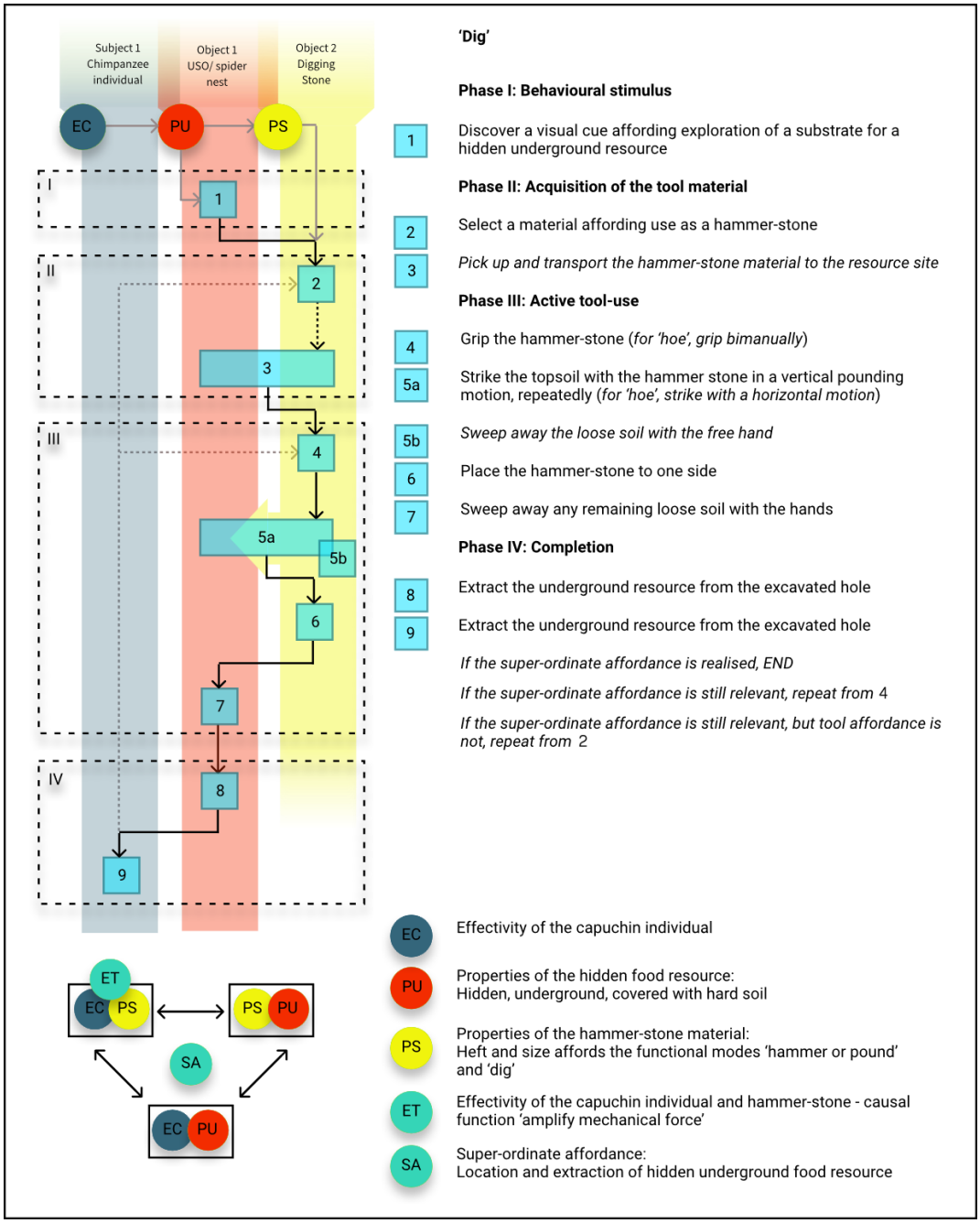
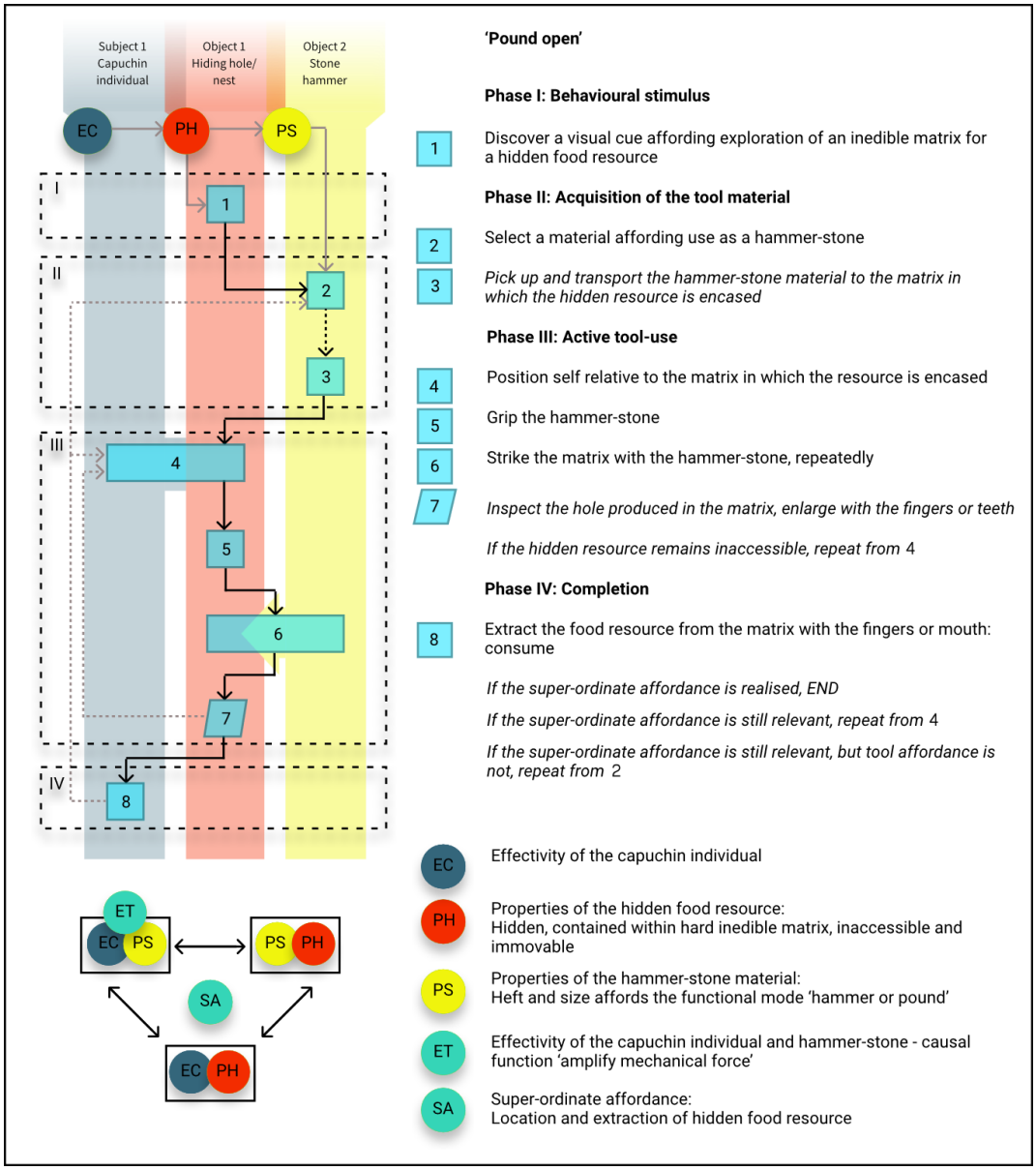


Figure 30 Cognigram for the SDC variant 'Pound open'



Pound open Besides hardened soil, the capuchins at SDC are also observed to use stone pounding tools to break down hard and inedible matrices in the search for vertebrate and invertebrate prey (Moura, 2004; Mannu and Ottoni, 2009; Falótico and Ottoni, 2016). Moura (Moura, 2004, p. 176) describes the behaviour as "an important technique in the destructive foraging repertoire" of Oitenta group, and provides a typical account of the behaviour. In this account, a male was observed to take a stone and transport it to a dry branch, then using the stone to repeatedly strike the branch before opening the crushed bark with his teeth. Figure 30 (p. 176) gives the behaviour as a single perception-action module, in which the super-ordinate affordance arises from 3 foci: the capuchin, stone material which forms the pounding stone, and the encasing matrix/resource within. Object order was taken to include 1 dynamic spatial relationship (between hammer-stone and the encasing matrix). The minimum operational sequence can be described by 8 critical actions (maximum 11), in 4 phases. Again, no modificatory actions besides optional transport were counted for the behaviour.

5.2.2 Causal cognition in subsistent with the primary causal function 'amplify mechanical force'[40]

Grades 1 and basic 3 causal cognition are present, with cognition causally coupled with the environment throughout the tool-using process such that interaction with tools and target items informs the subject's tool-using behaviour. Field experiments at FBV suggest tapping of piassava nuts (*Obrignya spp.*) on anvil surfaces provides visuo-haptic feedback about optimal positioning, and the most efficient axis on which to rest the nut within the anvil cavity so as to stabilise the nut and prevent fly-off during striking (Fragaszy, Lui, *et al.*, 2013; Mangalam and Fragaszy, 2015). At SDC, where Pedra furada and Bocão groups crack cashew nuts (Falótico and Ottoni, 2016), the kidney shape of the nuts presents a different challenge. Although lateral positioning of nuts on their flatter side provides a more stable placement, positioning the nut arch-up reduces the kinematic force necessary to crack its outer shell, an affordance which, from relative rates of observation, Falótico *et*

[40] Material from this section appears in Mosley (2020)

al. (2017) argue takes time and experience to learn. Besides nut-placement, Visalberghi, Spagnoletti *et al.* (2009) found capuchins selected and transported stone nut-cracking tools based on their functional affordances, and where visual perception provided insufficient information, sought out haptic and acoustic feedback through manipulative interaction: lifting, and or tapping prospective tools (Visalberghi, Addessi, et al., 2009). Similarly, rotation of the hammer-stone during the nut-cracking sequence, particularly by juveniles, suggests manipulative interaction provides visuo-haptic feedback about tool shape and size (Fragaszy *et al.*, 2019, 2020), which Westergaard & Suomi (1997) posit inform grip of cracking tools. Falótico & Ottoni (2016) show stones selected for tool-use at SDC were often transported and were on average, "heavier, larger, and rounder than the average of available stones" (p. 15), demonstrating clear material preference and perception of relevant artefact functional criteria. Further, evidence suggests experienced capuchins tool-users perceive the causality of their *though* tool-use, adjusting their posture, tool choice and striking force depending upon the properties of the tool used and item targeted, and on a strike-by-strike basis according to the changing status of nut-shells (Liu *et al.*, 2009; Fragaszy *et al.*, 2010; Mangalam and Fragaszy, 2015; Liu, Fragaszy and Visalberghi, 2016; Mangalam *et al.*, 2018; Mangalam, Rein and Fragaszy, 2018).

Returning to the SDC case, it is apparent that adjustments in tool choice reflect the changing relevance of competing target affordances. Cashew nuts contain a caustic liquid surrounding the nut kernel, and harden as they dry (Mitchell and Mori, 1987); and it might thereby be expected that heavier tools should be selected as the season progresses (harder shells requiring greater force to strike open). Yet against expectations, Luncz *et al.* (2016) found capuchins in the Pedra Furada group adjusted tool choice by selecting lighter stones for drier nuts. Since weight of tools correlated positively with size, and therefore surface area, Luncz *et al.* (2016) hypothesise that by selecting larger tools capuchins at SDC reduced the likelihood of direct contact with the caustic liquid released during cracking; in this sense the functional properties of the tool reflecting not only the causal

function of the tool to 'amplify mechanical force' but also to 'extend the users reach', providing an effective barrier between the skin and caustic product.

Besides individual material interaction, socially biased learning also informs tool behaviour for this variant (grade 2 cued-dyadic causal reasoning), with individuals' attention directed by, and deriving information from, others tool-using interactions. At FBV for example, Eschar *et al.* (2016) found capuchins aged 6 years or younger were significantly more likely to situate themselves near anvils, interact with, and perform percussive and striking behaviour with nuts, when other group members engaged in nut-cracking behaviour. In corroboration, Fragaszy *et al.* (2017) show onset of this effect occurs within one minute of other conspecifics' beginning to perform cracking, and diminishes slowly, with higher rates of nut interaction and presence at the anvil continuing for minutes after others had stopped cracking. Fragaszy *et al.,* (2017) theorize attention and working memory are enhanced by socially situated practice. This is particularly important for a skill like nut-cracking which requires an extended period of development of necessary but complex perceptuomotor skills. With regard to observation of others, Ottoni *et al.,* (2005) found juveniles at Tietê targeted observational models for their age, dominance rank, proficiency, and productivity, preferentially observing older, dominant males. Preferred models were also those which provided the greatest opportunity for scrounging, reinforcing the prospective notion that until proficient nut-cracking is learnt, food rewards and the perceptive cues derived from others tool-use provide incentive to continue engaging with tool and target materials (Ottoni and Izar, 2008).

As for the role of material engagement in behavioural development, studies demonstrate capuchins spend years practicing isolated components of the behavioural sequence prior to achieving proficiency, with capuchins at SDC achieving successful nut-cracking at approximately 2 years of age (de Resende, Ottoni and Fragaszy, 2008; Falótico, 2011; Eshchar *et al.*, 2016). According to de Resende *et al.* (2008), juveniles at Tietê National Park first begin to manipulate stones and nuts independently, often percussing nuts against a substrate, after which they quickly move on to

perform direct percussion of nuts with stones, and stones with nuts. The last, and seemingly most difficult, element of the sequence to develop is placement and release of nuts onto the anvil surface, and it is only when this element is achieved that non-efficient cracking emerges, followed six plus months later by efficient cracking. Capuchins, perhaps due to their predominantly arboreal ecology, do not usually release food items they are trying to break open until either they are successful, or lose interest. That juveniles continued to place other non-food and tool items onto anvils during cracking bouts even after learning efficient cracking suggests placement and release, overcoming the desire to maintain grip, required practice as much as did cracking actions; with the relevance of releasing the nut, as opposed to gripping it tightly, taking consistent time and practice to realise (de Resende, Ottoni and Fragaszy, 2008, p. 836).

Current degree of material constitution of cognition for this variant may vary by target and site since many of the target species can be, and are, processed without the aid of stone tools by other groups; for instance, capuchins at FBV employ a 'rubbing' technique to process cashew, and the increased risk of contact with CNSL has been used as a possible explanation for the absence of tool-assisted processing there (Sirianni and Visalberghi, 2013; Visalberghi *et al.*, 2016). However, since the rubbing technique has not been observed at SDC, it is plausible to suggest cracking and rubbing each represent community-specific responses to the toxic CNSL threat (L.V. Luncz *et al.*, 2016), in which case cracking *does* provide novel function at SDC (if not at FBV). As for evolutionary relevance of the super-ordinate affordance, conflicting evidence from other sites suggests nut-cracking, though perhaps not maintained by necessity, may once have arisen from it (Spagnoletti *et al.*, 2011; Emidio and Ferreira, 2012; Falótico, Siqueira and Ottoni, 2017). Indeed, tool-using populations of *S.libidinosus* are more likely to inhabit drier, more seasonal areas like cerrado and caatinga, where plant richness and abundance are lesser than in rainier, species rich habitats (Moura and Lee, 2004; Spagnoletti *et al.*, 2011; Mendes *et al.*, 2015; Barrett *et al.*, 2018). Though changes in climate may alter the relevance of the affordance, by increasing the scope and energetic efficiency of the extractive foraging process, cracking is likely to provide a significant group-level adaptational

advantage, to the extent Wright *et al.* (2008) speculate use of stone tools used in the cracking of palm nuts may have been a selective agent for the relatively short hindlimbs and larger forelimbs of robust capuchins. Archaeological evidence of long-term maintenance of the nut-cracking behavioural tradition at SDC suggests it plays an important role in feeding ecology at the site (Falótico *et al.*, 2019). This being the case, and given the universal trend for cracking amongst wild populations, it is concluded material cognition is maximally constitutive to the ongoing development of capuchin cognition.

Shifting to causal cognition in to other forms of stone-pounding tool-use, grade 1 is prerequisite to both digging and pounding tasks, as is grade 3, with failure to reflexively match the information garnered about size and weight of tools with the properties of the target unlikely to result in improvement in either skill (overall energetic efficiency) or success rate. Since Falótico *et al.* (2017) show capuchins select digging and pounding stones of differing size and weight dependent on the properties of the prey target and location, it can be assumed capuchins are able to perceive and apply said information, if only in a direct sense, through the tool and tasks' object affordances and complementarities. Stone pounding tool-use functions to extend both the agential and sensory self, such that perception is extended through the physical object in use (grade 3). Moura (2004) postulates digging tools provide haptic and/or acoustic feedback about the location of underground storage organs, arguing local human populations use a similar technique to locate underground tubers of *Spondias tuberosa* which, when full of water, can be heard beneath the soil by pounding the ground. Experimental and field observational evidence of capuchin foraging strategies supports Moura's claim. When visual information is insufficient, capuchins often use acoustic information, obtained from tap-scanning or tapping of items onto hard surfaces, in order to locate invertebrates or to test for fruit/nut ripeness (Terborgh, 1983; Panger *et al.*, 2002; Phillips, Grafton and Haas, 2003; Phillips *et al.*, 2004); and Phillips *et al.* (2003) posit that where visual cues are used to derive information about which sites afford investigation, acoustic tap-scanning is used to refine the search. Tools used to crack open tree bark and rock complexes are essentially tool-mediated forms

of the same behaviour, functionally combining exploratory and extractive activity into the same act. In the case of digging, visual cues of others tool-use, or of plants or webs above the surface may provide the initial visual clue, but it is the acoustic cues perceived during tool-use which may refine and locate prey targets. This may be particularly so for the *Thiloa* root, for which not all plant roots have USOs. Further supportive evidence is provided by Moura (2004), who found successful bouts of digging were longer than when unsuccessful, indicating use of the tool may provide positive perceptive reinforcement of the affordance relevance, digging stones confirming the presence of USOs even when the capuchin cannot see them.

As for social learning, grade 2 is also likely present in some basic form, as evidenced by customary spread of both behaviours throughout the group, with others tool-use no doubt crucial to uptake. As Falótico *et al.* (2017) point out, a large part of the variant's behavioural success is dependent upon correctly locating a hidden resource, which for different prey targets, reflects differing levels of difficulty, and may explain variation in rates of success between juveniles (more frequently unsuccessful) and adults (more frequently successful). One way in which juveniles may learn to identify resources is by re-visiting sites already excavated by other conspecifics, and non-conspecifics [in particular collared peccaries, *Pecari trajacu* (Falótico, Siqueira and Ottoni, 2017)]; the perceptual information provided by others' previous engagement facilitating future tool-use (grades 4 & 5 causal cognition). Whereas spider tunnels and *Thiloa* USOs are exhausted through excavation, *Octea* roots, are not and leave a visible signal which may scaffold juvenile digging behaviour by providing an easily found means of practice.

For both variations of pounding tool-use, material cognition meets the criteria for minimal constitution only. Though there is no doubt the behaviours are embodied, extended and distributed, tool-use does not provide a novel function (many items can be excavated, and matrices broken down by hand or with the teeth). Tool-use does, however, increase the scope and effectiveness of foraging for USOs and hidden invertebrates, through its contribution to the subject's effectivities,

their perceptual capabilities, and through the causal function 'amplify mechanical force'; potentially providing an adaptive advantage by increasing access to alternative food resources, decreasing feeding competition, and increasing nutrient intake while minimising energetic cost. This being said, in the case of capuchin digging tools specifically, USOs are not fall-back foods, being more accurately classed as filler-fall-back foods; "food that never fills up the whole diet, is not consumed during part of the season and is patchily distributed" (Falótico, Siqueira and Ottoni, 2017, p. 8). In experimental conditions, Westergaard and Suomi (1995) found captive capuchins provided with digging apparatus manufactured and used wooden tools to excavate buried rewards. They noted all capuchins only adopted a tool-assisted strategy if the soil was too hard to dig manually, leading to the hypothesis that where extractive foraging facilitates manual digging in primates, suitable ecological conditions were likely to foster tool-use (Westergaard and Suomi, 1995, p. 5). Following the study, capuchins in their study group continued to use digging tools, exploiting a range of, likely opportunistically available, materials. Flexibility in material selection suggests the perceived relevance of the digging affordance relies less on a specific material context, and more on a general material property: suitable hardness. Tool-use in this sense, appears more in line with the opportunity hypothesis, than with the necessity hypothesis: the one element clearly correlated with the behaviours expression being opportunity for material engagement, since performance is reliant upon availability of resources and appropriate stone materials; the latter being abundant at SDC, but virtually absent at FBV where suitable tool material is sparse (Visalberghi, Spagnoletti, *et al.*, 2009). Although capuchins at FBV could potentially use wooden tools, it is possible that either cultural perceptual factors prohibit this (as maybe the case for probe tools – see Section 5.3.4), or that the soil is simply too hard.

5.2.3 Probe tools

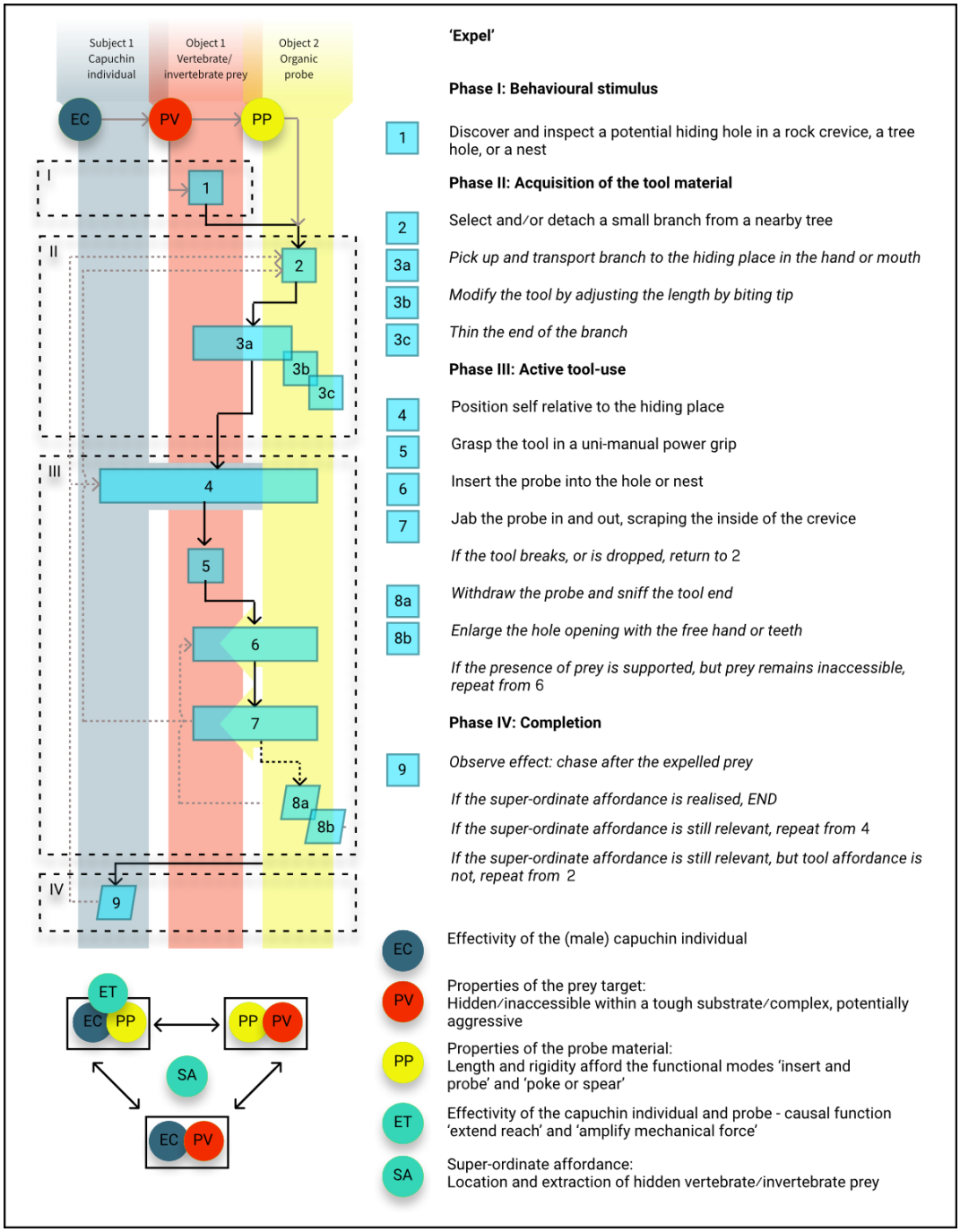
While several authors report use of probe-like tools in other capuchin species in semi-wild and semi-captive settings (Cooper and Harlow, 1961; Westergaard and Fragaszy, 1987; Chevalier-

Skolnikoff, 1990; Souto *et al.*, 2001), SDC is currently the only semi-wild *S.libidinosus* site at which probe tool-use is observed (Ottoni and Izar, 2008; Falótico and Ottoni, 2014; Cardoso and Ottoni, 2016). SDC capuchins use vegetative probe tools to access a variety of resources including vertebrates, invertebrates, honey, gum, wax, and water (Mannu and Ottoni, 2009; Falótico and Ottoni, 2014). Although a distinction is often made between probe tools used in subsistent contexts and those used as weapons (here classed as social variants), sub-divisions of subsistent tools based upon prey species or technique are not generally present within the capuchin literature. This presents an issue for inter-species comparison, since variant lumping or splitting determines repertoire richness, meaning overall complexity maybe artificially increased or decreased as a result of methodological choice. Therefore, to aid inter-species comparison between chimpanzee and capuchin repertoires, this thesis treats capuchin subsistent behaviours traditionally described under the catch-all 'probe tool-use' as heterogeneous, and divisible into three variant modes[41] : 'Expel', 'fluid dip', and 'open and probe'.

Expel Capuchins are known to predate several small vertebrate and arthropod species (Izawa, 1978, 1979; Butynski, 1982; Fedigan, 1990). Many of these species present a particular foraging challenge either because they live contained within protective nests or behind tree bark, or because they are able to hide in rock crevices or tree holes too small for capuchins to access. To predate out-of-reach prey, male capuchins sometimes exploit probe tools to expel these animals from their hiding places (Moura, 2004; Moura and Lee, 2004; Mannu and Ottoni, 2009; Falótico, 2011; Falótico and Ottoni, 2014). Probing episodes typically begin with discovery and inspection of a site affording probing (including observation of a prey animal hiding when chased), followed by detachment of a small branch from a nearby tree by hand or by mouth. Modifications are made while transporting the probe towards the target site, and include trimming of leaves from its distal end and thinning of the proximal tip (Mannu and Ottoni, 2009, p. 247; Falótico and Ottoni, 2014, p. 119).

[41] Classification is based on behavioural descriptions provided in the literature.

Figure 31 Cognigram for the SDC variant 'Expel'



The probe is inserted into the target's hiding place or nest, and moved vigorously in and out, until, if successful, the animal is expelled; at which point the capuchin attempts to catch and eat the expelled prey. The behavioural continuity exhibited by *S.libinosus* in their technical responses to vertebrate and invertebrate prey is in direct contrast with chimpanzee approaches which differ between prey types, with chimpanzees adopting a precision grip and finer grade tools when targeting invertebrates (see Sections 4.2.2 - 4.2.3). Although blonde capuchins have been reported to 'fish' for termites (Souto *et al.*, 2001), use of probe tools in the predation of termites at SDC seems less designed to encourage termites to climb or attach themselves to the probe, so much as to violently expel them from the nest (Falótico and Ottoni, 2014). The lack of finer-grade technique is no doubt a result of *S.libidinosus* feeding ecology; Falótico & Ottoni (2014) observe that when predating social insects, capuchins more often did so directly, by destroying the nest (see also Izawa, 1979, p. 70). Figure 31 (p. 185) gives 'expel' as a single perception-action module constituted by 3 foci: the capuchin, the organic material which forms the probe tool, and the target (invertebrate or small vertebrate). 2 spatial relationships were counted to Object order, 1 static (between probe and crevice) and 1 dynamic (between probe and target allospecific). The minimum critical sequence is formed of 7 actions (maximum = 10), in 4 phases. 2 modificatory actions are counted, including branch thinning and adjustment of tool length. Manufacturing mode is classed as reductive reshaping.

Fluid dip The technique employed by capuchins probing for fluids, e.g. honey or wax, is very similar to that of chimpanzee fluid-dipping, with modified probes being carefully inserted into wasp nests, then withdrawn and the coagulated fluid licked from the tip (Falótico and Ottoni, 2014). Figure 32 (p. 187) portrays fluid dipping as a single perception-action module, in which the super-ordinate affordance arises between interplay of 3 foci: the capuchin, the organic material which forms the probe, and a viscous trapped fluid. Object order includes 2 spatial relationships, 1 static (between the probe and the entrance to the nest containing honey) and 1 dynamic (between the

Figure 32 Cognigram for the SDC variant 'Fluid dip'

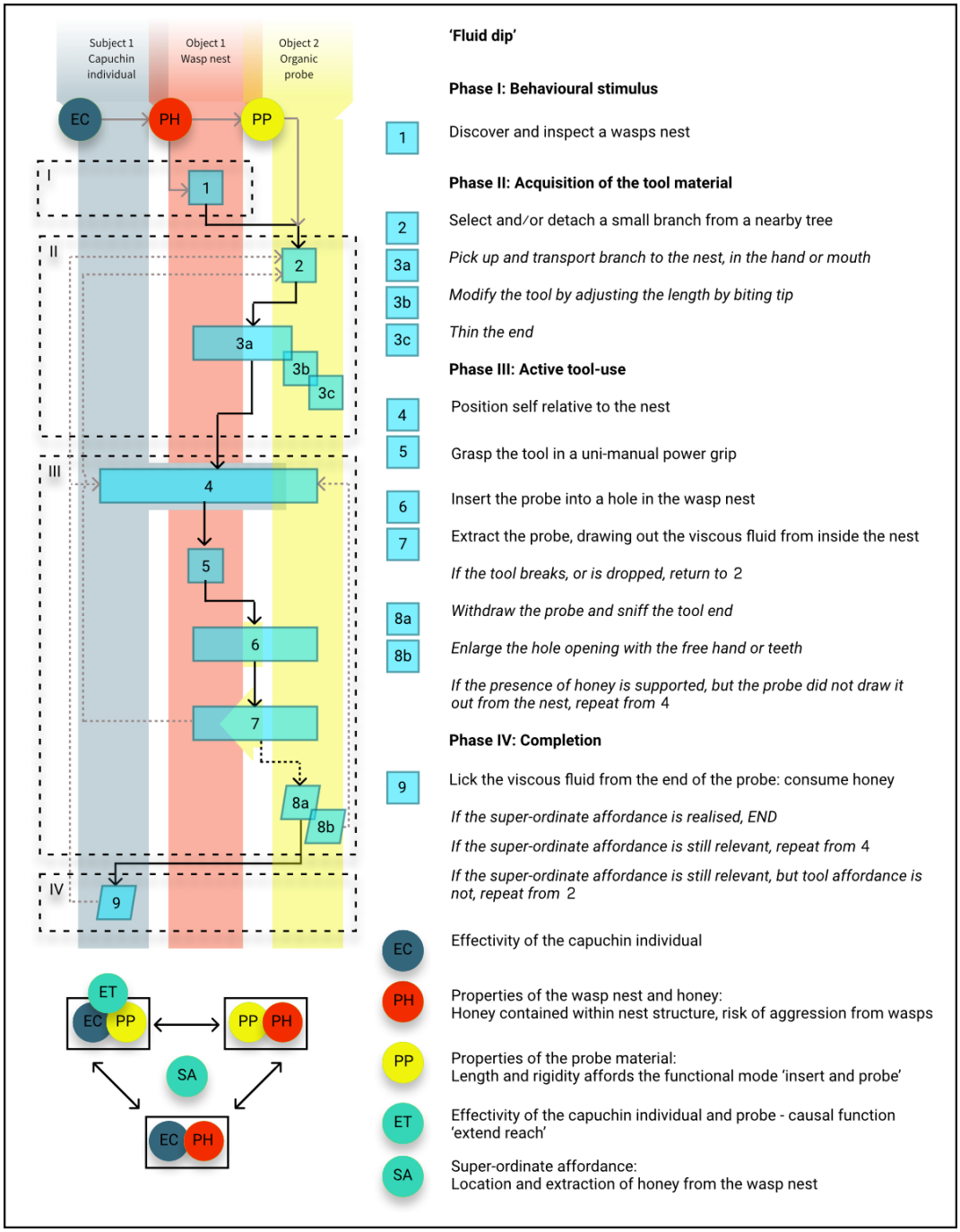
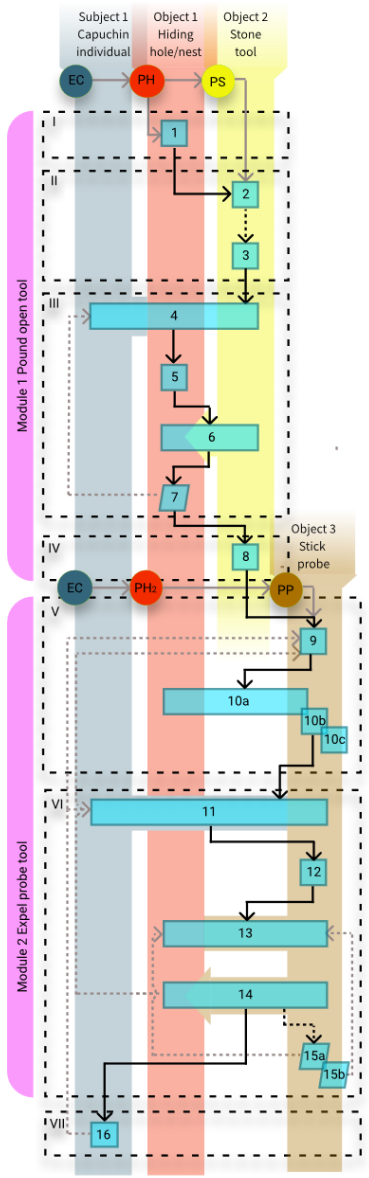


Figure 33 Cognigram for the SDC variant 'Open and probe'



'Open and probe'

Phase I: Behavioural stimulus

1 Discover a visual cue affording exploration of an inedible or tough matrix likely to contain a hidden food resource

Phase II: Acquisition of a tool material

2 Select a material affording use as a hammer-stone

3 *Pick up and transport the hammer-stone material to the hidden food resource*

Phase III: Active tool use

4 Position self relative to the matrix encasing the resource

5 Grip the hammer-stone

6 Strike the matrix with the hammer-stone, repeatedly

7 *Inspect the hole produced in the matrix, enlarge with fingers or teeth*

If the resource remains inaccessible, repeat from 4

Phase IV: Completion of sub-module

8 Place the hammer-stone to one side

Phase V: Acquisition of a tool material

9 Select and/or detach a small branch from a nearby tree

10a *Pick up and transport the branch to the hiding place, in the hand or mouth*

10b *Modify the tool by adjusting the length, biting the tip*

10c *Thin the tool tip*

Phase VI: Active tool use

11 Position self relative to the cracked matrix

12 Grasp the tool in a uni-manual power grip

13 Insert the probe forcefully into the hole in the cracked matrix

14 Jab the probe in and out, scraping the inside of the hole

If the tool breaks, or is dropped, return to 9

15a *Sniff the tip of the probe*

15b *Enlarge the hole opening with the hands or teeth*

If the presence of prey is supported, but prey remains inaccessible, repeat from 13

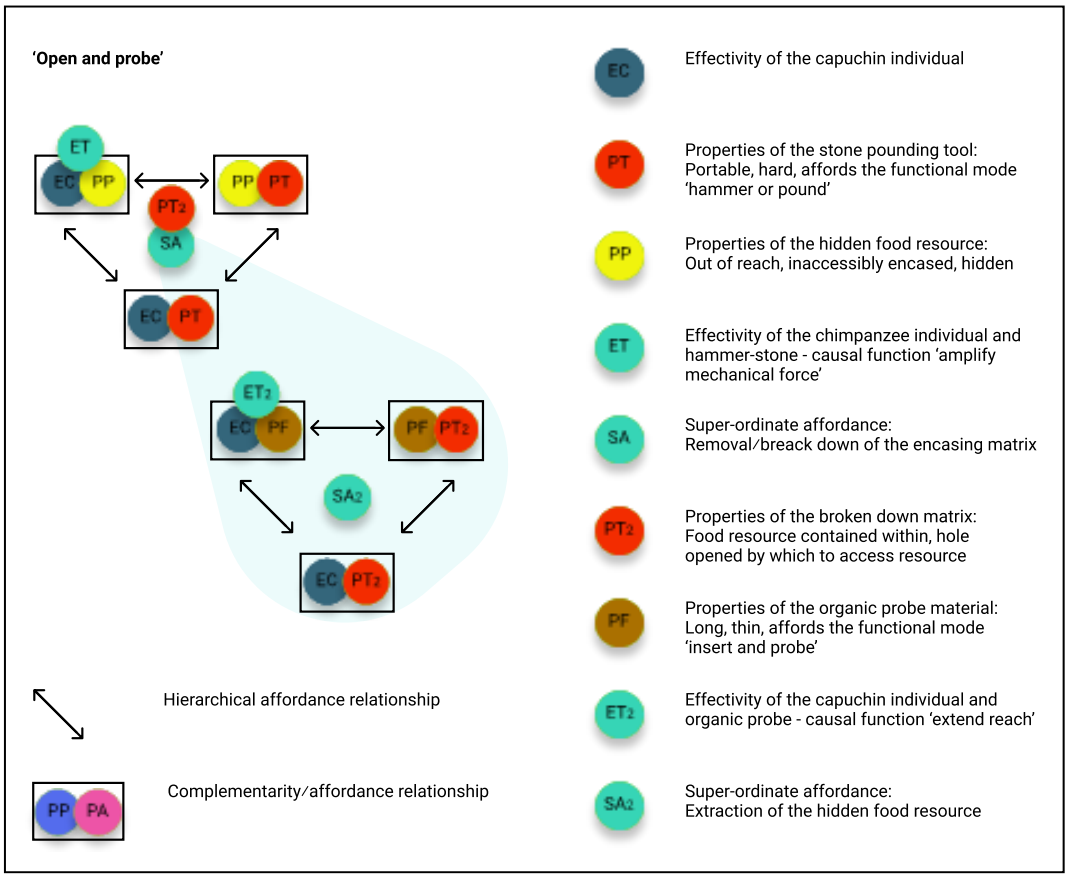
Phase VII: Completion

16 *Observe effect*: chase after expelled prey

If the super-ordinate affordance is realised, END

If the super-ordinate affordance is still relevant, repeat from 11

Figure 34 Affordance relationships making up the SDC variant 'Open and probe'



probe and the honey). The minimum operational sequence is described by 7 critical actions (maximum = 10), in 4 phases. Modifications include thinning of the branch, and adjustment of length. Manufacturing mode is, again, classed as reductive reshaping.

Open and probe Mannu & Ottoni (2009) report that, on a number of occasions, capuchins made "sequential" use of stone percussors and stick probes to access insect nests in rotten tree trunks and prey (in particular, lizards) hidden in rock crevices (see also Ottoni, 2015). Of the four examples given, in each, a male capuchin used a pounding stone to enlarge a hole in a substrate, tree, or rock complex, before detaching, modifying, and inserting a branch into the hole, "jabbing it vigorously" (Mannu and Ottoni, 2009, p. 248) to extract the hidden target. In several cases, tool-use was interspersed with epistemic actions such as sniffing of tools and manipulation of hole openings with either the fingers or mouth. Figure 33 (p. 188) & Figure 34 (p. 189) show the variant 'open and probe' as a composite perception-action sequence built from the sequential association of the modules 'pound open' and 'expel'(/'fluid dip'). A total 3 spatial relationships, 1 static (between probe and opening in the casing-matrix) and 2 dynamic (between hammer-stone and casing-matrix; probe and target resource). The minimum operational sequence comprises 12 critical actions (maximum = 16), in 7 phases. Modifications to the tool include a maximum of 2 possible actions: adjustment of tool length, and thinning of the distal end. Since the pounding and probing tools are used sequentially and not in conjunction, modification remains classed as reductive.

5.2.4 Causal cognition in SDC probe tools

Through its causal function, probe tool use extends the users reach and, by proxy, the user's perceptive boundary. On several occasions, Mannu & Ottoni (2009) observed tools being introduced only once, before being retrieved and sniffed, only to be abandoned, indicating the behaviour may often be opportunistically triggered by the site itself, which affords exploration, rather than by knowledge of a specific prey's being inside. That probe tool use is frequently interspersed with

sniffing of tool tips, and with manipulation of hiding place entrances (Mannu and Ottoni, 2009), supports this hypothesis, adding to the notion that probe tool use acts as a form of perceptual prosthesis by providing information about presence or absence, and the nature of hidden prey. Adjustment of tool forms during the tool-using process demonstrates an ongoing sensitivity to the complementarity between the tool's functional affordances, and the properties of the task at hand - in other words, a reflexive ability to respond to immediate cues as they arise as though tool-use were itself epistemic. Although Falótico & Ottoni (2014) found no significant difference in the average length of probe tools used by different groups, differences were found between tools used to target different species, with termite tools significantly longer and thicker than tools used to target tree holes, which were in turn longer than tools used to target rock crevices. By demonstrating a sensitivity to the ecology of prey type perhaps absent in technique, this supports the claim that SDC capuchins are able to respond to and situationally bring about the relevant functional properties of tools as they relate to a given task.

While the ontogeny of subsistent probe tool-use has yet to be clearly investigated, notable differences in success rate, which is positively correlated with age, indicate practice is a necessary part of the learning process, with juveniles rarely successful even when using modified tools (juveniles were successful in only 10% of observed episodes recorded by Falótico & Ottoni, (2014). Indeed, experimental evidence in captive settings indicates grades 1 and 3 causal cognition are critical to development of successful probe tool-use. Visalberghi and Trinca (1989) found that, when provided with dipping-apparatus, capuchins did not immediately comprehend the relevance of functional properties of objects, and instead selected and inserted shapes into openings at random, modifying selected objects only after they failed (Fragaszy, Visalberghi and Fedigan, 2004). These results suggest perception of the tool affordance only arose when interaction with the object as an extension of the user's reach provided extra information for which visual perception alone was insufficient. *S.libidinosus* perceptivity to probe tool-using affordances is, at least in part, influenced by their social ecology, with behavioural uptake subject to local patterns of socially-biased

transmission (grade 2 causal cognition). 'Cultural' or normative influence in this sense is manifest at both the regional and local levels; with inter-group discrepancies in probe tool-using (or lack thereof) unlikely to be explained by ecological dissimilarities between sites alone (Ottoni and Izar, 2008; Cardoso and Ottoni, 2016); and with demographic distribution showing a significant intra-group sex-bias – studies record up to 97% of probe tool episodes as having been performed by males, and the remaining 3% as having been performed by sub-adult females (Moura and Lee, 2010; Falótico and Ottoni, 2014).

Turning temporarily to local distribution, lack of adult female probe tool-using is surprising. While all *S.libidinosus* tool-use exhibits some level of male bias, of all the tools in the SDC repertoire, probe tool use is perhaps the least physically demanding and therefore the least likely to show bias (Moura and Lee, 2010). Further, females in captivity may solve probe tool problems as often and effectively as males (Visalberghi and Trinca, 1989; Visalberghi and Limongelli, 1994), so that it would seem neither physical nor cognitive factors should inhibit female probe tool use (Falótico and Ottoni, 2014, p. 121). Moura & Lee (2010) and Falótico & Ottoni (2014) discuss several possible explanations for the discrepancy, including differing male/female feeding ecologies and parental investment strategies, however, neither appears sufficient to explain the sex bias. Although males predate vertebrates more often than females, lizards comprise a significant percentage of female's vertebrate diet [61.1% (Falótico and Ottoni, 2014, p. 121)], suggesting both opportunity and incentive for tool use. As for paternal investment, probe tool-use is unlike other forms of capuchin tool use in that it does not produce scrounge-able leftovers or typically enable food sharing, and is therefore unlikely to provide much advantage to any offspring.

A more plausible explanation, though it currently lacks the research to support any firm claim, is that females, more so than males, lack the opportunity to observe and or interact with behavioural models and tool materials. From the SDC site, it appears vertical transmission is critical to variant spread. Of the 20% of probe tool-using episodes recorded by Falótico & Ottoni (2014, p.

19) observed by conspecifics, c.80% were observations made by juveniles or infants; with manipulation of abandoned tools by observers occurring in 38 events. Wild studies of *Sapajus* socio-ecology show that female in-group feeding competition is increased by tool-use, particularly when resources are usurpable (Verderane *et al.*, 2013) - as would be the case in the instance of probe tools used to expel vertebrates[42]. Indeed, at FBV, Spagnoletti *et al* (2013) report that despite there being no significant difference between the number of occasions in which male and females predated vertebrates individually (51.3% and 48.7% of all observed episodes of individual vertebrate predation, respectively), males were significantly more likely to participate in predation events in which two or more individuals targeted the same prey item, either together, at the same time, or one after the other (64.23% and 35.77% respectively). Adults and juveniles were similarly likely to participate in group predation episodes (Spagnoletti *et al.*, 2013). Assuming predation behaviour is similar between the SDC and FBV sites, female feeding competition could limit female exposure to others' predation techniques, and access to others' tools, critical to variant transmission.

Overall, material cognition meets the criteria for minimal constitution. Probe tools function to extend physical and perceptual parameters through peri-personal space, increasing the scope and effectiveness of predatory behaviours in a variety of foraging contexts by providing feedback about relevant task features; averting the energetically expensive need to destroy the protective matrices which hide prey targets; and reducing risk of injury. Constitution cannot be considered maximal since the predatory behaviours to which tool-use is applied are not novel, with many of the resources accessed still being predated without the use of probe tools, if only with less efficiency. In light of the captive studies discussed above, it would appear probe tool using affordances are comparatively difficult for capuchins to perceive[43], and perhaps, given a lack of behavioural overlap with their non-tool-using repertoire, technique may require an extended period of experimental investment to develop. Material engagement, both individually, through observing others, and

[42] s*ensu* Isbell & Pruetz, 1998: it is argued the vertebrate can easily be taken (either directly or indirectly) by a higher-ranking individual.
[43] In comparison to stone pounding tools

through interaction with others' tools thus appears critical to mastering skill and technique. At the macro-level, discrepancies between sites may reflect the relative difficulty of this extended learning process, exacerbated in the wild by low rates of return [success rates being the lowest of all other tools present in the SDC repertoire (Moura and Lee, 2010; Falótico and Ottoni, 2014)] and by a lack of rewards from others tool-use to scaffold attention towards the sustained interaction necessary for variant uptake and spread. When presented with dipping apparatus, capuchins at FBV failed to manufacture, use or re-use pre-inserted probe tools, suggesting the perceived relevance of tool and task affordances was reduced or altogether absent for individuals in the group (Cardoso and Ottoni, 2016).

While this could be a factor of inexperience, failure to recognise or be solicited by the tool affordances, even when made more salient (by pre-inserting the probes), could be more indicative of 'cultural override' (sensu Hicks *et al.*, 2020), with cultural preferences, or expertise from the pre-existing technical repertoire, potentially influencing (or inhibiting) the capuchins' perception of affordance relevance (Cardoso and Ottoni, 2016). Marshall-Pescini and Whiten (2009), Hrubesch, Preuschoft and van Schaik (2009), and Gruber et al. (2011) argue that chimpanzee learning of novel technical traits is similarly constrained by cultural 'conservatism', with experimental results suggesting that expertise (or at least functional mastery) of a given skill inhibited further exploration and adoption of novel techniques even where those techniques were ergonomically more efficient. An exception to this might be cultural override in the form of 'conformity', in which individuals bias towards 'approved' technical behaviours, which reflects a social pressure to conform to group norms (e.g. Luncz, Mundry and Boesch, 2012; van de Waal, Borgeaud and Whiten, 2013; Luncz and Boesch, 2014). That pre-existing technical repertoires can affect and inhibit learning of novel behaviours demonstrates a cultural bias to NHP technical cognition, and a normative affectivity to their technical affordance perception – reinforcing the concept of the technical mind as a particular set of skills which together produce an emergent perspective. In the social situation of technical ontogeny,

mind can be seen as a developing and distributed process of being, not just in the world, but also with others.[44]

5.2.5 Social variants

Determining functional orientation for tools used outside of the subsistence context posed a difficult challenge, since some of the behaviours listed in the following sections could equally have been placed here (e.g. 'scratch', and 'stone pound'), and the variant 'poking stick', placed elsewhere, according to subjective interpretation or case-specific context. As is, two variants have been classed as social tool use (on the basis that of primary context): 'poking stick (club/spear)', and 'aimed throw'.

Poking stick (club/spear) Anecdotal reports describe social tool-use by *S.libidinosus*, with poking and clubbing sticks incorporated into their agonistic and mobbing behavioural repertoires. Observations include dislodging and dropping of branches to deter intruders, 'clubbing' of snakes (*Bothrops spp.*) and a tortoise (*Stigmochelys pardalis*), and defensive use of sticks to repel other monkeys (Boinski, 1988; Chevalier-Skolnikoff, 1990; Vitale, Visalberghi and De Lillo, 1991; Hamilton and Fragaszy, 2014). At SDC, capuchins have been observed to use stick tools to threaten and/or contact non-conspecifics including snakes (*Bothrops spp.* and *Boa constrictor*), toads (*Leptodactyuls spp.*), spiders (tarantula), scorpions, and on one occasion a white eared opossum (*Didelphis albiventris*) (Mannu and Ottoni, 2009; Falótico and Ottoni, 2016; Falótico, Verderane, *et al.*, 2018). Typical use begins with an individual's or the group's discovery of an animal affording threat, followed by vocalisation and physical threat gestures characteristic of mobbing behaviour. A capuchin then breaks off a branch, and, positioning itself some distance from the perceived threatening other, reaches out in an attempt to contact the target with the stick, thrusting the stick a spear-like or clubbing gesture (Falótico and Ottoni, 2014 supplementary video 2). The precise

[44] This paragraph appears in Mosley (2020, p.7)

Figure 35 Cognigram for the SDC variant 'Poking stick' (club/spear)

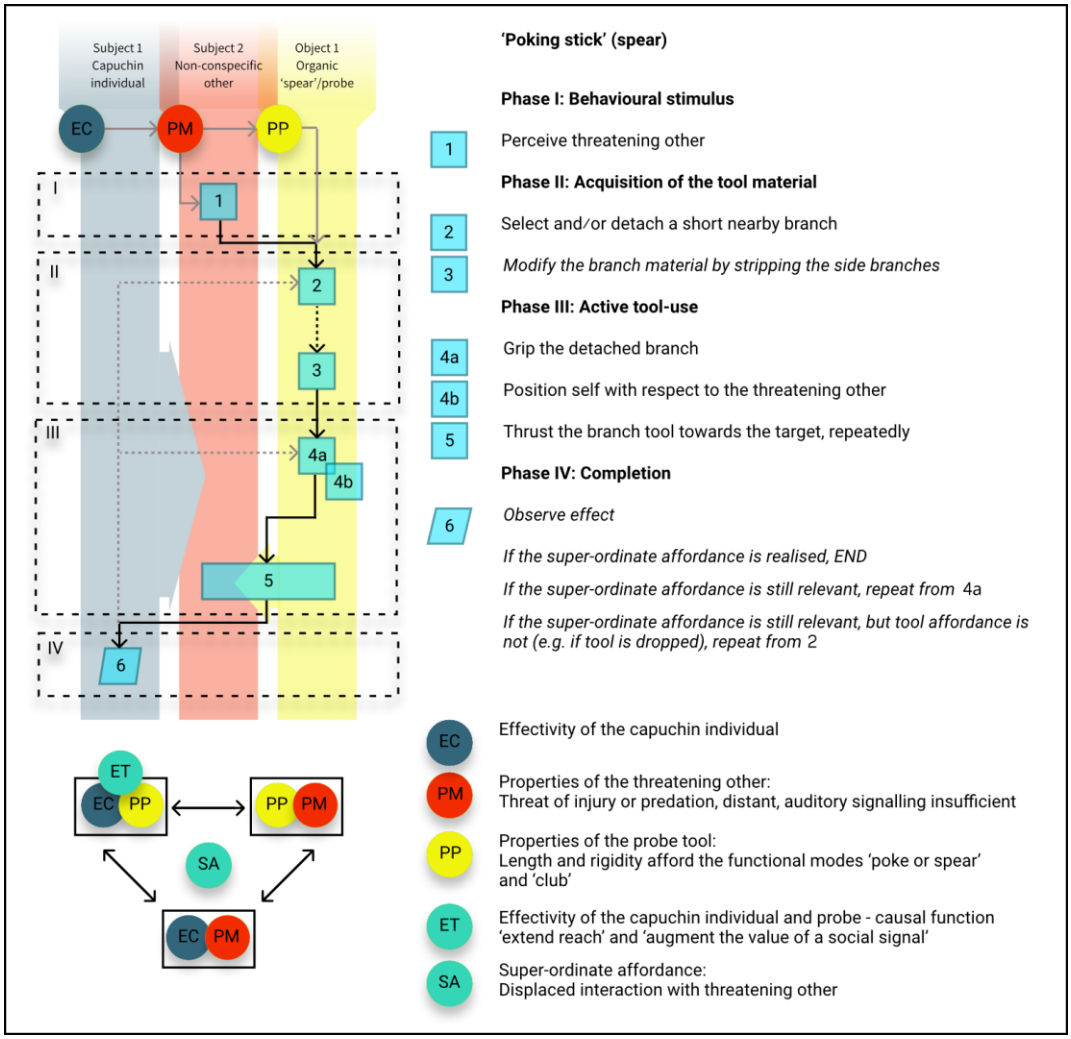
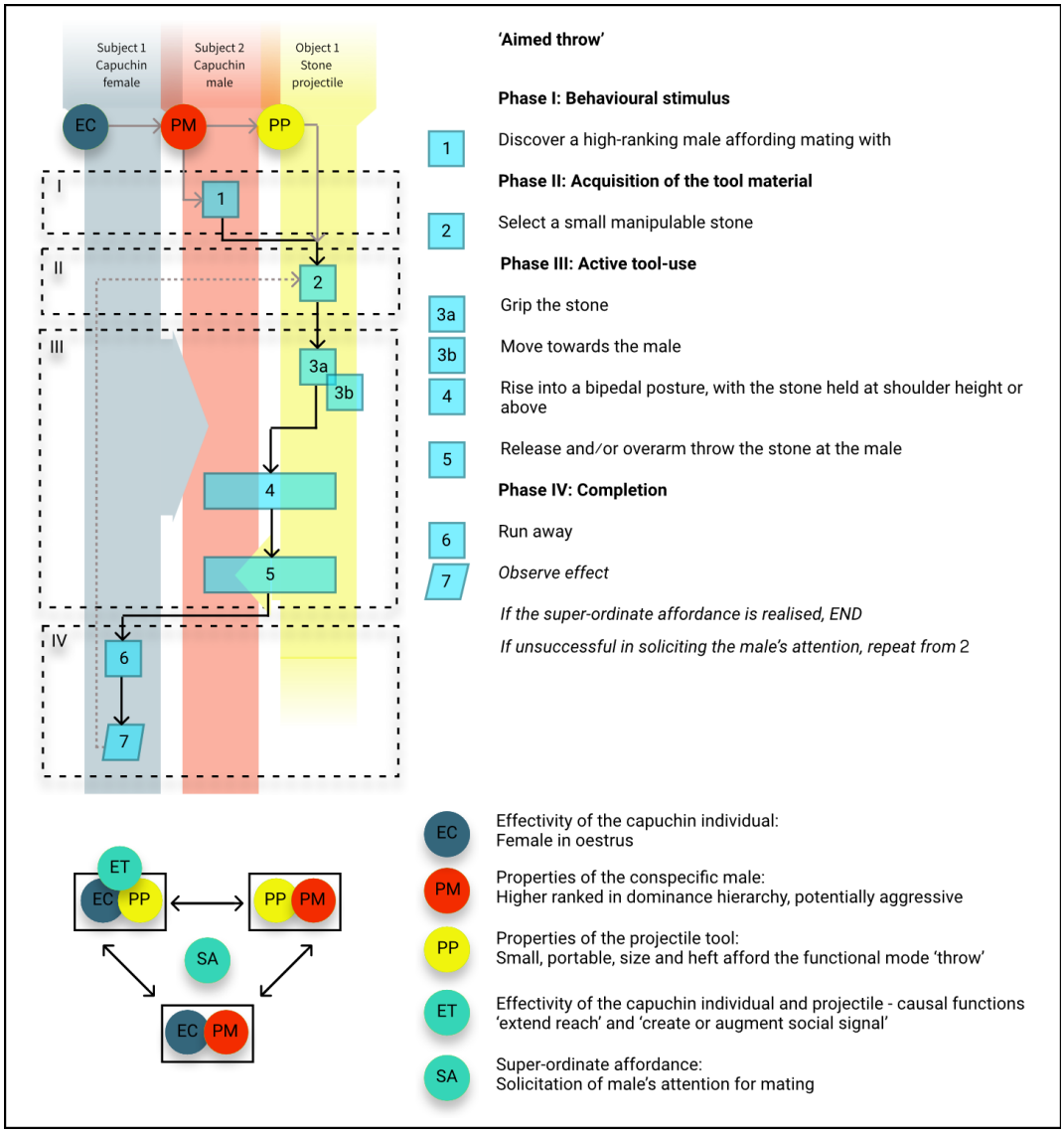


Figure 36 Cognigram for the SDC variant 'Aimed throw'



function of tool-use in this context is unclear, since success is hard to measure (i.e. whether tools did or did not reduce predators' latency in leaving an area), and since capuchins often failed to contact the target animal (Mannu and Ottoni, 2009, p. 248). On at least one occasion, technique was interspersed with sniffing of the tool tip (Falótico and Ottoni, 2014 supplementary video 2) suggesting the tool behaviour was either investigative in nature or was used to provide supplementary information by its user. Although modification does not appear to be a typical feature of this behaviour, in one episode (Falótico & Ottoni, 2014, supplementary video 2) a capuchin can be seen to modify an unused tool by stripping its side branches with the mouth. Reuse of tools is not reported, but seems unlikely given the variant's arboreal or elevated context; dropping of tools onto target animals is likely to render them inaccessible due to risk of incurring injury in re-acquisition. Given lack of striking precision, it is likely that tool-use in this context, rather than functioning as a weapon *per se*, serves to exaggerate the threat gesture in cases where the target predator may not easily perceive auditory or visual cues (following Crofoot, 2012; Curio, 1978); for example, when targeting venomous snakes (Christensen *et al.*, 2012; also cited by Crofoot, 2012). Taking the tools function as gestural rather than forceful, Figure 35 (p. 196) gives the use of a poking stick as a single perception-action with 3 system foci: the capuchin, organic material which forms the probe tool, and the target allospecific. 1 dynamic spatial relationship (between probe and allospecific) exists to count towards Object order. Minimum behavioural sequence is described in 5 critical actions (maximum = 6), in 4 phases, and includes 1 modification (besides detachment and transport): stripping of side branches, which was classed as reductive reshaping.

Aimed throw Capuchins in captivity are known to be capable of aimed throwing, and anecdotal observation of the behaviour in the wild suggest it is a universal, if rarely expressed, feature of capuchin behavioural repertoires (Westergaard and Suomi, 1994; Westergaard *et al.*, 1998, 2000; Evans and Westergaard, 2004; Shumaker, Walkup and Beck, 2011). At SDC, aimed throwing of small

stones is habitual amongst adult females of the Pedra furada group[45], and is performed as a communicative behaviour signalling sexual receptivity to high-ranking males (Falótico and Ottoni, 2013). The technical variant is not unique to the site, though use of stones rather than organic material is unusual; similar proceptive behaviours have been observed at FBV and in captivity (Carosi and Visalberghi, 2002; Falótico and Ottoni, 2013; Visalberghi *et al.*, 2017). According to Falótico & Ottoni (2013), to perform the behaviour females stood bipedally (sometimes tripedally) and held the stone either at or above shoulder level, projecting it towards the targeted male to create the effect of an overarm throw (Falótico and Ottoni, 2013). Though only 7 of the 42 episodes recorded during the period of Falótico & Ottoni's (2013) study resulted in the stone physically contacting the target, whether the stone struck or missed the targeted male to land nearby, elicited the same response: males looked towards the female, and, on occasion, subsequently threatened or chased her. Visalberghi *et al.* (2017) argue aimed throwing supplements 'touching-and-running' behaviours, in which females approach prospective mates quickly, push or touch them with an outstretched arm, and immediately run away (Carosi and Visalberghi, 2002). 'Touching-and running' behaviours are characteristic of the corresponding period of courtship, and although males' initial response to solicitation attempts by females is usually a lack of interest, higher ranking males are more likely to respond aggressively with threats or with chasing , in some cases resulting in slapping and biting females (Carosi and Visalberghi, 2002; Mendonça-Furtado *et al.*, 2014). In instances when risk of reprisal is particularly high, i.e. when targeting high ranking males, tool-use affords a means of closing the distance between individuals in order for the female to make contact, while maintaining a spatial agonistic buffer. Figure 36 (p. 197), visualises aimed throwing among SDC capuchins as a single perception-action module, in which the super-ordinate affordance is distributed across 3 foci: the female capuchin in oestrous, the stone material which forms the projectile, and the high-ranking capuchin male. 1 dynamic spatial relationship (between stone projectile and male capuchin) was

[45] No evidence of stone throwing as sexual solicitation by females has been reported for any of the other three groups at SDC (Mannu & Ottoni, 2009; Falótico, 2011; also cited by Falótico & Ottoni, 2013).

counted into Object order for the behaviour. The minimum operational sequence contains 7 critical actions (maximum = 7), in 4 phases. No manufacture is counted for the tool behaviour.

5.2.6 Causal cognition in capuchin social tool-use

Considering the material constitution of social tool-use, neither variant of this context provides a novel function, but both supplement pre-existing non-tool-using communicative behaviours, each by augmenting the value of a particular social signal. Speculatively, in the former case this involves a multi-modal exaggeration of the threat/mobbing signal in order to increase its perceptibility to a non-conspecific other - optimising time and energy expenditure; and in both cases, involves a functional extension of the signal through peri- and/or extra-personal space which physically distances the subject from the signal recipient – reducing probability of injury. Maximising efficiency whilst minimising the behaviours incumbent risks ought to bring about an adaptive reward. For the poking stick, the adaptive benefits of mobbing are potentially fourfold (following Dugatkin & Godin, 1992; FitzGibbon, 1994): by approaching the predator, mobbing provides information about the nature of the potential threat; reduces the probability of an immediate attack (both by encouraging the predator to move on and by eliminating the possibility of ambush); informs conspecifics of the potential threat, recruiting others to approach the threat as a collective, diluting the probability of individual predation, and strengthening coalitionary bonds; and finally, advertises the subject's quality to potential mates. For aimed throwing, the subject's benefits could be direct or indirect. For example, mating with higher-ranking males could facilitate access to controlled nutritional resources (Janson, 1984, 1986; Carosi, Linn and Visalberghi, 2005); but would also increase reproductive success long-term through the passing on of beneficial genetic traits to any resultant offspring. Since social tools improve the scope and efficiency of pre-existing non-tool-using behaviours, their material is considered minimally constitutive to cognition.

In terms of physical cognition, successful extension of the agential self through peri-personal space is underwritten by grades 1 and 3 causal cognition, and extension through extra-personal

space, by low level grade 6 (see Section 3.6.1.6). Captive experiments show skilled capuchin throwers recognise the functional affordances of projectiles (Evans and Westergaard, 2004); select materials by their weight (Cleveland *et al.*, 2003); and distinguish between stationary and moving targets, adjusting their behaviour accordingly (Westergaard and Suomi, 1994). Although there is no evidence that subsistent probe tool-use involves any level of causal understanding beyond grade 3 (self-mind reading), in a social context, resorting to the multi-modality of a mobbing signal facilitated by the poking stick could be indicative of basic grade 5 non conspecific mind-reading. In this scenario, it would be the non-conspecific other's reaction to the tool which informs future tool-use.

In terms of social cognition, both use of poking sticks and aimed throwing exhibit demographic distributions characteristic of transmission involving at least grade 2 cued-dyadic reasoning. As an exaggerated form of predator response, 'poking' sticks are specific to the site, and, as probe tools, exhibit significant male bias (Falótico and Ottoni, 2014). Aimed throwing, at least in the proceptive context of the SDC variant, is performed exclusively by adult females, with inter-group discrepancies in expression and material selectivity (Falótico and Ottoni, 2013; Visalberghi *et al.*, 2017).

With regards to material engagement, lacking a metric by which to measure the development of 'skill' in either form of social tool-use, it is difficult to interpret to what degree material interaction informs technique. One way in which material engagement might affect cognitive development is with regard to the ensignification of material as a communicator of risk. *S.libidinosus* are both predators and prey of snakes, and although differing behavioural responses indicate adult capuchins are able to discriminate between species which afford opportunity and those which afford threat (Falótico, Verderane, *et al.*, 2018), studies amongst other wild primate groups suggest this ability is absent in infants, taking time and experience to nurture (Mineka and Cook, 1988; Vitale, Visalberghi and De Lillo, 1991; Meno, Coss and Perry, 2013). Group mobbing behaviours produce relatively low risk situations through which juveniles may learn to recognise and

respond to predator threats (eg. Altmann, 1956; Bartecki & Heymann, 1987; Curio, 1978; FitzGibbon, 1994) Tool-use in these situations, could be perceived as a visual, material signal in lieu of alarm calling, providing information both about the snake, and how to respond to it.

Material engagement is also likely to shape material selectivity in aimed throwing. Falótico & Ottoni (2016, p. 439) hypothesise that the flexibility with which stone pounding tools are used, and the variety of subsistent contexts to which they are applied, drives further innovative forms of use such as stone throwing in oestrus display. As a counter-argument, Visalberghi *et al.* (2017) point out FBV females select inorganic and organic materials for their oestrus display, despite a lack of organic materials being utilised as tools in subsistent contexts. Rather, they suggest, capuchins are more likely to follow the same behavioural patterns of material selection as they would commonly use when throwing (or dropping/displacing) functioned as a deterrent to predators and intruders (Fragaszy, Visalberghi and Fedigan, 2004; Moura, 2006; Visalberghi *et al.*, 2017, p. 212). Further, in comparisons between terrestrial and arboreal species, terrestrial species tended to use stones, and arboreal species, branches; such that groups' material choice typically reflected the materials most ubiquitous within the species' habitats (Visalberghi *et al.*, 2017). At SDC, not only do capuchins spend greater periods of time on the ground than at FBV, but there is also a relative abundance of suitably sized stone material. This being said, there is no reason why the two hypotheses should be mutually exclusive, and indeed, that only PF group at SDC engage in stone throwing in oestrus display suggests opportunity for material interaction alone may not be sufficient for behavioural innovation to occur. After-all, although abundance of material may provide ample opportunity for interaction with stones, it is the flexible use of stone tools across a variety of contexts (many of which reap immediate reward) which provides motivation for sustained practical engagement, increasing the prospects of discovery of novel technical affordances.

5.2.7 Hygiene & comfort variants

There are three technical variants at SDC for which functional context is classed as 'hygiene':

'Nasal probe' and 'tooth pick' (described together under the title 'self-groom'), and 'self-scratch'. All are self-directed incidents of probe tool-use, and are included as anecdotally reported variants, present but not customary within the population.

Self-groom The variants 'nasal probe' and 'tooth pick' are reported only once in the literature[46], by Haslam & Falótico (2015), who observed a single female from the Jurubeba group use a series of tools in short succession, to probe her nose and mouth while being groomed by an adult male. Although according to the behavioural description provided by Haslam & Falótico (2015, pp. 212–213) the two variants were performed interspersed and occasionally by means of the same tool, their respective functions were not the same. Nasal probing involved careful insertion of a short probe into the nasal cavity, often triggering a sneeze. Tooth picking, in contrast, never elicited a sneeze reaction, and use of the tool was described as dynamic; the capuchin carefully placing the tool before appearing to work at the base of the teeth or gum, moving the tool in a rapid back and forth movement with respect to a specific location within the mouth. Since neither behaviour is prerequisite to the other, such that each could be performed in isolation, the variants 'Nasal probe' and 'tooth pick' are taken to form two separate perception action modules [which may form a compound ('self-groom')], as shown in Figure 37 (p. 204) and Figure 38 (p. 205), respectively. The super-ordinate affordance for nasal probing is spread over 3 foci: the capuchin, the material which forms the nasal probe, and the item lodged up the nose (or source of discomfort). Object order includes 1 dynamic spatial relationship (between the probe and nasal passage). Minimum operational sequence is of 6 critical actions (maximum = 6), in 4 phases, and includes no modifications to the tool form. The super-ordinate affordance for 'tooth pick' is also constituted by 3 foci: this time the capuchin, organic probe material, and the item causing irritation to the gums (as the source of discomfort). In this case, 2 spatial relationships were counted towards Object order, 1 static (between probe and mouth) and 1 dynamic (between probe tip and gums). Minimum

[46] 'tooth pick' has been observed by Perry *et al.* (Perry, Barrett and Godoy, 2017 in supplementary information) in *Cebus capucinus:* and was described as the subject "poking [a] stick in [their] own mouth between [the] teeth"

Figure 37 Cognigram for the SDC variant 'Nasal probe'

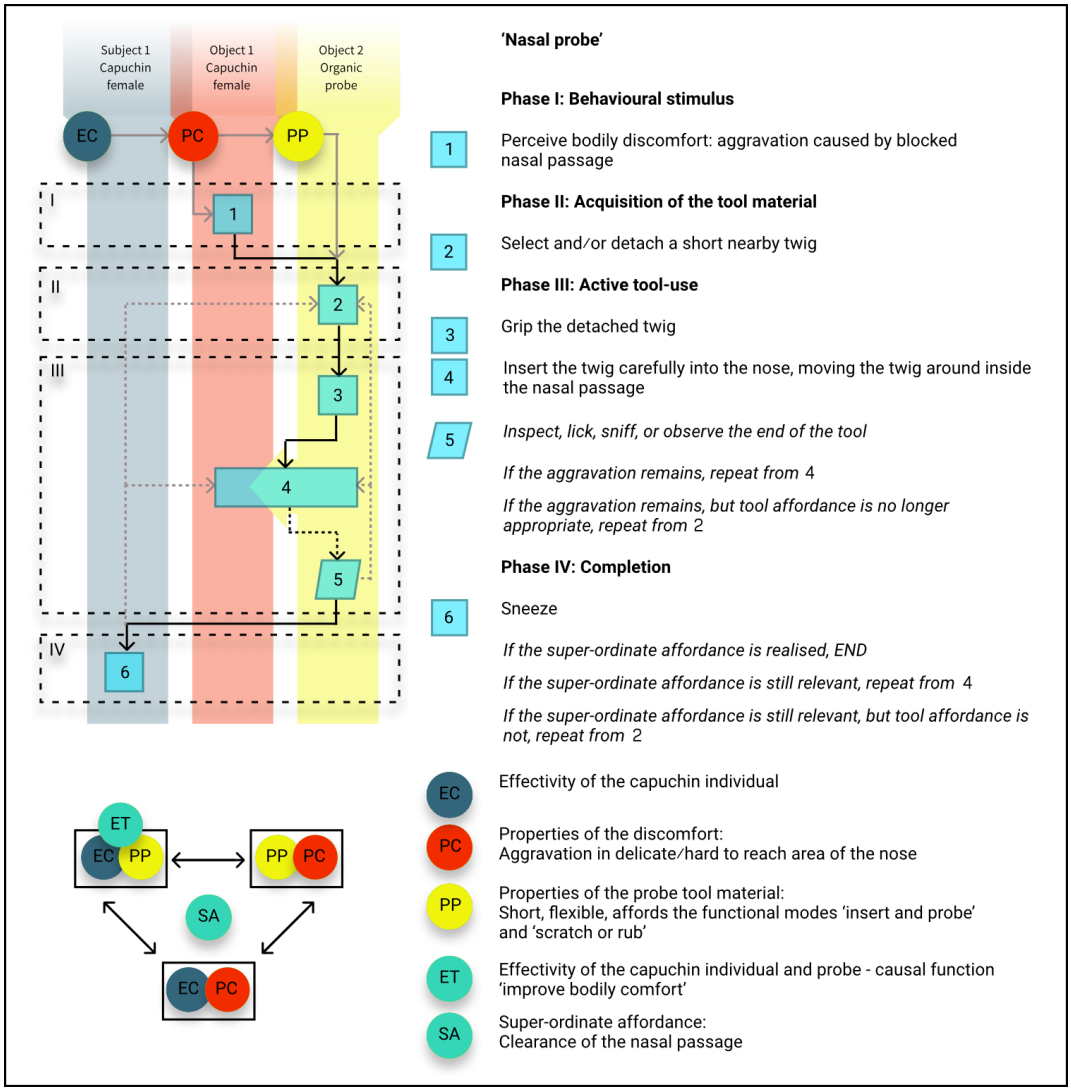
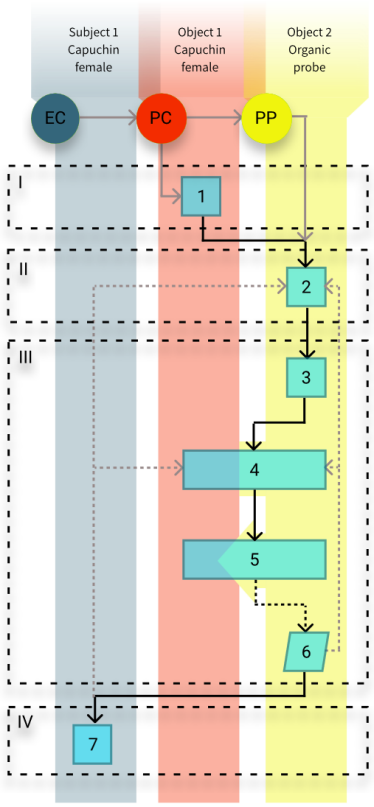


Figure 38 Cognigram for the SDC variant 'Tooth pick'



'Tooth pick'

Phase I: Behavioural stimulus

1 Perceive bodily discomfort: aggravation to the teeth or gums

Phase II: Acquisition of the tool material

2 Select and/or detach a short nearby twig

Phase III: Active tool-use

3 Grip the detached twig

4 Place the twig carefully against the base of the aggravated tooth/gum

5 Quickly and repeatedly move the tool side-to-side motion against the site of discomfort

6 *Inspect, lick, sniff, or observe the end of the tool*

If the aggravation remains, repeat from 4

If the aggravation remains, but tool affordance is no longer appropriate, repeat from 2

Phase IV: Completion

7 Successfully dislodge the aggravating material

If the super-ordinate affordance is realised, END

If the super-ordinate affordance is still relevant, repeat from 3

If the super-ordinate affordance is still relevant, but tool affordance is not, repeat from 2

EC Effectivity of the capuchin individual

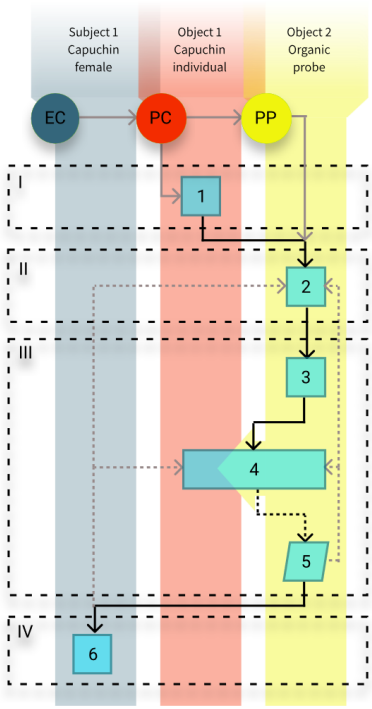
PC Properties of the discomfort:
Aggravation in delicate/hard to reach area of the mouth

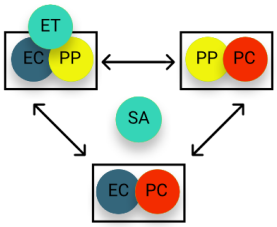
PP Properties of the probe tool:
Short and flexible, affords the functional mode 'scratch or rub'

ET Effectivity of the capuchin individual and probe - causal function 'improve bodily comfort'

SA Super-ordinate affordance:
Relief from discomfort

Figure 39 Cognigram for the SDC variant 'Scratch'





'Scratch'

Phase I: Behavioural stimulus

1 Perceive bodily discomfort: unknown (skin irritation?)

Phase II: Acquisition of the tool material

2 Select and/or detach a short nearby twig

Phase III: Active tool-use

3 Grip the detached twig

4 Press the distall end of the stick to the area of discomfort

5 *Inspect, lick, sniff, or observe the end of the tool*

If the aggravation remains, repeat from 4

If the aggravation remains, but tool affordance is no longer appropriate, repeat from 2

Phase IV: Completion

6 Alleviate discomfort

If the super-ordinate affordance is realised, END

If the super-ordinate affordance is still relevant, repeat from 4

If the super-ordinate affordance is still relevant, but tool affordance is not, repeat from 2

EC Effectivity of the capuchin individual

PC Properties of the discomfort:
Aggravation in delicate/hard to reach area of the body (forehead)

PP Properties of the probe tool material:
Short, flexible, affords the functional mode 'scratch or rub'

ET Effectivity of the capuchin individual and probe - causal function 'improve bodily comfort'

SA Super-ordinate affordance:
Alleviation of physical discomfort

operational sequence comprised 6 critical actions (maximum = 6), in 4 phases, and included no modifications. Reuse of the tool is reported, with more than one tool being used to serve both functions sequentially. Epistemic actions occur throughout the tools use, including frequent interspersed extraction and licking or sniffing of tool tips (Haslam and Falótico, 2015).

Scratch Falótico and Ottoni (2014, p. 119 and supplementary video 3) observed two incidents of individuals using sticks to groom themselves and others: in one incident, an adult male used a stick to 'scratch' his head, while in another an adult female is reported to have used a stick to 'scratch' the individual she was grooming. Figure 39 (p. 206) gives the behaviour as a single perception-action module distributed between 3 foci: the capuchin, the organic material which forms the probe, and the recipient conspecific. Object order includes 1 dynamic spatial relationship (between the probe and conspecific recipient). The minimum operational sequence is described by 5 critical actions (maximum = 5), in 4 phases, with no modificatory actions included.

5.2.8 Causal cognition in Capuchin Hygiene tool-use

For all hygiene variants, cognitive inference is severely limited by small sample size. Grades 1 and 3 are evident, in so much as the capuchin individuals who performed each variant were able to manage and direct the causal effects of hand-held tools. Given that the behaviours are only present in a handful of individuals (or even only in one), there is no reason to believe individuals derive relevant tool information from others' material interactions; and, indeed, Haslam & Falótico (2015) note that no individuals paid attention to the female individual during her tool-use besides the male present. Female innovation and use of probe tools supports the prospect raised in section X.X that the male sex bias in subsistent and social probe tool-using reflects a normative aspect to probe tool affordances and not a female in-capability. Although the sex bias did not appear to prohibit female innovation in a hygiene context, it is worth questioning to what degree observation by conspecifics was deleteriously affected by the subject's gender: i.e. whether sex bias reduced the perceived

relevance of information gained from another's material interaction, and de-incentivised observation. If so, it could provide a practical example of normative affordance values developed in one (or two) context(s), being transposed to another, without the need for complex 'representational' explanation.

Regarding material constitution, the causal relationship between environment and cognition is minimal. Hygiene variants supplement pre-existing grooming behaviours, presumably providing immediate affective rewards such as quicker or more effective physical relief. As self-directed behaviours, there is also the possibility that 'hygiene' tools are stress-related, and function to relieve or signal social or physical uncertainty, or as displacement activities, detracting attention away potential cues exposing weakness (Maestripieri *et al.*, 1992; Castles, Whiten and Aureli, 1999; Duboscq *et al.*, 2016; Whitehouse, Micheletta and Waller, 2017). Immediate rewards might or might not be translated into long term adaptive advantage such as improved general health, or where grooming is not self-directed, reciprocated grooming, stronger affiliative bonds and higher rates of social tolerance; entailing fitness benefits for all individuals involved (Dunbar, 1991; Parr *et al.*, 1997; Roberts and Sherratt, 1998; Barrett, Gaynor and Henzi, 2002; Lehmann, Korstjens and Dunbar, 2007).[47] At the same time, tool-use in allogrooming may be detrimental to its function, since probe tools subvert the need for physical touch, and thereby, the prospective neuro-biological mechanisms facilitating social bonding, e.g. oxytocin and endorphin release (Keverne, Martensz and Tuite, 1989; Dunbar, 2010). This may explain why social tool-use in a hygiene context is extremely rare across all tool-using animals (McGrew and Tutin, 1972), but particularly so for animals like *S.libidinosus* for whom "allogrooming relates to agonistic, coalitionary and dominance patterns" (Fragaszy, Visalberghi and Fedigan, 2004, p. 210).

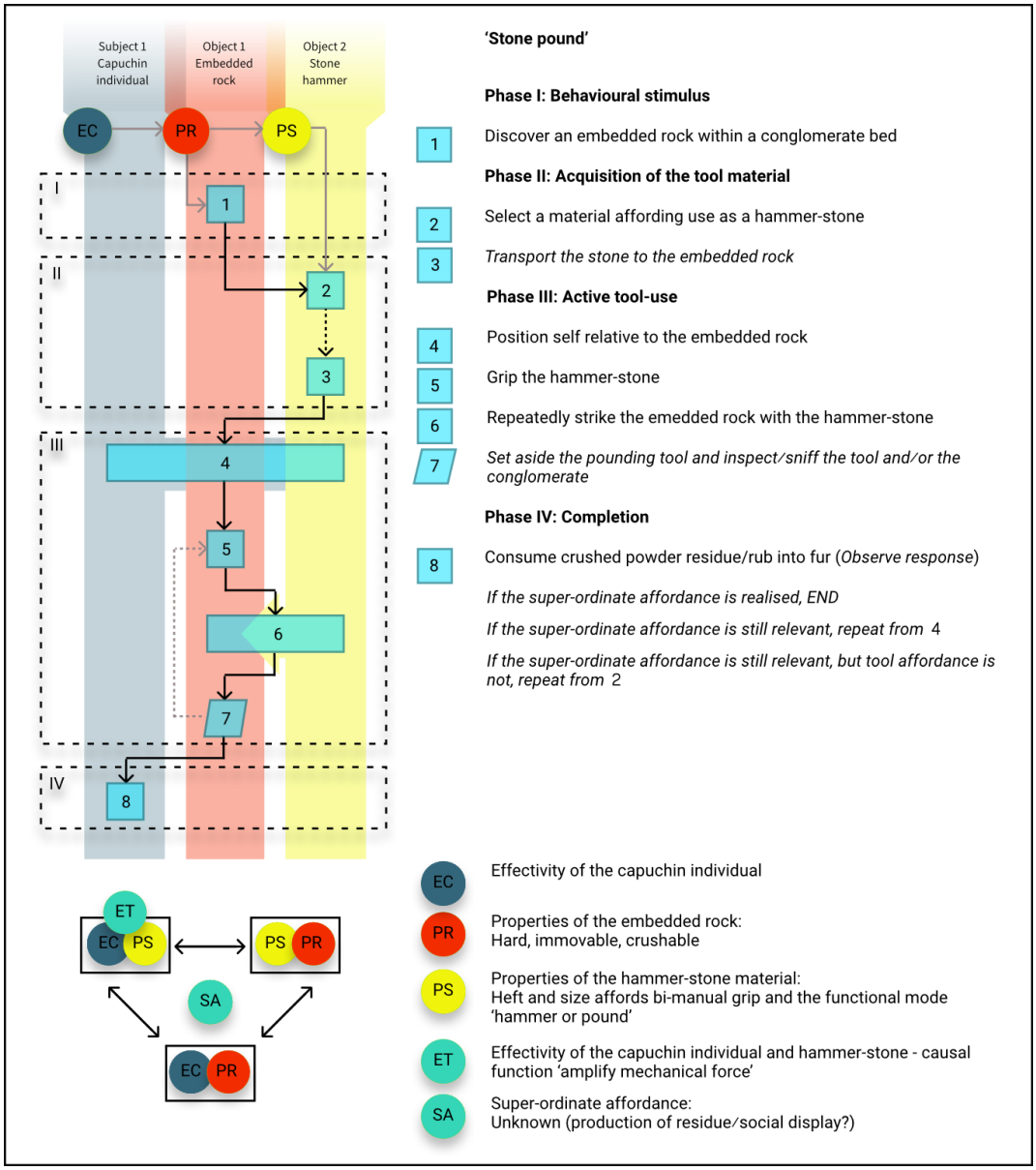
5.2.9 Other variants

[47] Parr et al. (1997) found that grooming dyads among *Cepus apella* did not match the patterns of affiliation among old world primates, suggesting the function and benefits of allogrooming in *Cebus* may differ. Patterns of affiliation do not detract from the notion that grooming strengthens affiliative bonds.

Stone pound Capuchins at SDC have been observed to use stone pounding tools to strike sandstone-embedded pebbles. Previous authors have suggested the behaviour may occur in an aggressive context, producing an auditory signal to deter predators (Moura, 2006). Others postulate pulverisation of the conglomerate produces a powdered quartzite, sandstone, or a lichen residue, presumably providing important minerals which the capuchins consume (Mannu and Ottoni, 2009; Falótico and Ottoni, 2016; Proffitt *et al.*, 2016). Technique is analogous to that of 'pound open', though in this instance the target is fixed to the substrate. In order to perform the behaviour, a capuchin individual grasps a portable stone of suitable size and mass, and repeatedly strikes it against the embedded rock. As Lombard *et al.* (2019) highlight, without knowledge of the behaviours specific function, rock pounding could be interpreted as either proper or proto- tool-use. To qualify as the former, it must be the portable stone which is manipulated to affect the embedded rock and not the properties of the embedded rock which are used to affect the qualities of the stone pounded against it. Although, as will be argued later, this ambiguity could affect the inference of causal cognition, it does not affect complexity in any other sense – with behavioural, focal, sequential, and object relationship complexities all the same for proto- and proper tool-use. Making no assumptions as to tool status, Figure 40 (p. 210) gives the variant 'stone pound' as a single perception-action module, in which the super-ordinate affordance is seen to rise through dynamic interplay of 3 foci: the capuchin individual, the portable stone material, and the stone material embedded in the conglomerate bed. 1 dynamic spatial relationship (between the portable stone material and the conglomerate rock) is counted to Object order. The minimum operational sequence includes 6 critical actions (maximum = 7), in 4 phases, with no modificatory actions included.

Grade 1 causal cognition must be present: the capuchin must be able to perceive, or at least be solicited by, the affordances of both materials as they relate to one another; Moura (2006) notes that many episodes began with the monkey moving around a rocky outcrop, tapping different stones

Figure 40 Cognigram for the SDC variant 'Stone pound'



prior to selection indicating direct interaction provided information about relative affordance relevance. That pounding activity is well distributed throughout the population [and with strong male-bias (95.2%: Falótico & Ottoni, 2016)], suggests grade 2 cued-dyadic causal reasoning is also present: presumably others' pounding behaviour serving to incite performance in a manner akin to that seen in Section 5.2.2 in regard to nut-cracking. Inter-group discrepancies are indicative of social learning, prospectively on several levels. On one level, discrepancies in the reported function of the behaviour could reflect group specific traditions (e.g. pulverisation versus anti-predator response). On another, if and where function is anti-predator response, discrepancies in exhibition could reflect group specific perception of predator risk For example, Moura (2006) describes rock-pounding as present in several groups within the SDC, with the variant most frequently elicited upon first or early encounters (in particular by Oitenta group); however, not all groups performed the behaviour, with several unhabituated groups simply fleeing when approached. While male bias could reflect the context of tool-use, with anti-predator aggressive displays predominantly performed by males (van Schaik and van Noordwijk, 1989); Falótico & Ottoni (2016) show stones used for this task were significantly heavier than those used to crack open encased foods (avg weight = 635 +- 589g), the physicality of which might limit female participation. Contradictorily, adults and juveniles amongst PF and BC groups were found to perform rock pounding almost as frequently (Falótico and Ottoni, 2016), suggesting (1) that the behaviour was neither an anti-predator response, nor (2) beyond the physical capacities of females. Frequent licking of the percussion spot, would support the hypothesis rock pounding by PF & BC groups functioned to pulverise the rock material and not as an anti-predator deterrent.

Skill acquisition and development of efficient technique should be similarly complex regardless of proto- or proper tool status; arguably the most difficult aspect of pounding stone tools, i.e. placement of the target item, being made redundant by the fixture of the conglomerate rock to the rock bed. What may differ between proto and proper tool-use is the sense in which the animal perceives the tool/proto-tool as an extension of their own agency. In the proto- case, there is no

need to believe that the monkey experiences the conglomerate 'anvil' as an extension of themselves, and so degree to which grade 3 can be inferred is subject to the inferred function of the tool. Similarly, no assumption can be made as regards degree of material constitution, other than that, as a base standard, the environment must be minimally constitutive to cognition. Without knowledge of function, no assumption can be made as to novelty. Adaptive advantages which might be gained through proto- or proper tool-use are also dependent upon function, though can at least be considered. If the behaviour functions as conspicuous display, repelling predators, then its costs and benefits are similar to those of mobbing behaviours (see 'poking stick' in Section 5.2.5), though in this instance without the additional benefit of providing a spatial buffer. If, however, the behaviour functions to produce a powdered residue for consumption, tool-use would provide access to whichever minerals that residue contained, giving tool-using individuals an adaptive advantage by increasing access to a potentially valuable nutritional resource.

5.3 Summary

5.3.1 Context and complexity

Tufted capuchins (*S.libidinosus*) are a generalist and opportunist species, characterised by their destructive foraging and extremely diversified diet (Terborgh, 1983; Fragaszy, Visalberghi and Fedigan, 2004). This extreme behavioural plasticity is reflected in a broad and flexible tool kit which uses inorganic and organic materials to target a wide variety of food resources (see Table 12, p. 215). Variant complexities range from simple single module operational sequences with low behavioural, sequential and focal complexities, to composite tools and more complex compound modules of up to five focal aspects (see Figure 41, p. 214).

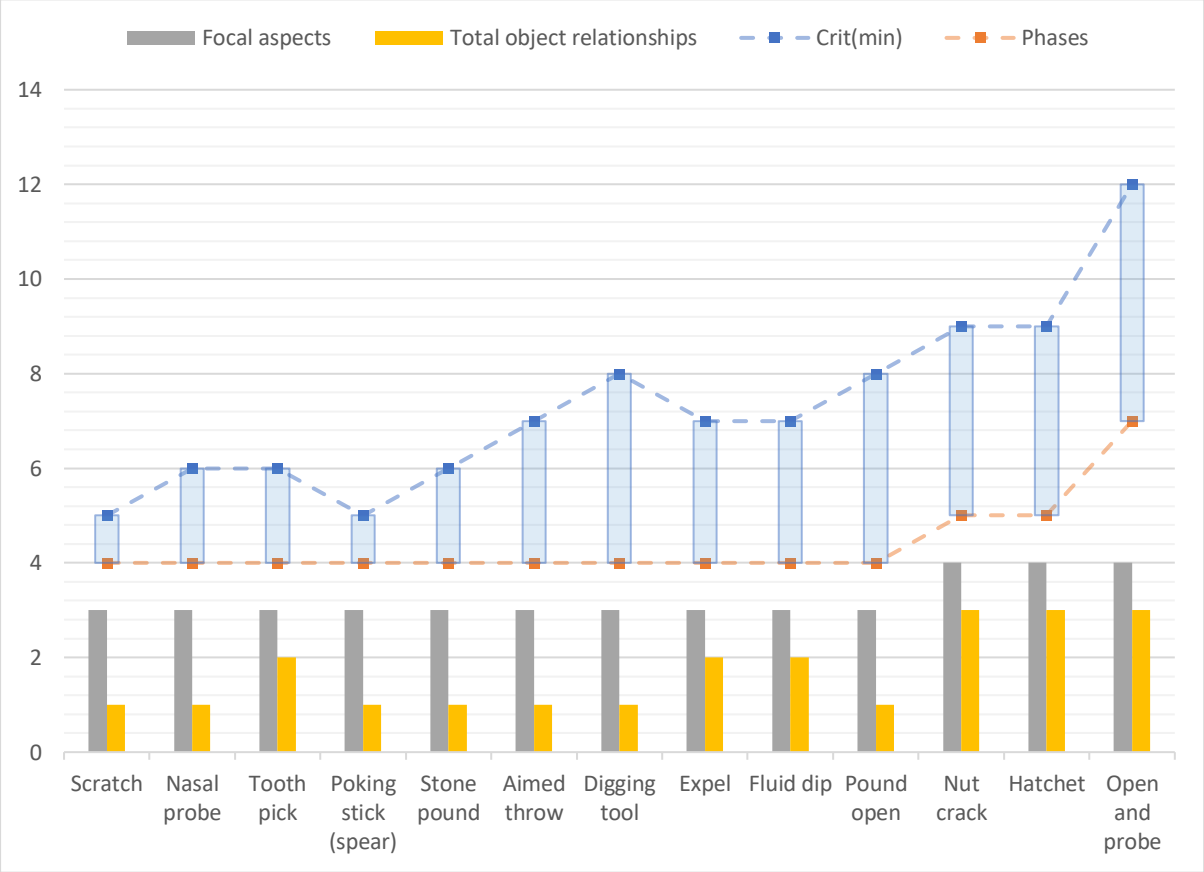
The predominant role of subsistents within the capuchin repertoire and their relatively high degree of complexity is likely to have been enabled, if not driven, by the particular mode of material

engagement they produce. In comparison with *S.libidinosus* hygiene and social variants, subsistents provide the most immediate returns, greatly expanding the scope and effectiveness of capuchin foraging capability. These rewards may benefit both the tool user and conspecific others, whose proximity, observational attention, and interaction with tool materials are incentivised by the scrounging opportunities tool-use provides. Although capuchin social tool-use and social hygiene tool-use can directly benefit their recipients, neither encourages behavioural transmission in the same way. In the former case this is because the recipient is either a non-conspecific or a conspecific male, and the behaviours are therefore inappropriate or irrelevant; and in the latter, it could be that tools used to groom others do not improve on the adaptive benefits achieved by non-tool-assisted reciprocity. Sustained and rewarded material engagement is necessary for transmission and ontogenetic development of longer, more complex behavioural sequences and greater numbers of spatial object relationships (e.g. nut-cracking), and for the refinement of object affordance recognition and individual skill.

Further, subsistents are the only *S.libidinosus* context which produce long-lasting changes to the physical environment. These changes include the physical remains of nut-cracking, pounding, and digging behaviours; such as accumulations of hammer and anvil stones (marked by CNSL stains and anvil pitting), nutshells, conchoidal flakes[48], and exposed digging sites (Visalberghi *et al.*, 2013; Haslam *et al.*, 2014; Proffitt *et al.*, 2016; Falótico, Coutinho, *et al.*, 2018); which, for each variant, may form an ontogenetic niche, focal points in the landscape that direct attention and scaffold future tool-use by subverting the more cognitively/physically challenging aspects of tool-use (Fragaszy, 2011; Fragaszy, Biro, *et al.*, 2013; Resende *et al.*, 2021). While situated learning creates a cyclical process of environmental and behavioural mutualistic influence, and an inter-generationally co-constructed, dynamic 'technique', distributing the cognitive workload across multiple generations has cumulative effect, again facilitating the development of longer, more complex behavioural sequences and object relationships.

[48] Though these are not used (Proffit *et al.,* 2016)

Figure 41 The relationship between problem solution distances and focal complexity/number of object relationships for technical variants at SDC



Borgo *et al.* (2013) argue that through extended experience, capuchins develop persistent, socially congruent (cf. Borgo and Vieu, 2009), artefact characterizations and categorisations based on attribution (or others previous attribution) of capacities to selected objects. This is evidenced by reuse of tools at accumulation sites, which occurs often with reduced, or entirely without, exploratory behaviours, such that the affordance of the stone tool is taken as apparent by its previous use, even when that previous use was not directly observed. Monkeys may even "wait in queue" (Borgo *et al.*, 2013, p. 380) to use a nut-cracking site, preferentially re-using the same pit exploited by the previous monkey (eg. Spagnoletti *et al.*, 2011). Since ensignification and artefact criteria are experientially developed, it should be expected that artefact categorisation is in alignment with local ecology.

Table 12 Tool forms, targets, and materials of Serra da Capivara variants

Tool form	Tool variant	Target	Tool material	Selectivity	Re-use	Modification
Stiff probe	Expel	Lizards, invertebrates	Tree stick, bark	Yes	Yes	Reduction
	Fluid dip	Honey, wax, water	Tree stick, bark	Yes	Yes	Reduction
	Open and probe	Invertebrates (bees)/ vertebrates	Stone, tree stick			Reduction
	Poking stick (spear)	Social (non-conspecific), dangerous snake species, white-eared opossum (*Didelphis albiventris*), scorpion	Tree stick, branch			Reduction
Stone pounders (and anvils)	Dig (dig/hoe)	USOs (*Thiloa glaucocarpa*), arthropod nests (*Actinopus sp.*), roots (*Octea sp.*)	Stone	Yes	Yes	
	Dig and pound	USOs (*Thiloa glaucocarpa*), roots (*Octea sp.*), inverrtebrates	Stone			
	Nut crack* (stone/wood/ hatchet)	Cashew, seeds (*manihot*, *Cordia rufescens*), jatoba fruits (*Hymenaea courbaril*), cactuses (*Opuntia sp.*)	Stone, tree branch/trunk	Yes	Yes	Linkage
	Pound open	Invertebrates, vertebrates	Stone	Yes		
	Stone pound	Quartzite (powder)	Stone	Yes		
Misc.	Aimed throw	Social (conspecific)	Stone	- Yes	-	
	Nasal probe	Hygiene	Grass stem, tree stick		- Yes	-
	Toothpick	Hygiene	Tree stick		- Yes	-
	Self-poke	Hygiene	Tree stick		-	-

This may explain why capuchins at SDC appear to be inorganic tool generalists (see Table 12, p. 215), exhibiting several variants with similar functions, while those at FBV are specialists. At FBV suitable hammer-stones are neither abundant nor portable (Visalberghi *et al.*, 2007), so that the experientially based criteria by which capuchins might come to identify stones as artefacts distinguished from their natural backgrounds - in essence, the criteria affecting perception of affordance relevance – is likely to be highly specific: as specific as, for example, the stone's being 'located at or on an anvil'. At SDC, in contrast, stones of suitable mass are both abundant and portable, so that deposition pattern and the context of prior engagement by which categorical criteria are constituted is more varied, and criteria are thereby more ambiguous. Hypothetically, ambiguous, or generalist criteria should enable a fluidity to tool-use, with which tool affordances are more easily transferred to new functional contexts; congruent with what we see at SDC.

5.3.2 Causal cognition and material engagement

At SDC, physical cognition is embodied, in the sense that tool-use is a physical process which takes place in a real-world context, and distributed, in that the tool use as a creative process takes place between subject and environment so that each plays a constitutive part. As prosthetic extensions of the agential self, tools extend the capuchins' physical capacities in all senses; their actions, the forces they generate, and their perceptive capacities are all extended through the mediative tool object. Grades 1 and 3 (in the form of self-mind-reading) causal cognition are evident throughout SDC capuchin tool-use, with material interaction informing affordance perception, and epistemic feedback through tool-use mitigating performance of technique.

As might be expected given the prevalence of stone-pounding variants, the causal function most represented in the SDC repertoire is 'amplification of mechanical force' (N = 7). These stone-pounding affordances appear particularly salient to capuchins, no doubt echoing a contingency between tool technique and species typical non-tool-assisted foraging techniques (e.g. tap-scanning

and object-banging); as well as a contingency between the primary modalities of sensory feedback. Both tool and non-tool forms of foraging involve a refinement of focus through the creation (via epistemic material interaction) of acoustic and haptic information (Visalberghi and Néel, 2003; Moura, 2004; Phillips *et al.*, 2004). Stone pounding tools, by emphasising acoustic and haptic feedback, effectively combine search and excavation/acquisition behaviours into the same manual gesture.

Regarding social cognition, SDC customary and habitual variants are, by definition, distributed. As there is no clear evidence of deliberate teaching (cf. Boesch, 1991b; Musgrave *et al.*, 2016), it is assumed that the majority of social learning at SDC occurs by grade 2 causal cognition, i.e. from the information derived through observation of others material interaction and tool-use, including object properties and affordances, but not including object causal functions or inferences about mental states. Significant sex bias of several variants (all probe tool-use) demonstrates the embedment of capuchin affordance perception and relevance within their species socio-ecology; with social structure and sub-group formation influencing the frequency and nature of social interactions, and thereby limiting or enhancing individuals' opportunities for variant inception. In comparison with apes, little is known about 'intentional' gestural communication among monkeys (Call and Tomasello, 2007; Pollick and de Waal, 2007; Arbib, Liebal and Pika, 2008; Molesti, Meguerditchian and Bourjade, 2020).[49] Capuchin natural visual signalling repertoires are typified by body posturing and orofacial signalling (Fragaszy, Visalberghi and Fedigan, 2004), and although captive studies demonstrate capuchins have some gestural ability when conditioned (Hattori, Kuroshima and Fujita, 2006, 2010; Essler *et al.*, 2017), these induced behaviours are neither natural nor, indeed, appear fully functional. Given their species' lack of gestural propensity, it is not particularly surprising that capuchins at SDC should exhibit only two social variants (and only one directed towards conspecifics).

[49] Where gesture is defined as communication by non-locomotory movement of the hands, feet, or limbs (Pollick & de Waal, 2007)

Case Study 3: Material engagement, tool-use and technical cognition amongst Burmese long-tailed macaques (Macaca fascicularis aurea) at Piak Nam Yai, Thailand.

6.1 The Case Study Site of Piak Nam Yai

Piak Nam Yai (9.34N, 98.28'E) is one of fifteen small islands situated in the Laem Son National marine park, Ranong Province, c.750m off the West coast of Thailand. Tool-use has been observed at the site since 2005 when a faunal survey assessing the impact of the 2004 tsunami found tool-use present in the Burmese and Burmese/common hybrid long-tailed macaque population inhabiting the island (Malaivijitnond *et al.*, 2007). The island includes several habitat types: mountainous tropical forest with freshwater streambeds make up the c.1.7km^2 interior, and the 5.4km coastline is comprised of rocky shore (66%), mangrove (29%), and sand beaches (5%) (Gumert, Hamada and Malaivijitnond, 2013; Falótico, Spagnoletti, *et al.*, 2017). As at the other case-study sites, the macaque population of Piak Nam Yai live in close proximity to humans, with rubber and oil palm plantations on the northern part of the island (Gumert, Hamada and Malaivijitnond, 2013). In 2011, a survey estimated nine groups of Burmese and Burmese/common hybrid long tailed macaques to be living on the island, and a total of 192 individuals, 41%[50] of which use stone tools (Gumert, Hamada and Malaivijitnond, 2013). Since published behavioural reports for PNY do not differentiate between groups, the PNY repertoire is discussed as a whole, and inter-group behavioural variation discussed only with relation to other sites.

6.1.1 The Piak Nam Yai repertoire and its place amongst the wider macaque technical catalogue

Of the lithic using NHPs, macaques are perhaps the least represented in the literature on NHP tool-use. Despite an overlooked report of observed tool use dating back to 1887 (Carpenter,

[50] 88% of the mature population (Gumert *et al.,* 2013)

1887), it is only relatively recently in 2005, with the discovery of stone tool-using in the wild population at PNY, that macaques have been recognised as customary tool-users (Malaivijitnond *et al.,* 2007). Prior to this discovery, and contradictory to what might be expected given macaques' high levels of manual dexterity and propensity for non-functional object manipulation (Huffman & Quiatt, 1986; Leca et al., 2007, 2008; Nahallage & Huffman, 2012), macaques have often been considered un-skilled tool-users (Panger 2007, p672; Macellini *et al.,* 2011), lacking behaviour demonstrative of the causal cognitive capacities typically associated with tool use and/or tool making (Natale *et al.,* 1986; Parker, 1977; Bandini & Tennie, 2018).

Although there are numerous anecdotal accounts of tool using by several macaque subspecies, reports of habitual lithic tool using remain exclusively associated with coastal populations (or hybrid populations) of *M.f.aurea* - a subspecies endemic to the islands spread throughout the Mergui Archipelago, and bounded within the Isthmus of Kra (Fooden, 1995; Gumert et al., 2019; Malaivijitnond et al., 2007). Besides PNY, Thao, and Phayam Islands, the oldest of the macaque field-sites, tool-using populations are now also reported off the West of Thailand at Yao Noi & Boi Yai Islands, Ao Phang-Nga National Park (hereafter YNI and BYI, respectively), and off the East Coast at Koram Island, Khao Sam Roi Yot National Park (hereafter SRY), Prachuap Khiri Khan Province (Gumert et al., 2009, 2013; Luncz et al., 2017; 2019).

Although behavioural and archaeological evidence demonstrate intra-group and inter-populational differences in the particular expression of tool-using techniques (Tan *et al.*, 2015; Luncz *et al.*, 2019), the existing literature suggests macaque technological repertoires are broadly homogenous; total repertoire richness is low (R = 4); all tool-use, subsistent based, of the causal mode 'hammer/pound', and with the primary causal function to 'amplify the user's mechanical force' (R = 2, S = 1, H = 0, E = 1). As published observations have been limited by both a lack of time depth, or to observations of activity at the shoreline (where populations are unhabituated or terrain prevents inland venture), it is acknowledged that *M.f.aurea* repertoires so far compiled may not be

fully representative of site or species-wide technological behaviour. This being said, the PNY repertoire, shown in Table 13 below, is consistent with current species patterns of behaviour.

Table 13 Technical variants observed at Piak Nam Yai since 2005

Functional Context	Variant	Population Distribution	Source/s
Subsistence	**Nut crack (face hammer/edge hammer)***	Customary	Malaivijitnond *et al.,* 2007, Tan *et al.,* 2015
	Axe-hammer	Customary	Gumert *et al.,* 2009, Gumert & Malaivijitnond, 2012, Tan *et al.,* 2015

- **Bold font denotes a variant involving complex and/or sequential tool-use**
  '*' Behaviours for which differing techniques (e.g. dig/hoe) are counted as independent variants

6.2 The technical repertoire of Piak Nam Yai

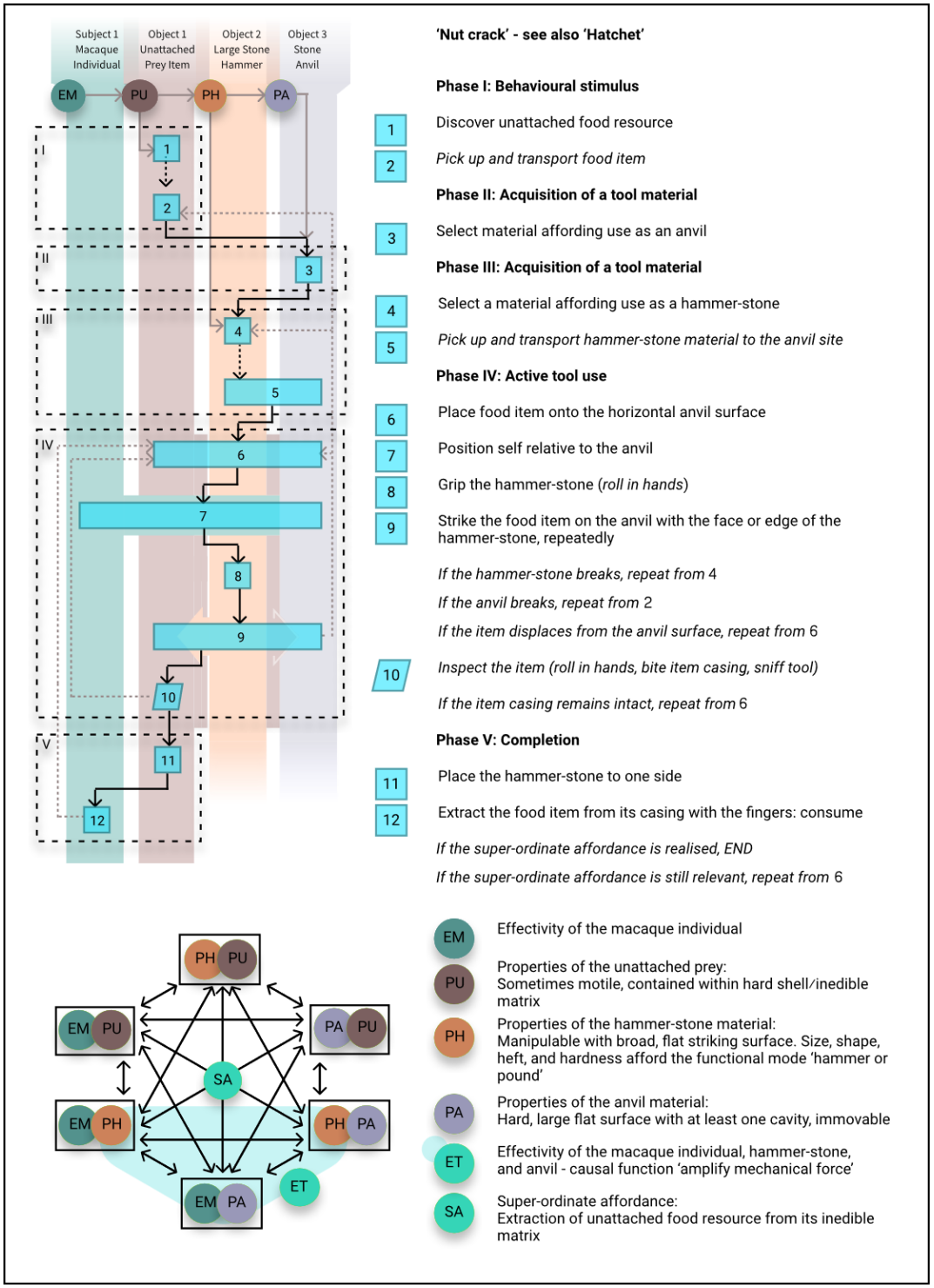
6.2.1 Subsistence stone pounding tools

Macaque stone tools used to crack open marine and encased foods have typically been classed into two broad categories: 'pound' and 'axe' hammering, also referred to as 'face/edge hammering' and 'point hammering', respectively (Gumert et al., 2009). For ease of comparison, and to maintain consistency between the case-studies, this thesis refers to pound hammering as 'nut-cracking'. It is recognised that this maybe confusing as within the literature pound hammering by macaques is more often associated with processing of marine food resources (and indeed at several sites may not include nuts at all); however, pound hammering and nut-cracking are behaviourally similar, and at PNY, nuts [e.g. seashore pandan (*Pananus tectorius*) and sea almonds (*Terminalia catappa*)] are one of the many food resources which this variant functions to process (Falótico et al., 2017; Gumert & Malaivijitnond, 2012). As distinct variants, nut-cracking (Pound hammering) and axe-hammering share considerable behavioural and functional overlap; one coarse and one precise, both involve use of a hammer-stone to open encased (primarily marine) food resources. The variants align roughly with two broad prey types: nut cracking with food resources which are

unattached/portable, and axe-hammering, with those which are not, for example sessile oysters attached to large boulders (Gumert et al., 2009).

Nut crack (face hammer/edge hammer) As for the other NHP species, nut-cracking is characterised by its functional mode, 'to pound', and organisation of three synchronous spatial elements - the portable food item being placed on an 'anvil' surface, to be used in conjunction with a hammer stone. A great deal of attention has been directed towards the precise behavioural sequence involved in macaque nut cracking, more so than for any other species, with technique having been shown to vary considerably between individuals and dependent upon the food type targeted (Gumert & Malaivijitnond, 2012; Tan et al., 2015). Critical actions in common describe a method in which, through the course of foraging behaviour, a prey item is discovered or dislodged and transported in either the cheek pouches or hands to a nearby anvil with a suitable hammerstone [the hammerstone being a large stone already present or requiring little transportation (Haslam, Pascual-Garrido, *et al.*, 2016)]. The tool user, in, or rising from, a seated position, (uni or bi-manually) grips the tool and repeatedly strikes the food item positioned horizontally beneath, with either the face or a long edge of the tool (Gumert et al., 2009; Tan et al., 2015). Where for more delicate target items, nut-cracking may require only a few heavy strikes, extraction of hard-shelled nuts, e.g. sea almonds and coconuts, involves a more protracted process; "sea almonds were typically placed on an anvil and smashed with a heavy stone… the macaque then picked up the nut and bit the damaged leathery exocarp away… the nut was replaced on the anvil and smashed again to open the harder mesocarp… [which] once opened, the macaque consumed" (Gumert & Malaivijitnond, 2012, p452). Due to the heavier nature of tools used, control over the tool and recoil appears hard to master, resulting in fumbling of the tool and subsequent adjustment of grip between strikes. Indeed, Gumert *et al.* (2009, p601) report heavier stone tools sometimes being used as 'fulcrums', lifted by an edge

Figure 42 Cognigram for the PNY variant 'Nut crack' (face hammer/edge hammer)

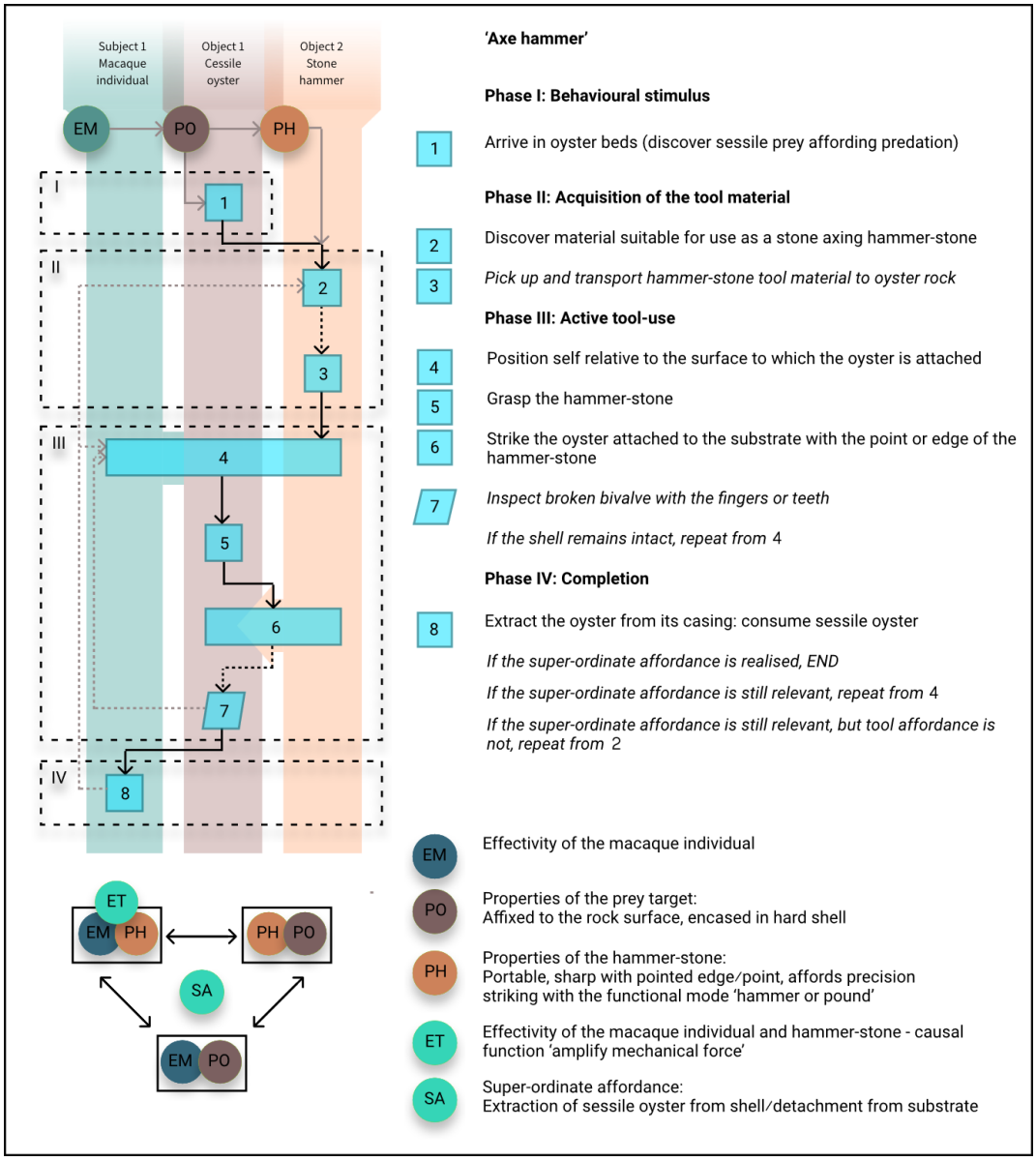


then ‘dropped’ onto prey resources. Whether or not ‘fulcrumming’ represents a technical variant in its own right, or simply an idiosyncratic and improvisational adaptation to overcome constraints upon tool manoeuvrability is unclear; for the sake of later comparison, it is treated as the latter, and larger, heavier stones, as an independent tool form, i.e. ‘fulcrum’. Figure 42 (p. 222) gives PNY nut-cracking behaviour as a single perception-action module, in which the super-ordinate affordance arises through dynamic interplay of 4 focal aspects: the macaque, hammer-stone, rock anvil, and food target (an unattached prey item). A total of 3 spatial relationships were counted towards Object order, 1 static (between the food item and anvil) and 2 dynamic (between the hammer-stone and food item; food item and anvil). Minimum behavioural sequence length comprises 8 critical actions (maximum = 12), in 5 phases, with optional transport of the tool and target occurring prior to and between tool-using bouts, and with an optional action to acknowledge inspection of the target item/breaking open of shell cases with the teeth during nut-cracking. Although no modificatory actions are included, use of the hammer-stone in conjunction with the anvil qualifies the modification mode as linkage.

Axe hammer Though functionally similar to nut-cracking, to the extent that the two forms are often used to sequentially process the same target item, axe-hammering does not require any placement of the food item, sessile oysters being attached to effective anvil surfaces.[51] Fixture to the rock surface means axe-hammering may occur in a variety of postures accommodating for orientation of the target item, so that the subject must alter strike angle in order to maximise accuracy. Gumert & Malaivijitnond (2012, p449) describe the processing of sessile oysters as follows: “macaques travelled to sessile oysters while carrying a small hammer stone and chipped off the

[51] Axe-hammering can result in prey resources becoming dislodged from the rock surface, or the rock to which the prey resource is attached may be portable, such that it (the food resource) can afford both forms of tool use.

Figure 43 Cognigram for the PNY variant 'Axe hammer'



unattached right valve… by striking at and breaking the hinge, before picking out and consuming the flesh from the still cemented left valve". While these small stone tools are most typically held in a precision grip, and used to repeatedly strike with the tool 'point', or more rarely, the tool 'edge', Gumert *et al.* (2009) and Tan *et al.* (2015) report that on some occasions, macaque individuals made use of augur (*Turritella attenuata*) and other shells also to strike sessile prey with the shell points in an overarm stabbing, or 'pick-like' gesture. Figure 43 (p. 224) shows axe-hammering as a single perception-action module, in this case, with the super-ordinate affordance arising from only 3 foci: the macaque, material which forms the hammer-stone or 'pick', and the attached prey target (sessile oyster or bi-valve). With the target already attached to an anvil-like surface, only 1 dynamic spatial relationship (between axe-hammer and target) was counted to Object order. Without object linkage or tool adjustment, minimum operational sequence length has 6 critical actions (maximum = 7), including no modifications, but with optional inspection and mouthing of the attached target. Haslam *et al.* (2016) report substantial tool re-use and high tool fidelity; although in the majority of episodes fewer than ten prey items were sequentially processed, in one exceptional case, 63 prey items were targeted in a single episode using the same tool. Transport of the tool occurs prior to and between tool-using bouts as the subject moves from bed to bed, with an average distance of 0.5m (Haslam *et al.*, 2016) and a maximum observed transport distance of c.90m (Gumert et al., 2009).

6.2.2 Causal cognition in PNY lithic tool-use

Ontogenetic studies of macaque stone tool-use indicate behavioural development arises through a process in which grades 1, 2 and 3 causal cognition are essential. In terms of grades 1 and 3, behavioural development takes place over several years, and begins with simple manipulations of single objects (primarily of stones and empty shells) within the first four to six months of age (Tan, 2017). At around age 1.5 years, simple object manipulation is replaced with a variety of non-functional combinatory manipulations, e.g. placing of objects onto anvils, and progresses to actions and combinations critical to variant method such as rubbing of stones or food items on boulder

surfaces, and ineffective percussive actions, shortly thereafter. From 2.5-3.5 years, individuals begin to produce actions and object combinations in the correct sequence to perform axing and pounding, after which Tan (2017) reports a period of idiosyncratic skill refinement after which there is no longer significant difference in strike accuracy with more mature tool-users. Tan (2017) also reports a gradual improvement in energetic efficiency, indicative of emergent expertise (and grade 3 causal cognition), with individuals producing fewer irrelevant actions, and requiring fewer striking actions to achieve success, over time. More proficient technique appears concurrent with greater tool fidelity, suggesting a fluid ability among more experienced tool users to adapt tooling movements to the properties of both the tool and task at hand. For nut-cracking this means a reduction in the time taken between strikes, and in the target items being displaced less often; and for axe-hammering, increased grip and better control, allowing for greater precision, reflected in reduced strike rate (Gumert *et al.,* 2011).

In discovery of object and tool affordances through individual material interaction, mature macaque tool users are able to select tool materials appropriate to the task at hand, matching tool affordances to variant mode and prey type (Gumert et al., 2009; Gumert & Malaivijitnond, 2013; at SRY, Luncz et al., 2017). Besides the difference in selected striking surface (i.e. point versus broad face), Gumert *et al.* (2009) found hammer stones used in nut-cracking to be significantly larger and heavier than those used in axe-hammering. Gumert & Malaivijitnond (2013), using a semi-experimental set-up, found an association between stone mass and food type for five food categories, with mass increasing with the degree of prey motility and hardness, and varying most between food categories processed in nut-cracking. This makes sense given that nut-cracking is used to process the widest variety of food resources (Gumert and Malaivijitnond, 2012). Where force transferred through a point results in a concentration of focus, force transferred through a broad, flat surface creates an even distribution of force across a wide area. By selecting tools based on mass, it would therefore seem macaque tool users are able to balance the trade-off between strike

accuracy and force transfer through selection of either larger, heavier, or smaller, more pointed tools.

Regarding social causal cognition, customary distribution throughout the adolescent/adult population, considered together with inter-site differences in tool expression, indicates social learning influences the developmental process of tool-using (Tan, 2017; Tan *et al.*, 2018; Luncz *et al.*, 2019). At SRY (Koram Island), Tan (2017; Tan *et al.*, 2018) found rates of observation of tool users were significantly higher amongst infants and juveniles than in adolescents or adults; and that the nature of non-tool using individuals' interactions with tool-users also differed with age. Non-tool using adults typically only interacted with tool-users when scrounging or supplanting them at a resource, while infants and juveniles were observed to carry out a wider range of epistemic engagements directed towards both tools and tool-related materials. These engagements included 'co-active' touching of tools that were being held, or in use, as well as explorative material interaction and manipulation of abandoned tool objects, leading Tan and colleagues (2018) to postulate naïve macaque tool-users *actively* seek out causal information in others tool-using that informs their own future tool-use. Mechanisms of social attention direction are likely echoed in *who* naïve individuals selected as behavioural models: not only are biases at SRY correlated with social and kin affiliation, i.e. those to whom proximity was more likely and greater tolerated; infants and juveniles were also found to preferentially observe more proficient tool-users, i.e. those producing greatest scrounging and learning opportunities (Tan *et al.,* 2018).

It is difficult to infer to what degree material constitutes technical cognition amongst *M.f.aurea*. Nut-cracking and axe-hammering appear to be two (sometimes novel) solutions to the same problem - i.e. breaking open of encased marine foods for consumption in inter-tidal zones – that, as opportunity has arisen, have expanded from the shoreline to the shore (cracking of sea almonds: Falótico, Spagnoletti, *et al.*, 2017) and, at Ao Phang-Nga island, inland into the adjacent forest (cracking of oil palm nuts: Luncz, Svensson, *et al.*, 2017). On the basis of direct observation

and archaeological evidence, Gumert & Malaivijitnond (2012) estimate the macaque population at PNY process at least 47 food species (37 genera) by means of tool-use; a significantly wider variety than among any other NHP. Although several of these species require a tool-assisted foraging strategy (e.g. coconuts, sea almonds and oil palm nuts), several others do not (e.g. many of the crustacean species) (*ibid*). Tool-use therefore only provides a novel function in a fraction of cases, while simply expanding scope and efficiency in many others. The degree to which material constitutes cognition, is dependent upon the adaptive advantage gained, both through granting access to those few previously inaccessible foods resources, and through the increase in efficiency with which other, priorly accessible food species are processed.

As Gumert and colleagues (2019a) write, macaque tool-use has strong ecological correlates, and is highly specific to coastal environments which are rich in both portable rock material to exploit and molluscs to predate. Although nut-cracking may draw activity away from the coast and into inland forests (Gumert, Kluck and Malaivijitnond, 2009; Falótico, Spagnoletti, *et al.*, 2017; Luncz, Svensson, *et al.*, 2017; Gumert, Tan and Malaivijitnond, 2019), tool-use in *M.f.aurea* is never disassociated from its coastal environment. With coastal environments making up only a fraction of *M.f.aurea's* expansive geographical distribution, it seems parsimonious to suggest ecological factors play or have previously played a strong, if not maximally constitutive, role in the species technical cognition. Indeed, when provided with tool and prey materials taken from the latter site, individuals from an inland population c.20km from SRY (where tool use is present) did not attempt to use or even interact with tools to crack open oysters, though they did unsuccessfully attempt to open the sessile oysters with their hands and mouths (personal observation).

Seeking to explain distribution, Gumert et al. (2019a) propose three non-exclusionary hypotheses, each with differing drivers and ascribed degrees of tool using's adaptive significance (laid out in Table 14, p. 229); the 'opportunity and disturbance' hypothesis (Gumert et al., 2019a,

p147), which considers distribution as an effect of anthropogenic influence, though acknowledged as one potentiality, is not discussed further as it does not relate to degree of constitution.

Table 14 Hypothetical scenarios explaining current distribution of tool using in M.f.aurea

	Insular isolation	**Opportunity and disturbance**	**Adaptation and selection**
Driver	Necessity	Opportunity	Unspecified
Adaptive significance/ Degree of constitution	Short term Minimally constitutive 'Cultural shift'	Unspecified	Long term Maximally constitutive 'Genetic selection'

According to both the 'Insular isolation' and 'Adaptation and selection' hypotheses, tool use is considered to provide an adaptive advantage to *M.f.aurea* individuals, with the primary difference between the hypotheses being the temporality of the advantage's effect: short term, or minimal, in the former, driving 'cultural shift', and long term and maximal in the latter, leading to selection for genetic predispositions supporting technical development. In the insular isolation hypothesis, Gumert et al. (2019a, p. 147) argue that with historical changes in sea level, land bridges connecting islands within the Mergui archipelago to the mainland would have become submerged, trapping small populations of *M.f.aurea* onto the islands and limiting their ranges. Without the ability to compensate by expanding the scope of their diet, trapped populations would likely have been forced instead, to expand into intertidal habitats - habitats which not only supported technical development by providing ample tool using opportunity (targetable resources and suitable tool materials being abundant), but within which technical affordance relevance would have been further bolstered by the scarcity of the island context. By enabling access to novel, hard-shelled food resources, Gumert et al. (2019a) speculate that tool using could have provided both the individual reproductive advantage, and group-level population carrying capacity necessary for survival and persistence of larger populations on small islands: pointing to the unusually large population density

at PNY relative to at other wild long-tailed macaque sites, for support (Gumert et al., 2013; also cited by Gumert et al., 2019a, p. 147). With the provision of a productive and relatively stable food resource, isolated macaque populations would have gradually focused less on their typical highly frugivorous feeding habitats in favour of more time spent engaging in tool-assisted processing of marine foods, resulting in a 'cultural shift' towards tool using (Gumert et al., 2009).

Though the insular isolation hypothesis might be able to explain geographic distribution of *M.f.aurea* tool-using, another recent study by Gumert *et al.* (2019b) found prevalence of tool-using behaviour to be strongly associated with subspecies morphological phenotype amongst the hybrid population of longtail macaques at SRY (*M.f.aurea*, *M.f.fascicularis,* and *M.f.a* x *M.f.f*). That tool-using was more prevalent among the one subspecies despite shared ecological conditions suggests tool using in *M.f.aurea* represents more than a simple 'cultural shift', and perhaps, as the 'Adaptation and specialisation' hypothesis proposes, a strong inheritable bias towards developing tool-use (Gumert et al., 2019a, 2019b).[52] In one hypothetical scenario, it is plausible that with insular isolation having driven an historical cultural shift towards tool using, the adaptive advantage gained might, over successive generations, have led to selection for attentional or manipulative predispositions readying development of technical skills (Gumert et al, 2019a, p. 147).

In either case, it seems more detailed information is needed to know the exact extent to which tool use has historically constituted, and continues to constitute technical cognition in the sub-species: neither hypothesis excludes the possibility that ecological pressures may act differently on macaque subspecies, nor the possibility that tool using has existed, or continues exist in more widespread locations yet to be discovered. However, what can be argued is that tool using has played a significant, likely maximally constitutive role in the adaptive behaviour of the *M.f.aurea* inhabiting inter-tidal regions.

[52] It is acknowledged that ecological pressures may act differently on the two subspecies.

6.3 Summary

6.3.1 Context and complexity

In summation, under suitable ecological conditions, Burmese long-tailed macaques (*M.f.aurea*) appear to be emergent lithic tool specialists: their repertoire of tool forms being limited range of simple and complex lithic tool forms, and occasionally hard organic tool materials (see Table 15, p. 232), all with the technical affordance to amplify mechanical force in common, and all used in the extractive/destructive processing of subsistent resources. As shown in Figure 44 (below), perhaps unsurprisingly given the lack of richness and high degree of behavioural overlap between variants, range of micro-aspect complexities is low, with focal ranges of 2-3 and a minimum behavioural complexity of 8 (axe-hammering) and maximum of 12 (nut cracking/hatcheting), respectively. Low diversity within the repertoire of fool forms masks, however, a richness of idiosyncratic techniques and breadth of prey species processed (see also Table 15, p. 232): reflective of *M.f.aurea*'s ecology as flexible foraging opportunists.

Figure 44 The relationship between problem solution distances and focal complexity/number of object relationships for technical variants at PNY

Table 15 Tool forms, targets and materials of Piak Nam Yai variants

Tool form	Tool variant	Target	Tool material	Selectivity	Re-use	Modification
Large stone pounder	Nut crack (face hammer/pound hammer)	Lizards, snails, bivalves, conches, crabs, nerites, oysters, fruits, seeds, nuts, other	Stone	Yes	Yes	Linkage
Pointed stone pounder	Axe-hammer	Bivalves, barnacles	Stone	Yes	Yes	None
Shell pick			Shell	-	-	None

6.3.2 Causal cognition and material engagement

Descriptions of Burmese long-tail's tool using emphasise its perceptual contiguity with their non-tool using foraging/behavioural repertoire. For example, Gumert & Malaivijitnond (2012, p455) write:

"Picking a nerite off a rock is little different than picking a berry off a branch, oyster colonies present themselves for harvest not to dissimilarly from fruiting trees, and handling a clam is little different than a hard fruit or nut… generalist primates capture insects in other environments, which involve capture techniques similar to those used in the capture of crabs along the shore"

Throughout the enskilment process, simple object manipulations from the natural foraging repertoire, like rubbing of food onto hard surfaces, are gradually re-moulded into skilled tooling gestures – familiar action trajectories gradually domesticated into novel skilled percussive strikes. Given macaques' natural predisposition for object manipulation (Huffman & Quiatt, 1986; Leca et al., 2011; Nahallage & Huffman, 2012), and capacity for complex hierarchical behaviours (Tan *et al.*, 2016), it makes sense that the lengthiest, and presumably most difficult, aspects of the enskilment process are mastery of critical action order and of percussive spatial relationships (Tan, 2017). Although social learning is clearly evident among the population at PNY, grade 3 experience of tool forms as extensions of the agential self appears more likely the productive of asocial individual object engagement. Though it cannot be ruled out as a result of observer bias, the observational methods used to describe technique in *M.f.aurea* being uniquely complex relative to those used among chimpanzee and capuchin ethological studies, a strong bias towards asocial learning could explain the relatively high degree of idiosyncrasy observed in individuals' technique, as described by Tan et al. (2015).

An interesting point is raised by Tan (2017), who notes that *M.f.aurea* juveniles appeared to experience functional object affordances in bouts of relevance: manipulations increasing in frequency throughout the first 6 months, declining, and then increasing again at around 1.5-2.5 years of age, coincidental with milestones of physical and neural development. Comparing this pattern with those observed in the development of object banging in human infants, in particular shared difficulty in controlling postural stability and movements of the distal arm joints, Tan (2017) suggests that tool use in *M.f.aurea* is likely developmentally constrained by limitations in physical maturation. However, conversely, it might be argued that such moments of physical and neural plasticity are critical both in motivating, and in determining the perceptual significance of behavioural plasticity (Montgomery, 2014): as the field of affordances shift relative to the developing individual, so the relevance of discovery through active material engagement, increases. Indeed, Tan (2017) found that individuals who had not developed tool use by the age of 3.5 years did not manipulate objects, or go on to develop tool using, suggesting a critical period for skill acquisition. That the closing of this critical period coincided with the age of completion for the myelination process, when neurons are rendered less plastic and subsequently less responsive to behavioural experiences, could indicate material engagement alone was not the key factor in determining potentiality for technical development, so much as associated degree of physical/neural plasticity.[53]

Burmese longtails present a unique behavioural context apart from other cases of primate tool using: although one the one hand, risk and necessity are increased by the insular context, and by tidal constraints on resource availability, on the other, the oyster beds in which tool using takes place are an essentially continuous, and highly visible (at low tide), resource, flush with suitable tool

[53] This does not exclude the argument that material engagement could induce temporary plasticity – simply that it may not always induce permanent changes, of the kind which might scaffold spontaneous technical development, i.e. certain explorative object manipulations (or object play) may no longer be perceptually relevant once meta-plasticity is reduced. One example of this might be the study by Byers & Walker (1995), who propose play to be not so much motor-training in the broad sense, so much as an influence to specific kinds of development.

materials. Archaeological surveys across several Burmese long-tail sites reveal how interplay between these contextual features, over generations of tool use, results in unique depositional patterns which meta-plastically influence populations' subsequent tool using, material selectivity, and reuse (Luncz *et al.*, 2019). At PNY, for example, Haslam et al. (2016) observed routine re-use, and transportation of tools short distances between prey resources within and outside of the oyster beds. While heavier tools were typically transported shorter distances (a factor of both materiality and prey mobility), and deposited *in situ,* on top or next to the anvil, close spatial association between prey resources enabled longer cumulative transport distances of smaller axing tools. Deposition in both kinds of tool using led to accumulation sites – the former, focally grounded by the raised anvils, and the latter, broadly (and abundantly) distributed throughout the oyster beds. Where reliable association between tool materials and tool use debris, at anvil sites would be expected to increase the likelihood of larger tool reuse in nut-cracking, extreme accumulation of smaller stone material throughout the oyster-beds may be expected to increase the perceptual relevance of tool-using more generally in that location as a processing-site: diversity of prey contexts contained therein potentially increasing the diversity of techniques and material forms employed. A relatively high degree of prey and context risk, associated with processing of motile prey, insular habitat and tidal constraints, rather than necessarily fostering increasing complexity of tool forms (which already include composite sets), ought to foster technical flexibility, and a resource-specialised repertoire comprising few, functionally overlapping tool forms.

The insular context of *M.f.aurea* tool using offers unique opportunity to explore the metaplastic effect of tool using among contained populations with access to limited resources, with differences in the relative influence of particular contextual aspects perhaps explaining inter-populational differences in technical behaviour, most archaeologically evident in material selectivity and reuse. For instance, Luncz, Tan et al. (2017) found that intensity of macaque tool use at PNY and SRY directly affected size of oysters available, macaques' selective preference of larger prey leading to resource depletion and attendant changes in tool size, consistent with the wider pattern of

primates adjusting tool to match prey size/hardness (Fragaszy *et al.*, 2010; Sirianni, Mundry and Boesch, 2010; Gumert, Hoong and Malaivijitnond, 2011; Gumert and Malaivijitnond, 2013). A second study by Luncz, Svensson et al. (2017) found as an exception, macaques at Lobi Bay selected larger stone tools to process marine snails than did macaques at the nearby site on BYI, despite on average, larger material being more abundant on the latter. Further, while oyster-processing hammerstones at the former site showed little percussive damage, the authors found central pitting indicative of substantial reuse evident on nut-cracking hammers from BYI. Though cultural preference cannot be ruled out, especially given greater material availability at BYI, the authors raise the interesting possibility that tidal effects and removal of stones from Lobi Bay could explain the observed pattern. As Luncz et al (2019) argue, these findings challenge the notion of archaeological assemblage composition as the product of 'pure' cultural choice subject to material constraint; further, Burmese long-tail tool use presents a case for understanding 'cultural' choice as socially influenced by engagement opportunity, and all its historical, cumulative, environmental and depositional factors.

7.1 Introduction

This chapter presents a comparison of the tool repertoires from the three case-study sites, including the broader context of their species' tool using. The first half of the chapter gives results of the comparison, split into aspects of macro- and then micro-complexity (per chapter 3). These results are then discussed with relation to the broader themes of this thesis in the discussion and conclusion.

7.2 Macro-complexity

The following section considers species-specific 'patterns' of tool using, in terms of macro-complexity, repertoire functional orientation, predominant causal functions, functional modes, and species 'universals. To accommodate for small sample sizes of both macaque and capuchin repertoires all statistical test used are nonparametric. Where the meaningfulness of these tests is further limited by differences in group distribution, results are discussed in terms of intuitive trends. Results are discussed altogether, in relation to the broader concepts of the thesis, including casual cognition, in Section 7.3 (beginning p. 255).

7.2.1 Repertoire richness and populational distribution

Of the three NHP case-studies, the richest repertoire was that of Bossou (*P.t.verus*): scoring highest in terms of total number of discrete variants, number of 'complex' variants (see Table 16, p. 239), and in overall repertoire diversity (see Table 17, p. 240; Table 19, p. 244; Table 20, p. 245). While Bossou exhibits the largest reported repertoire of all NHP sites (including for all sub-species of chimpanzee), *P.troglodytes* sites, in general, reported more technical variants on average, than did other species of NHP. Inter-species differences in repertoire size were not, however, significantly

different (Kruskal-Wallis H(2) = 4.46, p = 0.107), and the Serra da Capivara (*S.libidinosus*) repertoire, though considerably smaller than that of Bossou, was found to measure comparably with repertoires reported for other chimpanzee sites (see Figure 45, below; and Figure 47, p. 241): scoring within the broader range of all chimpanzee sites for total number of discrete variants, number of 'complex' variants, repertoire richness, heterogeneity, and evenness. The smallest of the three case-study sites, with the least complex repertoire, by all measures, was found to be Piak Nam Yai (*M.f.aurea*), with only 3 variants to the repertoire, and a high degree of homogeneity between those (see Table 17, p. 240; Table 19, p. 244; Table 20, p. 245). Both the repertoires reported from Burmese long-tailed macaque field sites scored lower than the averages for all three subspecies of chimpanzee, and for tufted capuchins. The smallest repertoire recorded at any site, was that of Fazenda Boa Vista (*S.libidinosus*), with only to variants reported as present or customary within the literature.

Figure 45 Chart showing macro-level complexity (total number of discrete variants) of repertoires for each sub-species

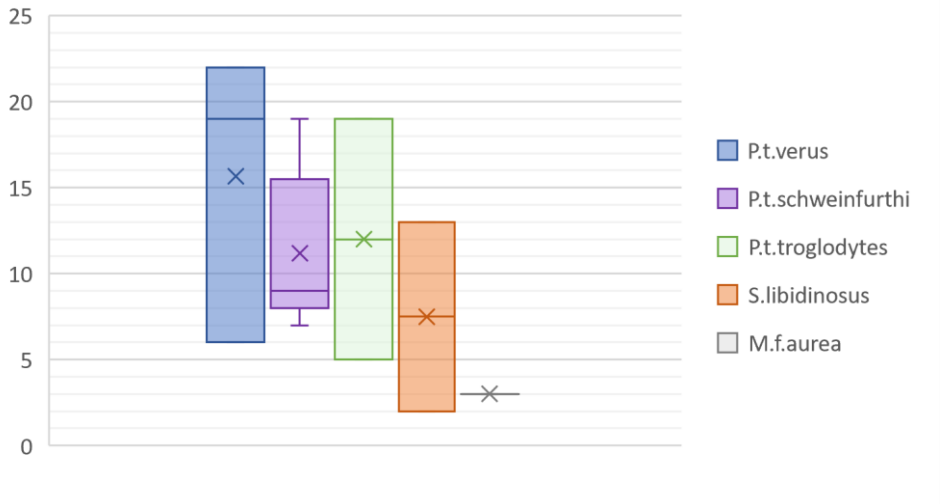


Table 16 Number of discrete technical variants for each of the case-study sites

Measure	Bossou	Serra da Capivara	Piak Nam Yai
Total repertoire size	22	13	3
Commonly expressed (%)	11 (54.5)	8 (61.4)	3 (100)
'Complex' variants	3	2	2
Composite variants	2	1	0

7.2.2 Species' repertoire orientation: functional context, modes, and causal functions.

7.2.2.1 Functional context

Subsistence tools form the predominant proportion of chimpanzee, capuchin, and macaque technical repertoires (see Table 17, p. 240, and Figure 46, p. 240), though the strength of this bias varies between species, intra-species, and between sites (see Figure 47, p. 241). While both macaque repertoires are wholly comprised of subsistence tools, capuchin and chimpanzee tool kits are comprised of variants for all functional contexts, including variants with hygiene/bodily comfort functions, variants used in social interactions, and variants for which the function was classed as 'other'. Only three repertoires (all *P.t.schweinfurthii*) reported repertoires for which less than 50% of variants were subsistents, of which only two reported repertoires for which subsistents were not the predominant functional context. These two sites were Kibale and Mahale M, at which hygiene/bodily comfort variants made the largest proportion of the technical repertoire.

Though perhaps uncommon among chimpanzee repertoires, hygiene-oriented tool kits are not unusual among the other apes. Indeed, comparative overviews of field studies reporting ape tool use demonstrate a high proportion, and in some cases the majority, of bonobo and orangutan technical variants function either for the purpose of self-hygiene or physical comfort; while

substantially fewer variants function in either foraging, or extractive foraging contexts (Hohmann and Fruth, 2003; Meulman and Van Schaik, 2013; Furuichi *et al.*, 2015).

Figure 46 Functional contextual orientation of NHP repertoires, as a percentage of species' total causal functional representation

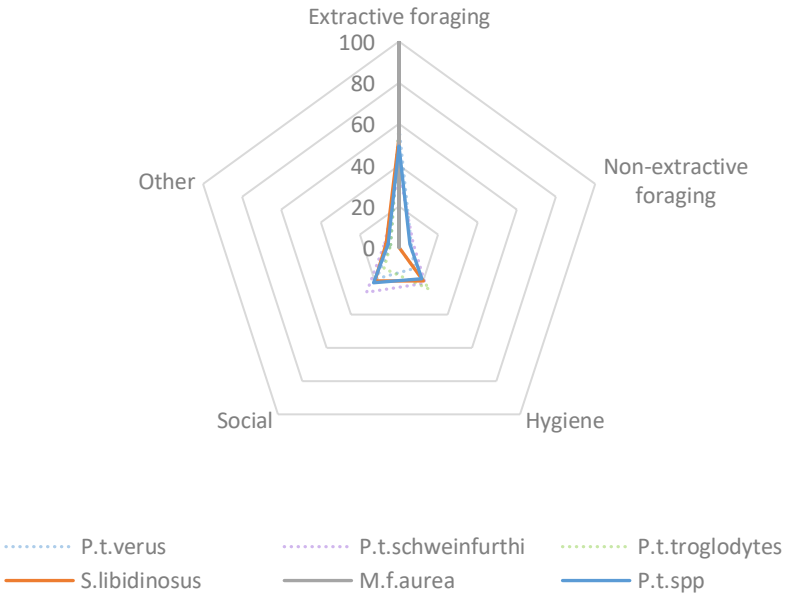
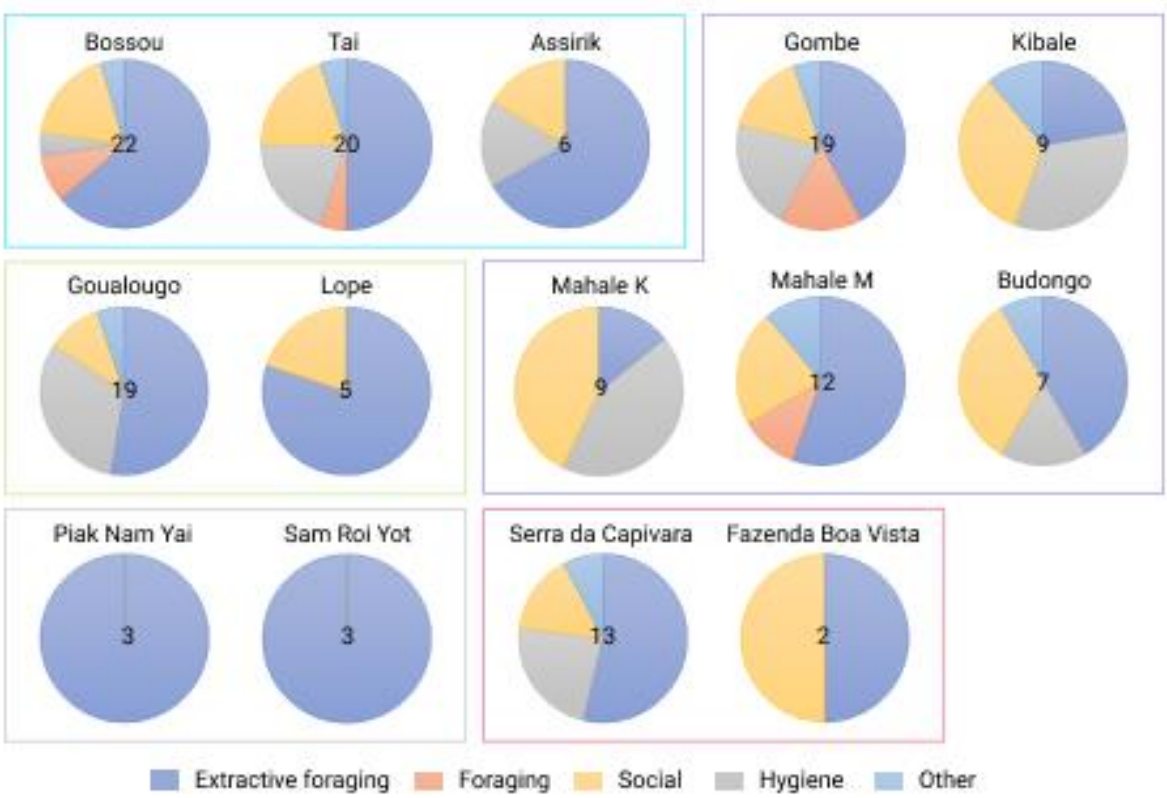


Table 17 SHE values for functional contexts present within the repertoires of the three case-study sites

Functional context	**Bossou (N = 22)**	**Serra da Capivara (N = 13)**	**Piak Nam Yai (N = 3)**
Richness (S)	5	4	1
Heterogeneity	1.09	1.16	0
Evenness	0.60	0.80	1
Primary functional context	Extractive foraging (64%)	Extractive foraging (54%)	Extractive foraging (100%)

Figure 47 Functional contextual orientation of site repertoires



- **Shown as a proportion of total repertoire size, grouped by sub-species. The number inside each pie-chart represents total number of discrete variants for the given repertoire. Blue: P.t.verus, Purple: P.t.schweinfurthii, Green: P.t.troglodytes, Red: S.libidinosus, Grey: M.f.aurea.**

While unlikely to predict manifestation of simple or *ad hoc*, technical abilities, extractive foraging *does* appear to be a precondition for the development of complex technical innovation (Parker & Gibson, 1979; Reader et al. 2001); such that the predominant subsistent context demonstrated across NHP case-study sites here, is likely to be the result of having selected those species and sites for their complex lithic tool use. Results of a principal components analyses of chimpanzee and orangutan tool catalogues conducted by Meulman & van Schaik (2010), suggest differences in contextual orientation reflect deeper differences in patterns of technical propensity. Repertoires characterised by a general foraging proficiency (i.e. higher number of extractive, and non-extractive foraging tools, and fewer tools in other non-subsistent contexts), e.g. chimpanzee and capuchin repertoires, were found more likely to be greater in total repertoire size, and with

more complex tools;[54] while hygiene and socially oriented kits, e.g. orangutan and bonobo repertoires, were found more likely to be smaller in total size, with fewer or no complex tool variants (*ibid.*).

Table 18 Rotated component matrix for principle components of lithic tool using NHP repertoires, using Varimax with Kaiser Normalisation. Positive factor loadings less than 0.4, and negative factor loadings greater than -0.4, have been excluded.

	All lithic using NHPs		***P.t.spp* & *S.libidinosus***		***P.t.spp* only**	
	Component		Component		Component	
	1 Foraging generalist	2 Foraging specialist	1 Generalist foraging	2 Generalist hygiene	1 Foraging	2 Hygiene
Total variants	.966		.874	.471	.754	.638
Total TUs	.744	.629	.969		.976	
Average TUs/variant		.776		*-.806*	.950	
'Complex' variants		.862	.931		.896	
Subsistence variants	.814	.523	.941		.931	
Extractive variants	.808	.531	.941		.930	
Hygiene variants	.757			.737		.865
Social variants	.823		.537	.536		.654
Other variants	.868		.630	.538	.416	.699

- **Negative factor loadings are in italics.**

A speculative PCA run across the NHP sites discussed within this thesis appears to confirm the pattern identified by Meulman & van Schaik (2013),[55] but also indicates some substantive differences between the NHP species. While differences between capuchin and chimpanzee

[54] Macaques may not have a large repertoire size, but all their variants are habitual, of which all but one is complex.

[55] Confirmation of the trend was expected as the same chimpanzee sites were used in Meulman & van Shaik's (2010) comparison – and since those same sites make up such a large proportion of the data compared here.

repertoires remain largely explained by the 'foraging' and 'hygiene' components, inclusion of the macaque repertoires into the PCA reverses the relationships between number of tools, complexity, and contextual orientation (see Table 18. p. 242).[56] Rather than by a division between contextual propensities, the lithic using species' repertoires could potentially instead be characterised as either foraging specialist (fewer, but more complex, extractive foraging tools) or foraging generalist (more, but on average less complex, tools, predominantly for extractive foraging, but also for a range of non-foraging contexts). Generalist and specialist tool kits are discussed further in Sections 7.2.3.2 (in relation to the complexity of tool forms) and 7.3.2 (with relation to the development of canonical affordances).

7.2.2.2 Functional mode and causal function

Though all three species are known to use similar tools, the primary functional mode was found to differ between the case-study sites (see Table 19, p. 244), with 'inserting and probing' variants making up one third of the Bossou chimpanzees' repertoire, in comparison to c.22% at SDC, and 0% at PNY. For both monkey sites, primary functional mode was hammering and pounding, comprising 33% and 100% of variant repertoires at SDC and PNY, respectively; in comparison to 25% at Bossou. While these primary functions were found to be typical for each respective species, chimpanzee technical repertoires, in general, were found to be richer and more diverse in their solicitation of modal affordances than were those of other species. The cumulative chimpanzee catalogue reported 15 unique functional modes in total, compared to 7 in wild capuchins, and only 1 in macaques.

Patterns of functional modality were reflected by NHP variant causal functions (see Table 20, p. 245; Figure 48, p. 245; and Figure 49, p. 246) with the majority of chimpanzee tools functioning to extend their users' reach (46% at Bossou, and 40% across all *P.t.spp.* sites) and the majority of

[56] Results should be considered purely speculative given the small sampling size for both monkey species and lack of variance (i.e. identical values) between the macaque sites.

capuchin and macaque tools, functioning to amplify their users' mechanical force (43.8% at SDC, and 42.7% of all *S.libidinosus* sites; 100% at PNY, and of all *M.f.aurea* sites). Again, chimpanzee repertoires were found to make use of a greater variety of tool causal functions (S = 5) than those of either capuchins (S = 4) or macaques (S = 1).

Overlap in the functional modes/causal functions employed by the different NHP species suggests some tooling affordances may be more readily solicited than others by primates. Of the 15 functional modes included in this thesis (see Table 3, p. 66), only one, 'hammer or pound', with the corresponding causal function 'amplification of the user's mechanical force', was common to all three species included within this thesis; while at least 5 others, listed by Shumaker et al. (2011) were absent altogether, including: 'cut', 'block', 'prop and climb', 'hang', and 'symbolise'.[57]

Table 19 Case study SHE values for repertoire functional mode

Functional mode	Bossou (N = 28)	Serra da Capivara (N = 18)	Piak Nam Yai (N = 3)
Richness (S)	11	7	1
Heterogeneity	2.01	1.56	0
Evenness	0.68	0.68	1
Predominant functional mode	Insert and probe (36%)	Hammer and pound (33%)	Hammer and pound (100%)

[57] Absence, here taken to exclude cases of captive primate tool using and more contentious cases (perhaps) typical of juvenile tool using, but absent among adults; notably 'symbolise', which has been argued to be present among chimpanzee juveniles engaging in stick doll play (Kahlenberg and Wrangham, 2010) but which is absent in adults; and 'contain', which is ambiguously present among chimpanzee juveniles engaging in leaf spooning, but often replaced by a more mature folding or sponging technique with the functional mode 'absorb' (Tonooka, 2001).

Figure 48 Causal functional orientation of NHP repertoires, as a percentage of species' total causal functional representation

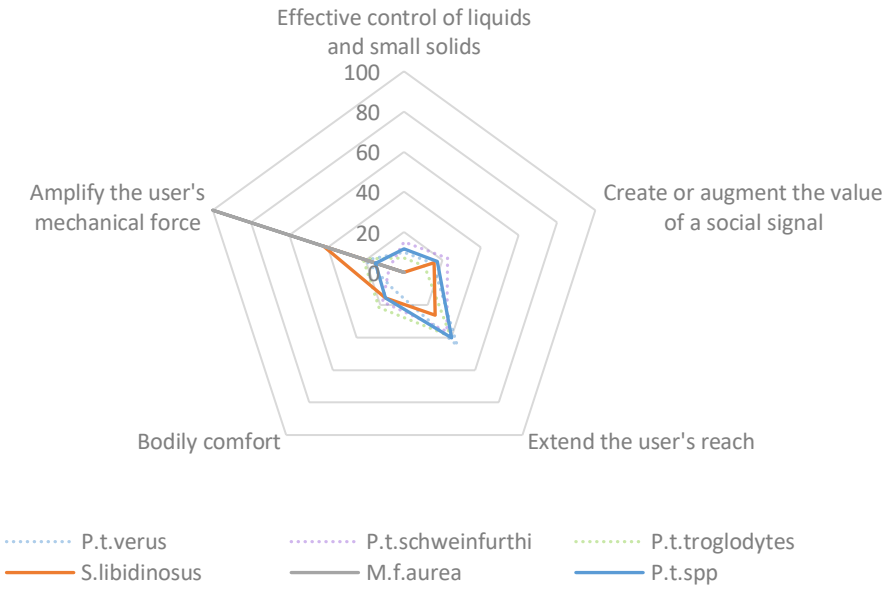
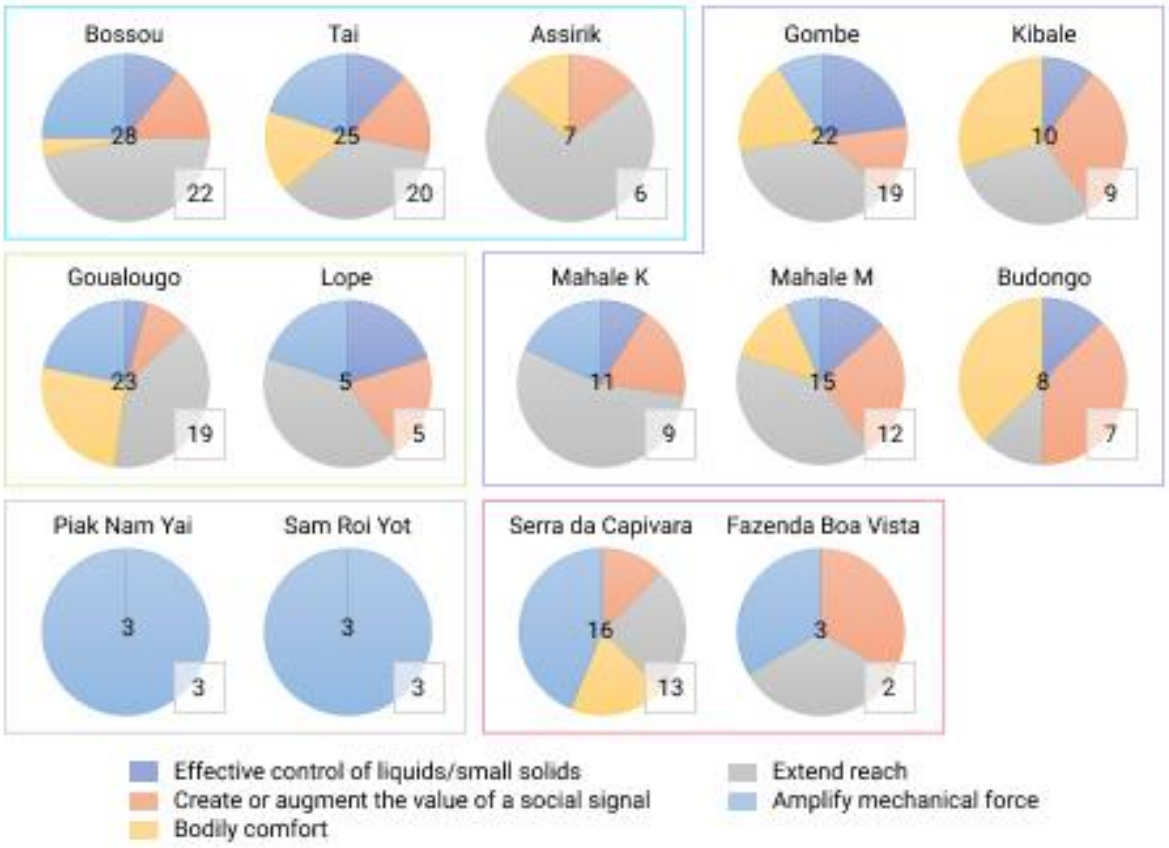


Table 20 Case study SHE values for repertoire causal function

Causal function	Bossou (N = 28)	Serra da Capivara (N = 16)	Piak Nam Yai (N = 3)
Richness (S)	5	4	1
Heterogeneity	1.34	1.28	0
Evenness	0.76	0.90	1
Predominant causal function	Extend the user's reach (46%)	Amplify the user's mechanical force (43.8%)	Amplify the user's mechanical force (100%)

Figure 49 Causal functional orientation of site repertoires



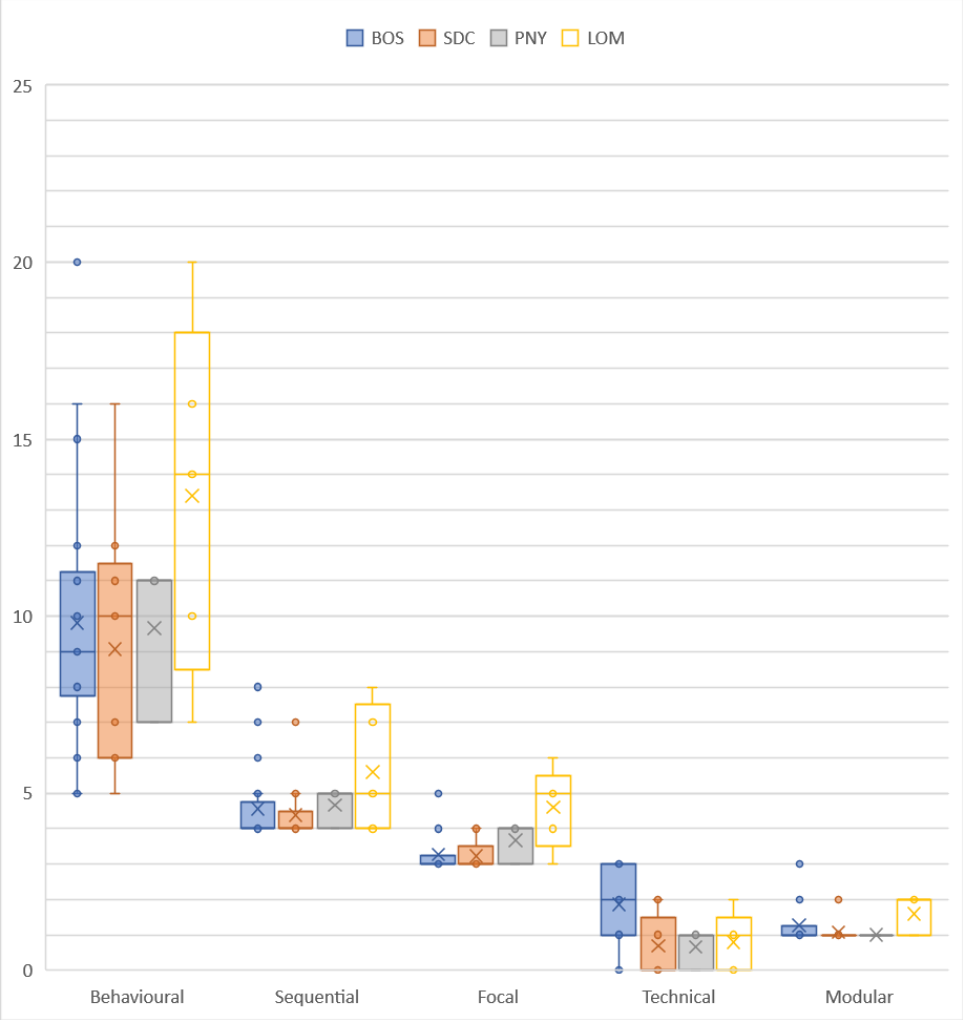
- **Shown as a proportion of the total number of causal functions present, grouped by sub-species. The number inside each pie-chart represents total number of causal functions present within a site's repertoire, and the number inside each small box, the site's total number of discrete variants. Blue: *P.t.verus,* Purple: *P.t.schweinfurthii,* Green: *P.t.troglodytes,* Red: *S.libidinosus,* Grey: *M.f.aurea.***

7.3 Micro-complexity and causal cognition

The following section focuses primarily on the case-study sites, to consider variant micro-complexity, exploring the relationships between behavioural, sequential, focal, technical, and modal complexities which might produce and/or characterise species' particular technical styles. NHP results are compared with hominin examples drawn from the literature. To give a view of relative overall non-random task complexity, variants were ranked by problem-solution distance [taken as the difference between behavioural and sequential complexities, following Lombard et al. (2019)] and by total number of spatial relationships (static and dynamic, simultaneous and sequential).

7.2.3.1 Behavioural, Sequential and Focal aspects

Figure 50 Graph showing variant complexity across micro-level aspects, for each of the main study sites; in comparison to Lomekwian lithic tool behaviours.



- **Scores for Lomekwian variants were adapted from Lombard et al. (2019), with re-created cognigrams shown in Appendix 3.**

Table 21 Micro-aspect values for case-study sites; in comparison to Lomekwian lithic tool behaviours. Scores for Lomekwian variants were adapted from Lombard & Haidle (Lombard, Högberg and Haidle, 2019)**, with re-created cognigrams shown in Appendix 3.**

Aspect	Bossou	Serra da Capivara	Piak Nam Yai	Lomekwi
Focal	N = 22	N = 13	N = 3	N = 5
Maximum	5	4	4	6
Average	3.3	3.2	3.7	4.6

Table 6 cont. Micro-aspect values for case-study sites; in comparison to Lomekwian lithic tool behaviours. Scores for Lomekwian variants were adapted from Lombard & Haidle (Lombard, Högberg and Haidle, 2019), with re-created cognigrams shown in Appendix 3.

Aspect	Bossou	Serra da Capivara	Piak Nam Yai	Lomekwi
Behavioural	N = 22	N = 13	N = 3	N = 5
Maximum	20	16	11	20
Average	9.8	9.1	9.6	13.4
Sequential	N = 22	N = 13	N = 3	N = 5
Maximum	7	7	5	8
Average	5	4	5	5.6
Technical	N = 18	N = 6	N = 2	N = 4
Maximum	3	2	1	2
Average	2	2	1	0.8
Modular	N = 22	N = 13	N = 3	N = 5
Maximum	3	2	1	2

While variants across the three sites displayed similar average levels for all micro-aspects of complexity, scoring within the lower ranges of those proposed for hominin Lomekwian tool using (see Figure 50, p. 247, and Table 21, p. 247),[58] a Kruskal-Wallis H test with pairwise comparisons demonstrated significant differences in variant complexity associated with functional context (problem-solution distance: $H(4) = 24.67$, $p = 0.000$; object relationships: $H(4) = 15.65$, $p = 0.004$). Consistent with the results of Section 7.2.2, extractive foraging variants were found to be significantly more complex than either hygiene (Problem-solution distance: $p = 0.003$) or social

[58] A Kruskal-Wallis U test revealed differences in micro-aspect complexities between species to be non-significant ($p > 0.05$).

(Problem-solution distance: p = 0.001; Object relationships: p = 0.005) variants.[59] Variants which ranked among the least complex belonged to social and hygiene contexts, and included 'Scratch' (SDC), 'leaf cushion', 'flailing stick or club', and 'leaf clip' (Bossou); each scoring 1 for problem-solution distance, and with only 1 spatial relationship between focal aspects. 'Nut-crack with anvil prop' (Bossou) was ranked most complex, with a problem-solution distance of 8 and a total of 4 spatial relationships between 5 focal aspects (inclusive of subject and tool object). Spatial relationships between focal aspects were more often than not either singular or sequential, with only the lithic cracking variants, and the chimpanzee variant 'push-pull' requiring management of multiple simultaneous spatial and affordance relationships.

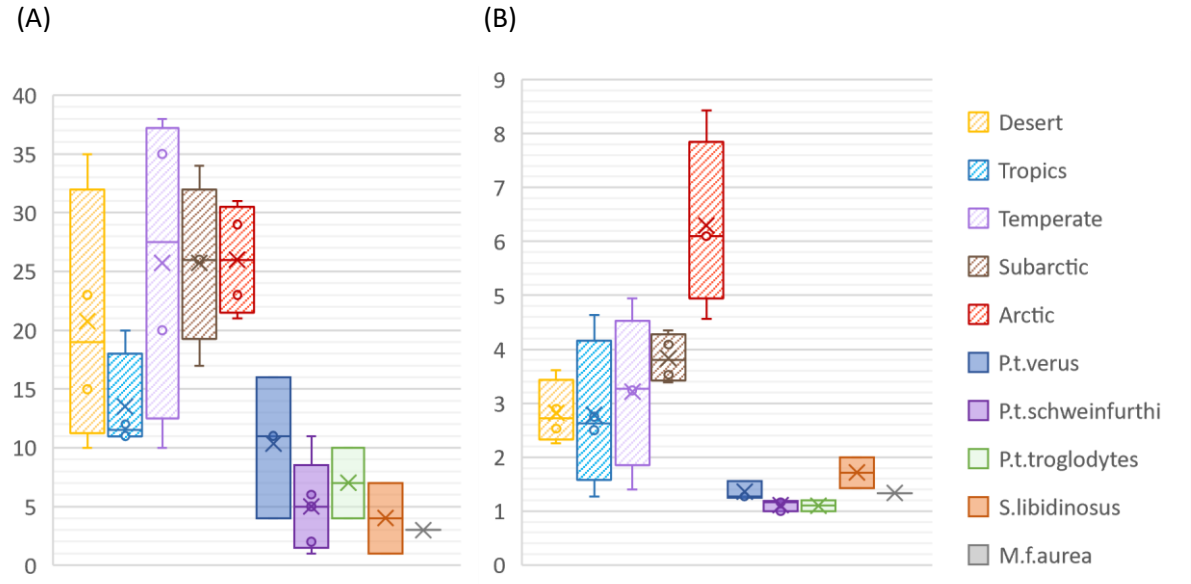
7.2.3.2 Technical complexity, manufacture mode, and tool association

A Kruskal-Wallis H test with pairwise comparisons showed differences in technical complexity between the functional contexts were less defined than for other aspects of micro-complexity ($H(4) = 12.121$, $p = 0.016$). Using post-hoc pairwise comparisons, extractive foraging subsistents were, however, again found to be typically more technically complex than social tools, overall ($p = 0.029$) and at Bossou ($H(4) = 11.186$, $p = 0.025$; pairwise: $p = 0.015$), though not at SDC ($H(3) = 1.929$, $p = 0.587$); most likely as a result of the differing material preferences between the species'.[60] Consistent with previous studies (e.g. McGrew, 1987; Westergaard, 1995), technical complexity of assemblages was found to be low at all NHP sites, though a greater number of organic inserting and probing tools used at Bossou corresponded with a higher total number of unique procedural units ($N \leq 8$), and higher average number of modifications per variant ($\bar{x} = 2.64$) than at either SDC ($N \leq 6$, $\bar{x} = 1.23$) or PNY ($N = 1$, $\bar{x} = 1.00$).[61]

[59] Independent results of KWU tests for each species tool kit are given in their respective case-study.
[60] No social tools are present in the PNY repertoire for an individual comparison.
[61] Total values are given as maximum estimates, inclusive of modifications such as biting to produce a brush tip in Bossou ant dipping, or lithic detachment in SDC stone pounding: i.e. modifications which have been speculated, but which lack certainty in purposiveness of the action. Average values are calculated from conservative total scores.

Though low, the number of unique procedural units present in the Bossou or SDC assemblages is not dissimilar to the conservative estimates made by Perreault et al. (2013) for lithic complexity found at early hominin sites; with assemblages dating from >2.35mya, at A.L 894, Hadar, Ethiopia, up to ca.200kya, at GhJh-74 in Kenya, scoring between 4-8 unique procedural units each (Perreault et al., 2013).[62] In fact, as shown in Figure 51 (below, p. 250), when NHP tool kits were scored using Oswalt's (1979) original system of techno-units, although total repertoire richness was generally less, average technical complexity per subsistent variant trended within the lower end of ranges given for modern hunter-gatherer food-gathering technological assemblages.

Figure 51 (A) Comparison between number of discrete subsistent variants in human and non-human primate repertoires; (B) Comparison between average number of techno-units per subsistent in human and non-human primate repertoires.



- **H.sapiens data are split into regional groups taken from Oswalt (1979, pp157-159, 173), adjusted to exclude variants which Oswalt classed as 'untended facilities' and which do not fulfil the tool use criteria adopted for this thesis.**

Quantitative similarity produced using either measure, disguises several notable qualitative differences between NHP and early hominin tool engagement. Indeed, Perreault et al.'s (2013) hominin estimates consider manufacturing of lithic tools only and are therefore likely to significantly

[62] Interestingly, Hovers (2009) directly likens the technical skill of Oldowan knappers at Hadar (A.L 894) to Bonobos', in terms of number of accidental flake scars produced.

underestimate technical complexity of the complete assemblage when inclusive of organic tools. Similarly, the comparison using Oswalt's measure is somewhat misleading, comparing technical complexity of tool forms with complexity of behavioural variants. In reality, NHPs employ only a few, simple, multi-functional tool forms to target a wide variety of resources, in some cases using the same tool form through multiple alternative functional modes, and even in more than one functional context.[63]

Table 22 Modes of manufacture present at NHP case-study sites and among their wider species contexts. Green: organic tool forms; Grey: lithic tool forms; White: absence; Dashed outline: indicates pattern is not present in wider context of species tool using.

Classification		Bossou	Serra da Capivara	Piak Nam Yai
Reshaping	Detachment	●	● ◌	○
	Reduction	●	●	○
	Replication	●	○	○
Association	Linkage	● ●	●	●
	Conjunction	○	○	○

Table 23 Association of tools at NHP case-study sites and among their wider species contexts. Green: organic tool forms; Grey: lithic tool forms; White: absence; Dashed outline: indicates pattern is not present in wider context of species tool using; Patterned fill; indicates pattern not present at site but present in wider context.

	Bossou	Serra da Capivara	Piak Nam Yai
Tool sets	●	◐ ●	○
Compound	● ●	●	● ▨
Meta-tools	●	○	○
Secondary	○	○	○

[63] Depending upon how tool forms are classified, total tool forms present among NHPs could range from 6 (with no accounting for material differences, e.g. wooden/stone or flexible/inflexible) to 10 or more (McGrew et al., 2019) .

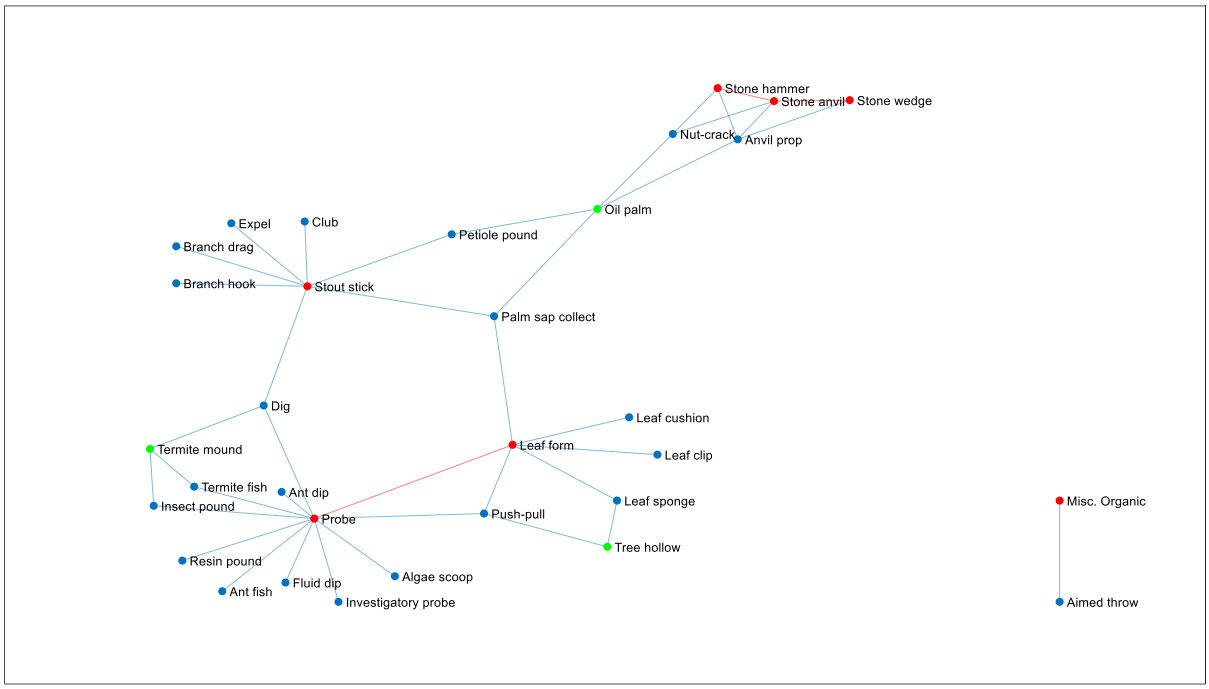
In addition, though all modes of manufacture characterised as reshaping, including procedural units classed as detachment, reduction, and replication, are present in chimpanzee and capuchin repertoires, their application is limited to manufacturing of organic tools (see Table 22, p. 251). With a single putative exception ('Stone pound', at SDC), NHP modified lithic variants, e.g. 'nut-crack' and 'pound-hammer', were always manufactured by linkage, with no evidence of reshaping beyond re-orientation through association, e.g. 'anvil prop' (also classed as linkage). Further, though all three NHPs produce tool kits comprised of multiple tools, tool association appears more limited than for early hominins - to the use of compound tools among macaques, compound and tool sets among capuchins, and compound tools, tool sets, and meta tools among chimpanzees, with no NHP species reported to use secondary tools (see

Table 23, p. 251). By contrast, tool making in Oldowan industrial complexes is typified by reductive reshaping of lithic materials. Tools are not only associated in sets, and as composites, but also through secondary tool use (Wynn *et al.*, 2011), leading some to make the significant distinction between tool manufacture – by means of basic reshaping – and tool crafting (e.g. McGrew et al., 2019). Perrault et al.'s measure of technical complexity, while successfully increasing resolution for NHP organic tool using, fails to capture the proposed increased cognitive difficulties of manufacturing by either conjunction, or for lithic materials, by reshaping by means of secondary tool use (i.e. grades 6 and 7 causal cognition).

As argued in the methodology (Chapter 3, Section 3.5.4.1), some reductivity caused in the measuring of technical complexity should be absorbed by the holistic approach taken, with conjunction methods and secondary tool-use both likely to be captured by increases in either focal, behavioural and sequential, or modular complexities, as well as by overall tool kit size and orientation. This being said, given the consistent and low scores in modular complexity for NHP variants, it does seem this aspect measure (and, modular complexity) may be more effective when a more diverse range of tools and tool kits are included into the comparison, i.e. with the inclusion of more modern hominin industrial complexes.

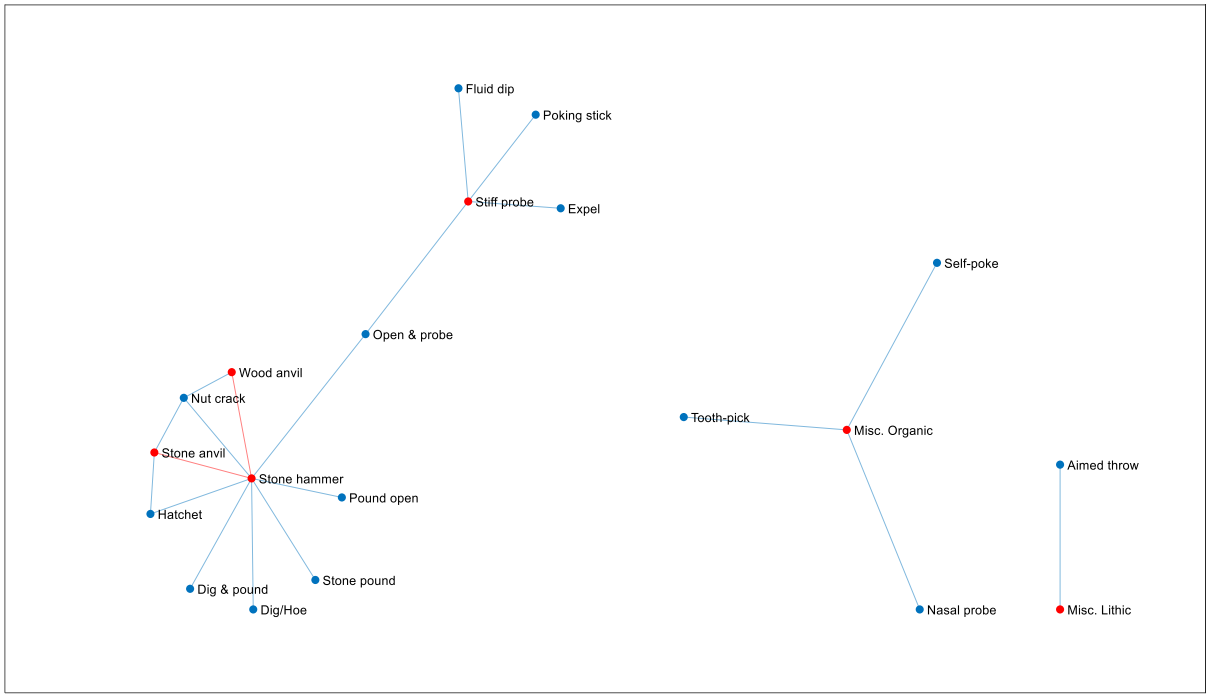
To explore patterns of material entanglement characterising NHP tool using (i.e. the meshwork constituting technical constellations), nodal network graphs were compiled for each of the case-study sites in MATLAB. Variants, tool forms, and important (or reliably concurrent) site locations were all assigned as nodes, with edges scored between variants and their associated tool forms, variants and site locations, and between composite tool forms. These technical networks are shown in Figure 52 (below), Figure 54 (p. 254), and Figure 54 (p. 254), and discussed throughout the following sections.

Figure 52 Material networks connecting technical variants of the Bossou repertoire.



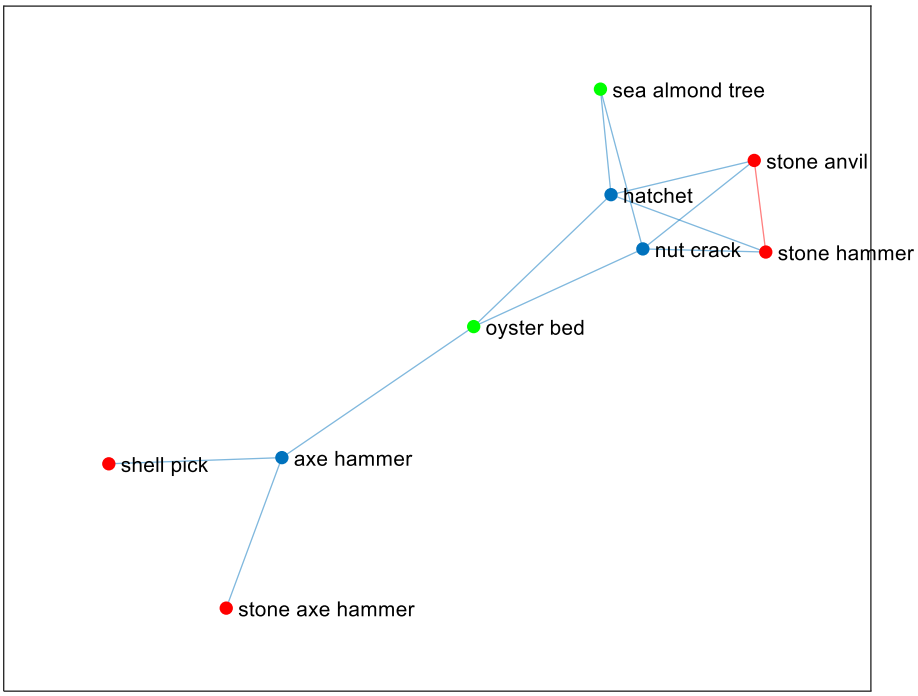
- **Blue: Variants; Red (Edge): Tool forms (Composite form); Green: Site locations**

Figure 53 Material networks connecting technical variants of the SDC repertoire.



- Blue: Variants; Red: Tool forms; Green: Site locations

Figure 54 Material networks connecting technical variants of the PNY repertoire.



- Material networks connecting technical variants of the SDC repertoire.

7.3 Discussion of results: overview of tool kits

Cross species comparisons nevertheless remain our best link to an invisible behavioural past, offering vital insight into our understanding of how hominin tool use, and meta-cognition might have evolved (McGrew et al., 2019; Wynn & McGrew, 1989; Wynn et al., 2011). However, their success is largely determined on the basis of species' suitability for comparison with early hominins, and more particularly, upon the frameworks by which species are compared. An overview of the case-studies included in this thesis, set in the broader context of lithic-using NHP tool use, reveals both unexpected similarities and considerable differences between the three primate species.

Perhaps the most obvious candidate for comparison given their close phylogeny, chimpanzees might be considered organic tool generalists; performing the greatest number of behavioural variants, by the most diverse range of functional modes/causal functions, across the widest range of functional contexts, of all the extant NHP species. Chimpanzee tool forms and tool making are also richer and more diverse than among either macaques or capuchins, as is tool association, with chimpanzee technical constellations connected by cross-contextual multi-functionality and linkage of organic tool forms, linkage of lithic tool forms, and by use of lithic meta-tools (see Figure 52, p. 253). Multi-functionality does, however, appear constrained to organic forms only, and chimpanzee lithic technology, though complex in terms of its focal and spatial relationships, is simple in function, being used to perform only a single variant in order to process a limited range of food resources.

Capuchin tool using appears similarly capable of being both generalist and flexible, but with multi-functionality connecting a greater number of variants through lithic, rather than organic tool forms, and through force-amplifying, rather than reach-extending causal functions (Figure 53, p. 254). An emergent proficiency for general percussive engagement with lithic materials appears evident in the manufacturing modes and in other forms of tool associations at SDC, with capuchins

at the case-study site the only wild NHPs known to associate lithic with organic materials in tool sets, to manufacture lithic tools by detachment, and to produce, if not to use, stone flakes. Comparative with chimpanzees, probe-tool using is diminished in distribution (present at SDC only), exhibits a contrary sexual-bias (male rather than female), and differs qualitatively, in material (stiff rather than flexible forms), performance and mode (lacking in precision, and more indicative of swiping or stabbing, than inserting).

Of the three NHPs, Burmese long-tailed macaques appear the truest lithic 'specialists' (see also McGrew et al., 2019), with the number of lithic tool forms constituting macaque repertoires, equalling, if not surpassing, the number shown in the capuchin repertoire at SDC, depending upon whether or not stone fulcrums are considered as a tool form in their own right (independent of stone pounders); and with macaques known to use their lithic subsistents to process more unique prey resources than either chimpanzees or capuchins, combined. Nevertheless, despite a wide variety of manipulative technical actions, macaque tool use appears quite limited, or at the very least, unvaried; macaque tool repertoires exhibit the fewest total tool forms, all in a single functional context, and all sharing a similar causal functions/modes. Tool association, is without exception, as composites, and tool manufacture is entirely restricted to linkage of lithic, or lithic with organic forms. As a result, macaque technical networks exhibit few connections between variants through shared tool forms, and a greater connection between variants (and tool forms) through shared site locations (see Figure 54, p. 254).

7.3.1 Grades 1 individual causal reasoning and 3 self-mindreading, and the phenomenology of technical enskilment: Material engagement and ontogeny[64]

In accordance with their own particular modes of material engagement, all three species have been shown to develop techniques managing hierarchical tool and target super-ordinate

[64] This section and the follow section 7.3.2 contain work published in Mosley (2020)

affordances, with processing of nuts by means of hammer and anvil composites in common. Individual causal reasoning and grade 3 self-mind reading (or the capacity for technical prosthesis) are evident throughout all three species of NHPs tool using; with epistemic actions being directed both towards and *through* tool objects. Skilled tool using among all species demonstrates a responsivity to the immediate changes in tool-task contingencies (e.g. modulation of strike amplitude between hammer strikes), and with expert tool users frequently appearing to combine functionally exploratory with pragmatic actions; in a literal sense, in their exploration of novel or threatening objects, e.g. in chimpanzees probing of snares (Sugiyama and Humle, 2011) and smelly substances on the ground (Ohashi, 2006), or capuchins probing of potentially dangerous predators (Falótico and Ottoni, 2014; Falótico, Verderane, *et al.*, 2018); and in a less obvious sense, in their subsistence tool using, in which exploratory and extractive activities were often achieved through the same actions. For example, in capuchin use of stone pounding tools to excavate under-ground storage organs (USOs), and invertebrates from behind bark (Mannu and Ottoni, 2009; Falótico and Ottoni, 2016) at SDC (Moura, 2004; Mannu and Ottoni, 2009; Falótico and Ottoni, 2016; Falótico, Siqueira and Ottoni, 2017), tool use not only functions to remove the dirt substrate, extending the agential self by amplifying the user's mechanical force, but in so doing, produces haptic and/or acoustic feedback by which the user is able to refine the focus of their effort and locate hidden food resources.

Grade 3 causal cognition (again, in the form of self-mind reading) is further evident in NHP tool selection. Each species displays a sensitivity to the material qualities of their tools and of task resources, matching form to function; and where manufacturing is necessary, does so often in anticipation of tool use. Although tool transport was not a particular focus for this thesis, many examples of the three lithic using NHP species used in compilation of the case-studies describe chimpanzees, capuchins and macaques bringing tool materials to sites for resource exploitation; whether perception/acquisition of the tool or perception of the target resource provide the impetus is unclear. Macaque tool transport, for instance, often occurs upon arrival at the oyster bed, where

an individual may pick up a small tool for axe-hammering, and carry it for some distance, still within the area of the food resource (Haslam, Pascual-Garrido, *et al.*, 2016); while chimpanzees, in contrast, are known to manufacture and bring tools to food resource sites, such that the act of engagement with tool materials may itself motivate the travel to a food resource – particularly if that food resource is farther away (e.g. Gruber et al., 2016).

Longitudinal studies of NHP technical behavioural ontogeny suggest perceptual learning of task contingencies, and subsequent emergent expertise (grade 3 self-mind reading), are the product of protracted interactive experience (grade 1 individual causal reasoning), with more hierarchically complex tool methods typically associated with greater periods of development (for reviews, see Biro, Sousa, & Matsuzawa, 2006; Fragaszy et al., 2013; Meulman, Seed, & Mann, 2013). Juvenile NHP tool users, even when able to achieve successful tool use, appear to lack the fluency and precision shown by more experienced individuals (e.g. Bril et al., 2012; Mangalam & Fragaszy, 2015); their techniques were often described as being clumsy or inefficient, and more frequently interspersed with purely epistemic interruptions such as exploratory handling of tools/targets between tooling actions (e.g. De Resende, Ottoni, & Fragaszy, 2008; Lonsdorf, 2005; Tan, 2017; Fragaszy et al., 2020). In capuchin digging stone tool use, for example, juvenile tool users typically failed to target the more visually imperceptible food resources targeted by adults, unless those resources had been visibly exposed by another conspecifics prior tool using, or by non-conspecific foraging activity (Falótico, Siqueira and Ottoni, 2017).

Reminiscent of Ihde's (1979, 1990) process of technological 'symbiosis', or the change from Heidegger's (1927/1996) 'present-at-hand' to 'ready-at-hand', changes from juvenile to mature tool using techniques suggest performances are gradually mitigated by an emergent sensitivity to the epistemic feedback produced through pragmatic tool using, achieved through a period of perceptual skill honing reliant upon, yet independent of successful perception of relevant tool and task object affordances and their order. In chimpanzee termite fishing, for instance, by 4.5 years, the majority of

juvenile tool users had successfully learned the correct sequence of choosing a hole in the termite mound, to manufacture probe tools, and were able to successfully insert their tools into the mound; yet, technique of insertion was either too forceful, or to the incorrect depth, and so ineffective for catching termites (Lonsdorf, 2005). Attention, rather than being directed through the tool to the target, was still being directed to the tool and target; perception of the more embedded affordances of the tool using task only occurred in the active subjective experience of a tool as an extension of the agential self, an experience which was only achieved through subsequent practice once the critical sequence had been established.

For Ihde, the immediacy and eventual transparency of a tool's phenomenological osmosis is directly reflective of the relative ergonomic 'fit' between tool and task, and tool and user (Ihde, 1990, p73). The more optimum the ergonomic interface between the tool and task, the more complete 'symbiosis' can be achieved: the more intuitive the tool to its user, the quicker that symbiosis can be realised. In a very mundane sense, similarities between the primate species are, in this respect, unsurprising, given similarities in their functional anatomy and exposure to a similar range of naturally occurring materials from which to produce tool forms. Where behavioural repertoires overlap, however, stylistic permutations, as well as differences in associated functional mode/causal function, likely mirror ecological differences between the NHP species natural ecological, foraging predispositions; for example, in the different principle causal functions shown by chimpanzees and both capuchin and macaques, with the former engaging more in fine-motor control, gestural tool use which extends the users reach, mirroring their non-tool-assisted processing of fleshy fruits (Corp & Byrne, 2002), an early inclination for 'inserting' manipulatory actions (Hayashi et al., 2005), and natural propensity for gestural communication (Hobaiter and Byrne, 2011, 2014); and the latter species' engaging more in tapping, or pounding lithic behaviours which amplify the users mechanical force, mirroring both capuchin's natural destructive foraging and search behaviours (Fragaszy & Adams-Curtis, 1991), and macaques innate predisposition towards stone-handling (Huffman and Quiatt, 1986).

As argued by Fragaszy & Mangalam (2018), since technical enskilment (i.e. perceiving to learn) takes place in the context of learning to perceive, both being functions of experience, learning of tool using affordances is also more likely to be enhanced when tool actions are congruent with species-typical explorative and play behaviours, and constrained when incongruent with ecologically relevant behaviours. As one of the most intuitively complex NHP tool behaviours (Matsuzawa, 1996), chimpanzee, capuchin, and macaque individuals spend years practicing isolated components of nut-cracking technique, with patterns of component expression postulated to reflect species-specific ecological bias (De Resende et al., 2008; Tan, 2017). For chimpanzee and macaque juveniles, ontogeny begins with the performance of simple object manipulations of nuts and stones from c.1.5 years and 4-6 months respectively, gradually transitioning into performance of non-functional object associations (e.g. placing of objects on anvils), followed by functional object combinations (e.g. ineffective percussive actions), prior to the manifestation of successful nut-cracking tool-use at c.3.5 and 2.5-3.5 years of age, respectively (chimpanzees: Boesch & Boesch-Achermann, 2000; Inoue-Nakamura & Matsuzawa, 1997; macaques: Tan, 2017). In contrast, exhibition of percussive actions by tufted capuchin juveniles appears at a comparatively high frequency early in development (from c.5-8 months), while placement and release of food items onto anvil surfaces, appears comparatively late, anticipating the realisation of successful nut-cracking (at c.2y), and with proficient technique typically expressed c.6 months later (de Resende, Ottoni and Fragaszy, 2008).

As discussed in chapter 6, percussion of objects onto surfaces is a routine aspect of capuchin exploratory foraging behaviour, and is highly prevalent among juveniles of the species (De Resende et al., 2008; Fragaszy & Adams-Curtis, 1991), to a degree which captive studies (e.g. Takeshita et al., 2005; also cited by De Resende et al., 2008), and a diet of predominantly un-encased, fleshy fruits, suggest, for chimpanzees and in-land macaques it is perhaps not. Conversely, releasing food resources onto anvils takes consistent time and practice for capuchins to realise, with the affordance in direct competition with the more natural instinct, relevant in their arboreal feeding context, to release encased food resources only having either successfully broken them open, or having lost

interest (De Resende et al., 2008, p836). Regional differences in feeding ecology may similarly contribute to explaining expression, or lack of expression, of nut-cracking behaviours between the chimpanzee subspecies', with proto-tool-like food processing involving object-substrate banging having been described among some western populations of *P.t.verus* and not among populations of either *P.t.schweinfurthii* or *P.t.troglodytes* (McGrew *et al.*, 2003). Gumert & Malaivijitnond (2012) postulate that among inland macaque populations, frugivorous diets comprise fewer foods requiring percussive extraction, such that the increased rate of consumption of shelled marine organisms associated with coastal environments may increase these populations likelihood, and readiness, to develop predisposed object manipulations into percussive tool actions (see also Tan, 2017). Interestingly, where tool use is present among *M.f.aurea*, Tan (2017) notes that the early tool using percussive actions used by juveniles more resemble species-typical non-tool assisted exploratory rubbing-actions of foods on substrates, transformed into swiping-like 'u-shaped' motions and finally into effective cracking actions, demonstrating a cumulative progression of action affordances, each emergent from the other as juveniles refined their perceptual understanding of the tool function.

7.3.2 Grades 2 cued-dyadic, 3 conspecific mindreading, 4 detached cued-dyadic causal reasoning, and 5 non-conspecific mindreading: Temporalities of material engagement in the ontogenetic niche

While studies of causal reasoning in 'theory of mind' (cf. Premack & Woodruff, 1978) suggest that NHPs are unlikely to perceive tools as agential extensions of a tool using other [i.e. to 'mind read' (cf. Lombard & Gärdenfors, 2017)], case-study examples for all three NHP species suggest observation of conspecific others' material interactions nevertheless directs attention towards the perceptible affordances of tools and target objects (Call, Carpenter, & Tomasello, 2005; Fragaszy & Visalberghi, 2004; Penn & Povinelli, 2007; Tomasello, 1996; though see Froese, 2015; Froese & Leavens, 2014; Whiten, McGuigan, Marshall-Pescini, & Hopper, 2009). Variants which were classed

as either customary or habitual were present at each of the case-study sites, while in their broader contexts, each of the three NHPs displays significant intra-species variation in the expression of tool using. Populations of the same species exhibit unique repertoire compositions, stylistic differences in variant techniques (e.g. Falótico & Ottoni, 2016; Tan et al., 2015; Tonooka, 2001; Yamakoshi & Myowa-Yamakoshi, 2004), and group-specific material preferences (e.g.Luncz et al., 2012, 2019; Visalberghi et al., 2017) which cannot be accounted for by a purely ecological explanation. Social tool use among chimpanzees, alongside their extensive gestural repertoire suggests that with increasing familiarity, or repeated contextual reuse of a social tool, grade 3 conspecific mindreading was emergent – to the extent that social tool using could be used to reliably induce a culturally-dependent behavioural response.

Although evidence of purposive teaching (including tool transfer) was absent at the case-study sites, proximity to tool using others was nevertheless important in bringing access to both suitable behavioural models and tool materials, and thereby opportunities for individual learning through engagement with the materials used in others' tool using processes. Purposive or not, studies of social learning show that, within tolerance constraints, more skilled, technically proficient individuals were the prefered behavioural model for all three species, suggesting that in scenarios where the immediate rewards from unskilled tool using are low, the sustained attention and interaction with tool and target materials required for development is indirectly incentivised by proximity to tool using others, and the by opportunity for scrounging (Ottoni et al., 2005; Ottoni & Izar, 2008; Tan et al., 2018). Juveniles of all primate lithic tool using species display an interest in the tool materials of conspecifics, frequently touching, and sniffing tools (Biro et al., 2006; Eschar et al., 2016; Tan et al., 2018), with these behaviours and presumably tool-action affordances made more salient when nearby others were themselves engaged in tool using (Eschar et al., 2016; Fragaszy et al., 2017).

Throughout the case-studies, tool re-use was seen to scaffold the learning processes in more complex tool using behaviours, such as chimpanzee pestle-pounding (Yamakoshi, 2011; Yamakoshi & Sugiyama, 1995), leaf folding/sponging (Tonooka, Tomonaga and Matsuzawa, 1997; Tonooka, 2001), and NHP probe tool use (Falótico and Ottoni, 2014; Musgrave *et al.*, 2016), providing the appropriate practical context in which to hone perceptual skill, while bypassing the need for delicate or physically challenging tool acquisition/modification (Fragaszy et al., 2017; Musgrave et al., 2020). Interestingly, at sites where active attention direction [e.g. through direct tool transfer (e.g. Musgrave et al., 2016) or exaggeration of the tooling action (e.g. Masataka et al., 2009)] has been observed, teaching appears positively correlated with degree of task complexity (Musgrave *et al.*, 2020) - a potential indicator both of grade 3 conspecific mindreading among familiar adult-juvenile dyads, and of an entanglement between grade 3 self-mindreading emergent from, and grade 3 conspecific-mindreading being used to scaffold development of future, complex technologies.

In this latter respect, socio-ecological context appears important, not simply in the conventional sense because it can act to help or hinder access to behavioural models/materials as outlined above, but also in the ways and temporalities in which it can alter the context in which materials are accessed. Through their shaping of the ontogenetic niche (cf. Stotz, 2017; West & King, 1987; West, King, & Arberg, 1988), tool-using others' material interactions direct attention in a longitudinal sense, through the creation of long-lasting tool artefacts, and in the shaping and scaffolding of the environment (Fragaszy, 2011). Sites of accumulated tool materials and target resource residues form focal points on the landscape, providing key opportunities to encounter situational affordances in their appropriate use contexts (Fragaszy, 2011; Fragaszy et al., 2013). The same reasons why some forms of tool use proliferate while others diminish is likely a factor of their materiality (which actions they produce), their object permanence (how conspicuous they are), and the reliability of their ecological context (how diverse/variable is their context and use through time).

Taking an example from the case-studies, it seems likely the same reasons why probe-tool-use is not well expressed often or widely among capuchin groups, may explain why use of stone pounding tools are so comparatively prolific. Capuchin probe tool forms are perishable, take place arboreally/in elevated contexts, and/or target motile prey, with typically low rates of return in non-scroungable rewards (Falotico & Ottoni, 2014; Falotico, 2018); meaning tool materials are unlikely to accumlate in order to attract attention, and nor is attention incentivised by scrounging opportunity. In contrast, stone pounding tool use is far more conspicuous, in both the immediate and longitudinal sense: it often takes place terrestrially and in a group context, produces a lot of sound to attract attention (Coelho et al., 2015; Eshchar et al., 2016; Fragaszy et al., 2017), and produces profound non-perishable effects on the environment including accumulations of hammers and nut casings, on and around anvils, distinguishable patterns of pitting on anvil surfaces, and in cashew processing, long-lasting CNSL stains on tools and anvils (Visalberghi *et al.*, 2013; Haslam *et al.*, 2014; Falótico *et al.*, 2019). In chimpanzees, the ecology of probe tool using is different enough that it is not affected in the same way: at Bossou, insect predation takes place in a social context, of mother and infant, and primarily at the nest or mound (Humle and Matsuzawa, 2002; Sanz and Morgan, 2007); where tools can accumulate around a focal locus, and tool acquisition can leave distinctive tree scarring within the immediate area (Pascual-Garrido, 2019).

As redistribution of materials can create accumulation sites, so it can deplete the diversity of contexts within which a material is found, drawing attention away from alternative uses, decreasing likelihood of behavioural innovation in novel contexts and contributing to cultural override (*sensu* Hicks et al., 2020) through the emergence of strict canonical artefact categorisations (grade 4 causal cognition). As hypothesised in the second case-study, more ambiguous criteria, should in theory, lend a fluidity to tool-use which might facilitate cross-context transfer of functional affordances; congruent with the diverse repertoire we see at sites like SDC and PNY, or in chimpanzee organic tool-using. More strict criteria, should, in contrast, lead to highly specialised tool using, with fewer tool associations; and congruent with what is seen at both FBV and at chimpanzee sites like Budongo

(elaborated upon in the next section). The role of the oil palm in the Bossou repertoire, as a landmark associating several different forms of more complex tool using, indicates the strength of the effect exerted by strictness of context is likely to be mitigated by richness of non-tool-related affordances of the same target resource; chimpanzees exploit numerous parts of the oil palm, rather than simply the nuts, or the palm petioles, or palm-sap, and so it makes sense that tool using, though highly concentrated and therefore highly visible around these landmarks, provides strict contexts for numerous functions. Grade 4 may thus already be present among several NHP tool using groups, in particular among chimpanzees and capuchins, as best evidenced by cultural override, or inability to recognise tool affordances present in the wider species catalogue, even when artificially made more salient (e.g. Cardoso & Ottoni, 2016; Gruber et al., 2011, 2012); and in immediate reuse of tools at tool sites, in the absence of prior proprioceptive behaviours (Spagnoletti *et al.*, 2011; Borgo *et al.*, 2013; Resende *et al.*, 2021). Emergence of grade 4 causal cognition is more complicated in *M.f.aurea* where the coastal habitat comprises an abundance of relatively homogenous suitable tool materials, and a more or less spatially continuous food resource; in fact, in such a situation, it might be that the coastal habitat as a processing site is, itself, a canonical affordance – as would explain macaque individuals' often picking up tool materials upon arrival to the oyster beds, and transporting them around the area.

7.3.2.1 The extractive foraging context: an ideal scaffold for complex tool use?

From an MET perspective, there are several facets of extractive foraging tool use which might make it (1) more prevalent than other tooling contexts, and (2) more likely to produce complex forms, in particular for species which naturally engage in non-tool assisted extractive foraging. These reasons include: extractive foraging species' ecological attentional predispositions and the context of their juvenile play behaviour; tool using reward types and their relative timescales of return; and the relative social and archaeological visibility of extractive foraging behaviours in comparison to other tool types.

Regarding species' ecological disposition, evidence suggests a strong connection between extractive foraging, and both intelligence and fine-level motor skills (Parker and Gibson, 1977; Reader, Hager and Laland, 2011; Parker, 2015); with behavioural flexibility often being required to compensate for any absence in anatomical structural specialisation (van Schaik, Deaner and Merrill, 1999). Higher innovation rates amongst extractive foragers (Reader et al., 2011) further suggest discovery of objects' functional affordances is likely supported by the extractive foraging context, in particular where non-tool assisted foraging repertoires involve either hierarchical or combinatorial object manipulation, such as prickly pear cactus processing (e.g. Tan *et al.,* 2016), or object-substrate banging (Adams-Curtis & Fragaszy, 1991).

Apparent differences in intrinsic motivation for object manipulation between chimpanzees and bonobos (as extractive foragers and non-extractive foraging, social tool users, respectively) correspond with strong differences in attentional bias found between captive individuals of the same species'. Studies by Koops *et al.* (2015a, 2015b) found object play occurred significantly more frequently, both in solo contexts and as a proportion of total play time, among chimpanzees than bonobos; while a captive study by Kano *et al.* (2015) found chimpanzee individuals biased their attention towards action target objects, and bonobos towards key features associated with social cuing (e.g. target faces or mouths). That the objects manipulated by chimpanzees became more tool like with age (Koops et al. 2015) could indicate *Pan* species differences in motivation and attentional disposition, though perhaps intrinsic in origin, are ontogenetically reinforced, with play behaviour honing perceptual skill in chimpanzees while consolidating the attentional relevance of objects functional affordances (see also Kano et al., 2015).

In this respect, direct and indirect rewards from tool using are likely to function as a mechanism for perceptual reinforcement and for motivating object engagement, with differences in the reward types of particular functional contexts likely to explain correspondent levels of innovation and technical complexity; a key argument of this thesis being that sustained material

engagement is critical to the development of skill in complex tool techniques. Indeed, all customary complex subsistent variants described in chapters 4, 5, and 6, produce both direct and indirect rewards to both tool user and proximate learners which might be considered to foster and support action target object attention and material engagement. With nut-cracking taken as the primary example: for the user, tool use produces both immediate food rewards and varying long term adaptive benefits through increased access to otherwise inaccessible nutrient resources; and for the proximate learner, produces scroungable food rewards.

Examples of social and hygiene tool using rewards, in contrast, seem less likely to promote sustained material engagement. Rewards for social tool users are largely dependent on the reliability of their technique inducing a particular behavioural response in others, such that direct returns are unlikely prior to the realisation of successful tool use, while there are no apparent indirect rewards to non-tool users which might encourage their own engagement. Indeed, in the capuchin social tool-use reported for SDC, the main reward seems to be a reduction in the antagonistic behaviour directed towards, and experienced by the tool user (e.g. aimed throw), with unsuccessful tool use being at best, ineffective, and at worst, increasing potential risk (e.g. aimed throw and poke/spear). Likewise hygiene tool use, though more likely to be directly rewarding for individual tool users when self-directed, is unlikely to provide indirect rewards to others, with social hygiene tool use potentially diminishing many of the affective rewards associated with touch-based grooming.

As discussed in the previous section, social and material visibility also play a key role in the shaping of NHP technical ontogenetic niches, giving some clue as to why some tool traditions persist where others diminish. As probe tool using flourishes or flounders among chimpanzees and capuchins, so it is that the relative conspicuousness of the extractive foraging context, its activities and artefacts, may increase the likelihood of developing more complex techniques. Comparing the extractive and social/hygiene variants from Bossou, both insect predation and nut-cracking activities are spatially focused, the latter around the oil palm, and both almost exclusively terrestrial, such

that they are both highly visible and allow for accumulation of tools around the focal target; offering opportunity for both social learning and tool material interactions/reuse. Both types of behaviour take place in a social context, of mother and infant, but perhaps also in the presence of other conspecifics, nut-cracking in particular producing enough noise that, even when engaged in privately, it draws the attention of conspecific others. In contrast, neither social nor hygiene tools have a particular geographical locus, and neither accumulate materials to facilitate tool reuse; the former often taking place arboreally or utilising perishable materials, and the latter, effectively exhausting the tools functionality through use. While Bossou's social tooling, may be highly attention directing, wild chimpanzee hygiene variants are without exception, self-directed, limiting their visibility to conspecifics, and thereby their amenability to long-term complexification.

Several authors have suggested smaller, hygiene oriented tool kits may be a 'cultural' characteristic of *P.t.schweinfurthii* groups living in the northern part of the western Rift Valley escarpment (Reynolds, 2005; Watts, 2008). At both Sonso (Budongo) and Kibale (Kanyawara and Ngogo), for example, variants used to affect bodily comfort are not only more abundant, but also used more frequently than at other sites (McGrew, 2010), while tool assisted insectivory is comparatively rare (or altogether absent). Interestingly, where present, insect predation is performed either with slender leafy stems or even detached leaves, rather than stick tools (Watts, 2008; Mugisha, Zuberbühler and Hobaiter, 2016), leading Gruber (2013) to suggest anthropogenic landscape changes, including deforestation and a subsequent increase in the number of more readily available food resources, may have led to a loss of stick-based tool behaviours among these chimpanzee communities. While the recent discoveries of honey-digging stick tool use among intermediary and fringe chimpanzee populations complicate this picture (Hicks *et al.*, 2019; McLennan, Lorenti, *et al.*, 2019; McLennan, Rohen, *et al.*, 2019), in light of the argument developed in this section, it is worth considering whether, and how, these communities' material choices may be contributing to, or constraining, the development of more complex extractive foraging traditions.

7.3.3 Grades 6 inanimate causal reasoning & 7 causal network understanding: general patterns and the context in technical evolution

Hallmarks of human and likely early hominin tool using, very little evidence exists for either grade 6 inanimate causal reasoning or grade 7 causal network understanding, among the NHP species. Indeed, in regards to cumulative culture and its ratcheting effect (*cf.* Tennie et al., 2009), cultural adaptations beyond the scope of a single individual's life-span have often been conceived of as a unique human achievement, the pinnacle of truly 'cultural' living, with many putative animal examples having been either criticised as false positives, products of reading development from cross-sectional rather than longitudinal data (Dean et al., 2014). This has particularly been the case in instances of chimpanzee technical innovation, where, in the absence of an archaeological record for comparison, regional differences in effectivity between analogous, perhaps ecologically predisposed, techniques and tool forms create an illusion of cultural ratcheting; e.g. purposive brush-tip modification of probe forms at Goualougo (Sanz & Morgan, 2009; see also Schofield et al., 2018, p114), or moss-sponging as an efficacious material selection innovation to leaf-sponging, at Budongo (Gruber *et al.*, 2015; Lamon *et al.*, 2018).

The findings of the previous sections of this dissertation, however, contribute to a growing body of research arguing for a more holistic understanding of culture, as an inherently cumulative process, embodied in the concept of ontogenetic niche construction (e.g. Schofield et al., 2018; Tan, 2017): the ontogentic niche being recognised as the essentially metaplastic developmental context of mind through material engagments, a distributed system geo-temporally extended beyond the individual. As Schofield and colleagues (2018) argue, in so far as culture is an emergent product of the changing ontogenetic niche, shifts in relationality need not be unidirectionally progressive, each generation's tool using more complex or more efficient; as evidenced in the case-studies, as tool use may increase resource opportunity, so overuse can deplete it (e.g. Luncz et al., 2017); relative

adaptational advantage may shift demographic to rapidly increase population growth, or create bottlenecks, and technological loss (Henrich, 2004; Vaesen, 2012a; Kolodny, Creanza and Feldman, 2015). As hominin archaeology examples fluctuating cultural innovation, loss, and recursion, so NHP cultures are equally capable, under the correct circumstances, to develop in effeciency (Schofield et al., 2018). As such, it is in terms of strength and direction of this cumulative effect, perhaps rather than in its kind, that we may consider there to be a substantial difference between human and NHP tool using; opening up an alternative, novel angle for future research into the materiality of hominin tool use and how it might have enabled the development of emergent modes of complex cognition like grade 7?

Perhaps the most substantial difference between NHP and hominin modes of material engagement is longevity and ownership of tool forms. NHP tools are almost without exception *ad hoc* and single-use – that is, for the majority of cases, manufacture remains married to use, and while reuse may occur, tool ownership is not apparent. Between use episodes, tools are left at processing sites, or are simply abandoned, rather than kept, carried, or cared for. Modern human tool forms, in contrast, are all of the above, with many tools permanent fixtures in a repertoire in which form is fundamentally linked by multiple-realisability of function/resource, as opposed to function by multi-functionality of form (as in NHPs). Form persistence coincides with form specialisation, with modern human tool forms involving significantly longer manufacturing chains, with objects and raw materials wound into complex chains of effectivity (following Lombard & Haidle, 2012).[65] Rather than by direct affordances of tools as they fit target resources, human technologies are tied together by the 'meta-affordances' of tool forms and materials; actions in which attention is directed towards the affordance itself, rather than the direct or contextualised moment of affordance realisation – in essence, "focus is upon means, not ends" (Wynn, 2020, p10).

[65] Effectivity in this sense being akin to Heidegger's (1927/1996) notion of 'for-the-sake-of'

For Wynn (2020), meta-cognition, and the higher levels of causal network understanding necessary for these kind of associations (i.e. grade 7 causal network understanding), are likely to have their base in simpler perceptual processes; in particular, in the perception of 'displaced affordances', i.e. "the detection of features not directly available to perception" (*ibid,* p10). These include (1) embedded affordances, i.e. intervening actions which regenerate direct-action affordances such as modification of a tool or target prior to tool use; (2) remote affordances, i.e. affordances displaced through time or over distance such as tool transport to a more remote, anticipated target resource; and finally, (3) emergent meta-affordances, i.e. the enactive signification of objects and materials as *useful*, independent of a direct contextual association, as exemplified by long-distance carrying and the reproduction of recognisable tool forms. As a case in point, Acheulean handaxes represent perhaps the earliest example of a material instantiation of a meta-affordance, with basic form emergent from the coalescing of specific ergonomic features, followed by subsequent over-determination, suggestive of a gradual shift from focus upon specific function, to the utility, or reproducibility of the handaxes form itself (Overmann & Wynn, 2019a, 2019b; Wynn, 2020). As the handaxe's material persistence would have scaffolded, or enabled, increasing displacement between material, production, and performance affordances, so their displacement would have reinforced the relevance of the handaxe's form as a meta-affordance, and thereby, its persistency. In the confluence of increasingly remote and embedded affordances, attentional focus is shifted from target to tool form.

The transient nature of NHP tool using is likely to inhibit similar significant entanglements which might permit emergence of meta-cognition. Clustering of variants by modular PSD indicates simple NHP technologies may be subject to attentional constraints, limiting behavioural and sequential complexity per module. Since modularisation in NHP tool using is strongly tied with number of tool forms utilised, at a ratio of just over 1 module per tool form, it seems plausible to hypothesise that the *ad hoc* nature of NHP tool using, and the direct marriage of manufacture with use, while on the one hand scaffolding the increase in working memory and capacity to perceive

embedded affordances necessary for more complex variants/tool modification (association by linkage increasing PSD cumulatively per module), on the other, presents an energetic ceiling to variant complexity (the need to manufacture tools limits the number of tool forms which can be linked together, and thereby the total number of modules/PSD). A shift towards the use of more persistent tool forms by hominins would have bypassed such a limitation by displacing manufacturing processes through time/space, exponentially extending the capacity for variant linkage, working memory (PSD), and consequently perception of more complex embedded affordances.

Risk is highly likely to have been a significant driver in such a shift, being inherent to displacement; tool manufacture, maintanence and transport are energetically costly, and performed in anticipation, rather than with guarantee, of success. Indeed, technical complexity and repertoire richness, as proxies of specialisation (and thereby persistence), have both been hypothesised as factors of risk, with Torrence (1989) having found environmental variability (as a proxy for risk) positively influenced overall richness and complexity of tool forms (measured in TUs) comprising modern hunter-gatherer subsistence repertoires (an effect evident in Figure 51, p. 250; lattitude being a proxy of environmental variability). Profundity of this effect, however, is likely a direct factor of degree of material cognitive constitution; as degree of consitution increases, so risk increases (on the basis that much to gain, means much to lose), and with risk, tool complexity, number of distinct tool forms, and total time spent manufacturing - until at some point, presumably the energetic costs of either making or transporting specialised tool forms so outweigh the benefits of *ad hoc* tool using, it is no longer resource, or energetically, efficient to continue making and discarding tools (i.e. the risk of failure exceeds the net energetic benefits of making and using *ad hoc,* but is outweighed by the net energetic benefits of making, maintaining, and reusing).[66]

[66] This level of risk can only be associated with tools which are maximally constitutive to cognition: i.e. tools used to access otherwise inaccessible resources or which alter the scope and effectivity of bodily skills in ways

Understanding the perceptual relevance of displaced affordances to be enhanced by risk, and risk by degree of material constitution could contribute to explaining the substantial differences evident between hominin and NHP tool transport distances. As Wynn (2020) notes, the longest transport distances typically recorded in NHPs are orders of magnitude smaller than the >10km reported for Oldowant tool makers/users at Olduvai Gorge or Kanjera South: c.65 sequential trips in the same direction for chimpanzees, c.131 for macaques, and c.620 for capuchins (Carvalho *et al.*, 2008; Visalberghi, Spagnoletti, *et al.*, 2009; Haslam, Pascual-Garrido, *et al.*, 2016)! Although Gruber (2016) found chimpanzees spent greater time manufacturing tools when travelling to more distant target resources, suggesting effort to mitigate the risk of failure was increased with degree of remote displacment of the target affordance; the minimal degree of material cognitive consitution characterising chimpanzee probe tool using (and all other NHP tool using), may simply fail to reach a level sufficient for risk to act as a catalyst to the virtuous circle driving persistency and emergent higher cognition supporting long-distance transport in hominins. With risk level limitting the perceptual relevance of displaced affordances and object persistency, it is possible to hypothesise NHP tool repertoires are further subject to a cap on repertoire size (i.e. total number of replicable tool forms); hence, although Kaplan et al (2020) demonstrate chimpanzee behavioural diversity, including diversity in tool using (i.e. behavioural repertoire), is increased in populations subject to greater environmental variability, total number of tool forms, and thereby technical variants, falls within a tight range significantly beneath that exhibitted by hominins (see results Section 7.2.3).

As one candidate example of an early technology approaching the threshold, or 'tipping point' to cumulative metaplastic change, among the Oldowan technological complex, the ability to consistently produce a flaked lithic cutting-edge, used to process large vertebrate prey, combines a novel and highly rewarding (i.e. maximally constitutive) function ('to cut or incise') with a persistent tool material. Increased dietary breadth and access to high value resources of protein and fat would

otherwise unachievable, with rewards which directly enhance adaptive success of the individual (e.g. bow and arrow use, or fire making tools in colder climates).

provide a significant energetic advantage, postulated to have fueled increased brain growth (Aiello & Wheeler, 1995; Domínguez-Rodrigo et al., 2014), as well as potential social rewards in instances of group resource sharing, postulated to promote prosociality and leading to periodic population-expansion (Matás & Yravedra, 2022; Speth, 2010; Tomasello et al., 2012); yet would have offset by significant risk, including (1) low or unreliable encounter rate, potentially exacerbated in the case of hunting by (2) unreliable rates of return, (3) injury incurred through hunting activity, and (4) increased inter-species competition with other carnivores, leading to (5) increased predation risk. A positive feedback loop between the positive rewards of tool use, and increasing ability to mitigate risk via the metaplastic of these rewards (for example, via increased prosociality and trust), is likely to have reinforced the perceptual relevance of technological investment, (for example, more complex manufacture and higher levels of tool curation), and dependency leading to, as Toth & Schick describe the pattern of Oldowan sites after 2mya, a "substantial immersion into culturally mediated, tool-centred adaptation, which enterred into complex interplay with cognitive evolution" (2018, p. 27). Evidence which could support a theory of greater technical investment includes the appearance of Oldowan sites in a greater number of localities, tool 'curation' [e.g. of spheroids and pounders demonstrating heavy long-term reuse (Schick & Toth, 1994; Toth & Schick, 2018)], and increasing tool complexity over time [e.g. a trend from simple flakes towards those with greater levels of retouch, and larger flakes produced from larger cores (Braun & Harris, 2003, 2009; Toth & Schick, 2018)].

Rather than explaining later-stage tool kit/form specialisation, the role of risk on NHP technical engagement, or indeed any minimally consitutive form of material culture, maybe simply be to exacerbate predisposed manipulative behaviours, or the perceived relevance of functional object affordances, leading to the manifestation of tool using, or among populations where tool use is already prevalent, instantiation of specific, more complex tool using behaviours, e.g. nut-cracking at Bossou (Sanz & Morgan, 2013; Yamakoshi, 1998). Among macaques, populational isolation and the increased survival challenges associated with island habitats, in combination with increased

processing of encased/shelled food resources, are hypothesised to have manifested complex tool using from a pre-existing, innate predisposition for stone handling and object play (Tan, 2017; Gumert et al., 2019). Risks associated with processing of motile prey may also explain the relative specialisation of macaque lithic tool forms – *M.f.aurea* being the only species to engage in lithic tool use to consistently target live, mobile prey, and to use multiple lithic tool forms to the same ends.

Conclusion

8.1 Summary

This thesis has applied a material engagement theory framework to explore complexity and causal cognition in NHP tool using. Case-studies of *P.troglodytes*, *S.libidinosus*, and *M.f.aurea* support a view of technical cognition as an ontological process extended beyond the mind and individual, with a number of implications for the use of non-human primate species as comparative models for hominin technical/intellectual evolution. As argued in chapters 1 and 2, conflict between anthropocentric and ecological agendas mean that 'tool use' and 'cognition' have become inherently unstable concepts (Preston, 1998; Bayne et al., 2019). Even as approaches have shifted away from classic anthropocentric notions of symbolism and the intelligent capacity for internal representation/computation as defining features of tool using, continuing explicit assumptions that tool use is a phenomenon apart from either body or environment implicitly beg the same question of technical cognition and the mind. With technical cognition divorced from mechanical action, by the very nature of the problem, it is impossible to conceive how animals think, or even if they do. The ontogenetic niche, though recognised as important, is limitted to its interpretation as an empty causal shell, a flexible, but essentially a-cognitive mold for cognitive development. By recognising the mind and techncial cognition as developmental processes of becoming, emergent through interaction, MET enables a research perspective in which animal minds, rather than needing invocation, can be constituted by their particular modes of being in the world. Tools, environmental objects, and even other con-specifics, are not viewed as merely causal to cognition, but as consitutive to it. The ontogenetic niche is an overarching, and multi-vectored, temporality of mind, in which an individual's single instance of tool using is but one cross-section, and for which cumulative culture is but a momentary trajectory.

In taking the body *as* the mind, an unavoidable consequence of the MET conceptual framework includes a recognition of different non-human primates' tool-using as constituted by fundamentally different cognitive processes. Consequently, the value of cross-species comparison should not be seen as in the 'recreation' of the cognitive features of a 'Last common ancestor', or such-like, but in the potential for general insight into how cognitive technical processes unfold as a product of the transactional relationship between organisms and their material environments. In this respect, it is also a conclusion of this thesis that traditional hypotheses of primate technical evolution, by failing to integrate mind with matter, provide insufficient explanation for *how* tool use occurs, and the link between technical and cognitive development. In the Neo-Darwinist framework, whether an adaptive or epiphenomenal response to a social or environmental problem, the requisite cognitive capacities for tool-use are seen to precede their behavioural application (e.g. Fox, Van Schaik, Sitompul, & Wright, 2004; Parker & Gibson, 1977); environmental constraints are argued to act as causal *selective* forces, justifying *why* tool using occurs, but neglecting explanation of *how* it is organisms come to be susceptible to solicitation by tool affordances in the first place. Reframed in light of the MET framework, environmental problems are seen as situational attitudes of the environment-organism system. Opportunity, resource scarcity, and other material factors of risk, are less drivers of cognitive evolution, so much as they are constitutive parts of it; increasing or decreasing the relevance of tool using affordances (e.g. Grund *et al.*, 2019), as they increase or decrease contexts for their discovery (e.g. Koops, Visalberghi, & Van Schaik, 2014).

A multi-temporal developmental framework like metaplasticity, applied to the concept of tool use, demonstrates how simple material agencies and individual tool using processes can come together to produce emergent levels of cognitive complexity; helping to develop a theory on the nature of tool-using and technical cognition which is both generalist and species-specific, but above all, both fundamentally non-anthropocentric and non-individualistic. In so doing, the findings of this thesis are relevant to ongoing discussion both in the broader fields of anthropocentric cognitive archaeology and non-human evolutionary psychology surrounding the nature of organism-

environmental relationships, and their role in the shaping of tool ontogeny and technical cognition/behaviour.

8.2 Constraints of the current framework and future directions

The results of the case-studies included in this thesis suggest that shifting of the cognigram method outside of the head can provide a potentially useful methodology for future studies wishing to make use of the MET framework in order to operationalise complexity in behaviour/cognitive systems, or to explore changes in style or performance across populations or over time. One fallback of the methodological framework developed by this thesis is its degree of resolution, which is too low to pick out variation in the complexity between the different NHP variants. Alternatively, it may simply be that low-variation is a characteristic of the kind of technical engagement NHP tool use constitutes – something which seems likely given that other methodologies have previously arrived at similarly limitted results (McGrew, 1987; Westergaard, 1995).If so, the methodology would benefit from an expansion of the *kinds* of tool using included (e.g. including more permanent tool forms, or tool forms which are more maximally constitutive to cognition). The focus, in this case, might be on identifying potential past tipping points in the relationship between aspects of variant complexity and tool permanance, and degrees of constitution. For example, does degree of constitution scaffold particular aspects of variant complexity, and is there a limit to this effect? Might tool permanance reflect this limit? If so, can this account for low variance among tool forms with a lower degree of material-cognitive constitution?

Another interesting avenue for potential future research could be simulative modelling of attention direction in affordance landscapes to explore how tool materiality and socio-ecology could foster or scaffold the development of partiuclar technological patterns, through affordance encounter rate and likelihood of uptake. Alternatively, a similar framework could be applied to hominin archaeological sites: exploring the relationship depositional pattern and types of material,

with tool repertoire richness and heterogeneity, strictness or flexibility, association and permanance of tool forms.

Abraham, W. C. and Bear, M. F. (1996) 'Metaplasticity: the plasticity of synaptic plasticity', *Trends in Neurosciences*, 19(4), pp. 126–130. doi: 10.1016/S0166-2236(96)80018-X.

Adams, F. and Aizawa, K. (2010a) 'Defending the bounds of cognition', in Menary, R. (ed.) *The extended mind*. Cambridge, MA: MIT Press, pp. 67–80.

Adams, F. and Aizawa, K. (2010b) *The bounds of cognition*. Malden, MA: Blackwell.

Adebidi Sowunmi, M. (1999) 'The significance of the oil palm (Elaeis guineensis Jacq.) in the late Holocene environments of west and west central Africa', *Vegetation History and Archaeobotany*, 8(3), pp. 199–210. doi: 10.1007/bf02342720.

Adler, J. and Tso, W. W. (1974) '"Decision"-making in bacteria: Chemotactic response of escherichia coli to conflicting stimuli', *Science*, 184, pp. 1292–1294. doi: 10.1126/science.184.4143.1292.

Adolph, K. E. (2020) 'An ecological approach to learning in (not and) development', *Human Development*, 63((S3-4)), pp. 180–201. doi: 10.1159/000503823.

Adolph, K. E. and Kretch, K. S. (2015) 'Gibson's Theory of Perceptual Learning', in Wright, J. D. (ed.) *International Encyclopedia of the Social & Behavioral Sciences*. 2nd edn. Oxford: Elsevier, pp. 127–134. doi: 10.1016/B978-0-08-097086-8.23096-1.

Aiello, L., & Wheeler, P. (1995). The expensive tissue hypothesis: The brain and the digestive system in humans and primate evolution. *Current Anthropology*, *36*(2), 199–221. https://doi.org/10.1086/204350

Albrecht, H. and Dunnett, S. C. (1971) *Chimpanzees in Western Africa*. Munich: R. Piper & Co.

Allen, C. (2017) 'On (not) defining cognition', *Synthese*, 194, pp. 4233–4249. doi: 10.1007/s11229-

017-1454-4.

Almeida-Warren, K. *et al.* (2017) 'Raw material procurement for termite fishing tools by wild chimpanzees in the Issa valley, Western Tanzania', *American Journal of Physical Anthropology*, 164(2), pp. 292–304. doi: 10.1002/ajpa.23269.

Altmann, S. A. (1956) 'Avian Mobbing Behavior and Predator Recognition', *The Condor*, 58(4), pp. 241–253. doi: 10.2307/1364703.

Ambrose, S. H. (2001) 'Paleolithic technology and human evolution', *Science*, 291(5509), pp. 1748–1753. doi: 10.1126/science.1059487.

Anderson, J. R., Williamson, E. A. and Carter, J. (1983) 'Chimpanzees of Sapo forest, Liberia: Density, nests, tools, and meat-eating', *Primates*, 24(4), pp. 594–601. doi: 10.1007/bf02381692.

Andrews, K. (2014) *The animal mind: An introduction to the philosophy of animal cognition*. London: Routledge.

Arbib, M. A., Liebal, K. and Pika, S. (2008) 'Primate vocalization, gesture, and the evolution of human language.', *Current anthropology*, 49(6), pp. 1053–1076. doi: 10.1086/593015.

Arroyo, A. *et al.* (2021) 'Use-wear and residue analysis of pounding tools used by wild capuchin monkeys (Sapajus libidinosus) from Serra da Capivara', *Journal of Archaeological Science: Reports*, 35, p. 102690. doi: 10.1016/j.jasrep.2020.102690.

Audouze, F. (2002) 'Leroi-Gouhran, a philosopher of technique and evolution', *Anthropological Research*, 10(4), pp. 277–306.

Avarguès-Weber, A., Dawson, E. H. and Chittka, L. (2013) 'Mechanisms of social learning across species boundaries', *Journal of Zoology*, 290(1), pp. 1–11. doi: 10.1111/jzo.12015.

Baber, C., Parekh, M. and Cengiz, T. G. (2014) 'Tool use as distributed cognition: How tools help,

hinder and define manual skill', *Frontiers in Psychology*, 5, p. 116. doi: 10.3389/fpsyg.2014.00116.

Baddeley, A. D., Thomson, N. and Buchanan, M. (1975) 'Word length and the structure of short-term memory', *Journal of Verbal Learning and Verbal Behavior*, 14(6), pp. 575–589. doi: 10.1016/S0022-5371(75)80045-4.

Baggs, E. and Chemero, A. (2021) 'Radical embodiment in two directions', *Synthese*, 198(s9), pp. 2175–2190. doi: https://doi.org/10.1007/s11229-018-02020-9.

Bar-Yosef, O. (2002) 'The upper Paleolithic revolution', *Annual Review of Anthropology*, 31, pp. 363–393. doi: 10.1146/annurev.anthro.31.040402.085416.

Barad, K. (2003) 'Posthumanist performativity. Toward an understanding of how matter comes to matter', *Signs. Journal of women in culture and society*, 28(3), pp. 801–831. doi: doi.org/10.1086/345321.

Barad, K. (2007) *Meeting the universe halfway*. Durham, NC: Duke University Press.

Barrett, B. J. *et al.* (2018) 'Habitual stone-tool-aided extractive foraging in white-faced capuchins, Cebus capucinus', *Royal Society Open Science*, 5(8), p. 181002. doi: 10.1098/rsos.181002.

Barrett, L. (2015) 'A better kind of continuity', *Southern Journal of Philosophy*, 53(Spindel supplement), pp. 28–49. doi: 10.1111/sjp.12123.

Barrett, L., Gaynor, D. and Henzi, S. P. (2002) 'A dynamic interaction between aggression and grooming reciprocity among female chacma baboons', *Animal Behaviour*, 63(6), pp. 1047–1053. doi: https://doi.org/10.1006/anbe.2002.3008.

Barrett, L. and Henzi, P. (2005) 'The social nature of primate cognition', *Proceedings of the Royal Society B: Biological Sciences*, 272(1575), pp. 1865–1875. doi: 10.1098/rspb.2005.3200.

Barrett, L., Henzi, P. and Rendall, D. (2007) 'Social brains, simple minds: Does social complexity really

require cognitive complexity?', *Philosophical Transactions of the Royal Society B: Biological Sciences*, 362(1480), pp. 561–575. doi: 10.1098/rstb.2006.1995.

Bartecki, U. and Heymann, E. W. (1987) 'Field observation of snake-mobbing in a group of saddle-back tamarins, Saguinus fuscicollis nigrifons', *Folia Primatologica*, 48(3–4), pp. 199–202. doi: 10.1159/000156296.

Barton, R. (2006) 'Chimp comparisons won't explain human evolution', *Nature*, 443(7112), p. 632. doi: 10.1038/443632d.

Bateson, G. (1973) *Steps to an Ecology of Mind. Collected essays in anthropology, psychiatry, evolution, and epistemology*. St Albans: Paladin.

Bayne, T. *et al.* (2019) 'What is cognition?', *Current Biology*, 29(13), pp. R608–R615. doi: 10.1016/j.cub.2019.05.044.

Beck, B. B. (1980) *Animal Tool Behaviour*. New York: Garland.

Bender, A. (2020) 'What Is Causal Cognition?', *Frontiers in Psychology*, 11, p. 3. doi: 10.3389/fpsyg.2020.00003.

Benito-Calvo, A. *et al.* (2015) 'First GIS analysis of modern stone tools used by wild chimpanzees (Pan troglodytes verus) in Bossou, Guinea, West Africa', *PLoS ONE*, 10(3), p. e0121613. doi: 10.1371/journal.pone.0121613.

Bensa, A. and Creswell, R. (1996) 'A propos de la technologie culturelle: Entretion avec Robert Creswell', *Genesis*, 24(1), pp. 120–136.

Bermejo, M. and Illera, G. (1999) 'Tool-set for termite-fishing and hone extraction by wild chimpanzees in the Lossi Forest, Congo', *Primates*, 40(4), pp. 619–627. doi: 10.1007/BF02574837.

Bingham, G. P., Schmidt, R. C. and Rosenblum, L. D. (1989) 'Hefting for a maximum distance throw: A

smart perceptual mechanism', *Journal of Experimental Psychology: Human Perception and Performance*, 15(3), pp. 507–528. doi: 10.1037/0096-1523.15.3.507.

Biro, B., Haslam, M. and Rutz, C. (2013) 'Tool use as adaptation', *Phil Trans R Soc B: Biological Sciences*, 368(1639), p. 20120408. doi: 10.1098/rstb.2012.0408.

Biro, D., Sousa, C. and Matsuzawa, T. (2006) 'Ontogeny and cultural propagation of tool use by wild chimpanzees at Bossou, Guinea: Case studies in nut cracking and leaf folding', in Matsuzawa, T., Tomonaga, M., and Tanaka, M. (eds) *Cognitive Development in Chimpanzees*. Tokyo: Springer, pp. 468–508. doi: https://doi.org/10.1007/4-431-30248-4_28.

Boden, M. A. (1994) 'Précis of the creative mind: Myths and mechanisms', *Behavioral and Brain Sciences*, 17(3), pp. 519–531. doi: 10.1017/S0140525X0003569X.

Boden, M. A. (1996) 'Creativity', in Boden, M. A. (ed.) *Artificial Intelligence: A handbook in perception and cognition*. San Diego: Academic Press, pp. 267–291. doi: 10.1016/B978-012161964-0/50011-X.

Boesch, C. (1991a) 'Handedness in wild chimpanzees', *International Journal of Primatology*, 12(6), pp. 541–558. doi: 10.1007/bf02547669.

Boesch, C. (1991b) 'Teaching among wild chimpanzees', *Animal Behaviour*, 41, pp. 530–532. doi: 10.1016/S0003-3472(05)80857-7.

Boesch, C. *et al.* (1994) 'Is nut cracking in wild chimpanzees a cultural behaviour?', *Journal of Human Evolution*, 26(4), pp. 325–338. doi: 10.1006/jhev.1994.1020.

Boesch, C. (1995) 'Innovation in wild chimpanzees (Pan troglodytes)', *International Journal of Primatology*, 16(1), pp. 1–16. doi: 10.1007/bf02700150.

Boesch, C. (2013) 'Ecology and cognition of tool use in chimpanzees', in Sanz, C. M. and Boesch, C. (eds) *Tool use in animals Cognition and ecology*. Cambridge: Cambridge University Press, pp. 21–47.

Boesch, C. *et al.* (2016) 'Chimpanzees routinely fish for algae with tools during the dry season in Bakoun, Guinea', *American Journal of Primatology*, 9999, pp. 1–7. doi: 10.1002/ajp.22613.

Boesch, C. *et al.* (2017) 'Technical intelligence and culture: Nut cracking in humans and chimpanzees', *American Journal of Physical Anthropology*, 163(2), pp. 339–355. doi: 10.1002/ajpa.23211.

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

Boesch, C. and Boesch, H. (1981) 'Sex differences in the use of natural hammers by wild chimpanzees: A preliminary report', *Journal of Human Evolution*, 10, pp. 585–593. doi: 10.1016/s0047-2484(81)80049-8.

Boesch, C. and Boesch, H. (1983) 'Optimisation of nut-cracking with natural hammers by wild chimpanzees', *Behaviour*, 83(3–4), pp. 265–286. doi: 10.1163/156853983x00192.

Boesch, C. and Boesch, H. (1989) 'Hunting behaviour of wild chimpanzees in the Tai National Park', *American Journal of Physical Anthropology*, 78(4), pp. 547–573. doi: 10.1002/ajpa.1330780410.

Boesch, C. and Boesch, H. (1990) 'Tool use and tool making in wild chimpanzees', *Folia Primatologica*, 54, pp. 86–99. doi: 10.1159/000156428.

Boesch, C., Head, J. and Robbins, M. M. (2009) 'Complex tool sets for honey extraction among chimpanzees in Loango National Park, Gabon', *Journal of Human Evolution*, 56(6), pp. 560–569. doi: 10.1016/j.jhevol.2009.04.001.

Boesch, C. and Tomasello, M. (1998) 'Chimpanzee and human cultures', *Current Anthropology*, 39(5), pp. 591–614. doi: 10.1086/204785.

Bogart, S. L. and Pruetz, J. D. (2011) 'Insectivory of savanna chimpanzees (Pan troglogytes verus) at Fongoli, Senegal', *American Journal of Physical Anthropology*, 145(1), pp. 11–20. doi:

10.1002/ajpa.21452.

Boinski, S. (1988) 'Use of a club by a wild white-faced capuchin (Cebus capucinus) to attack a venomous snake (Bothrops asper)', *American Journal of Primatology*. doi: 10.1002/ajp.1350140208.

Borgo, S. *et al.* (2013) 'Artifact and artifact categorization: Comparing humans and capuchin monkeys', *Review of Philosophy and Psychology*, 4, pp. 375–389. doi: 10.1007/s13164-013-0144-5.

Borgo, S. and Vieu, L. (2006) 'From physical artefacts to products', in *2nd International Workshop on Formal Ontologies Meet Industry, FOMI 2006*. Institute of Cognitive Sciences and Technologies, ISTC-CNR, pp. 85–99.

Borgo, S. and Vieu, L. (2009) 'Artefacts in formal ontology', *Philosophy of Technology and Engineering Sciences*, pp. 273–307. doi: 10.1016/B978-0-444-51667-1.50015-X.

Bourdieu, P. (1977) *Outline of a theory of practice*, *Outline of a Theory of Practice*. Edited by R. Nice. New York: Cambridge University Press. doi: 10.1017/cbo9780511812507.

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

Boyd, R. and Richerson, P. J. (1996) 'Why culture is common, but cultural evolution is rare', in Runciman, W. G., Smith, J. M., and Dunbar, R. I. M. (eds) *Evolution of social behaviour patterns in primates and man*. Oxford: Oxford University Press, pp. 77–93. doi: citeulike-article-id:1339814.

Braun, D. R., & Harris, J. W. K. (2003). Technological developments in the Oldowan of Koobi Gora: Innovative techniques of artifact analysis. In J. M. Moreno, R. M. Torcal, & I. T. Sainz (Eds.), *Oldowan: Rather more than smashing stones* (pp. 117–144). University of Autonoma Press.

Braun, D. R., & Harris, J. W. K. (2009). Plio-Pleistocene technological variation: A view from the KBS member, Koobi Fora formation. In K. Schick & N. Toth (Eds.), *The cutting edge: New approaches to the archaeology of human origins* (pp. 17–31). Stone Age Institute.

Breuer, T., Ndoundou-Hockemba, M. and Fishlock, V. (2005) 'First observation of tool use in wild gorillas', *PLoS Biology*, 3(11), p. e380. doi: 10.1371/journal.pbio.0030380.

Brezillon, M. (1968) *La Denomination des Objets de Pierre Taillee*. Paris: Centre National de la Reherche Scientifique.

Bril, B. *et al.* (2009) 'Tool use as a way to assess cognition: How do captive chimpanzees handle the weight of the hammer when cracking a nut?', *Animal Cognition*, 12(2), pp. 217–235. doi: 10.1007/s10071-008-0184.

Bril, B. *et al.* (2012) 'Functional mastery of percussive technology in nut-cracking and stone-flaking actions: Experimental comparison and implications for the evolution of the human brain', *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365(1585), pp. 59–74. doi: 10.1098/rstb.2011.0147.

Bril, B., Dietrich, G. and Hirata, S. (2011) 'A Gibsonian motor analysis of the nut-cracking technique', in Matsuzawa, T., Humle, T., and Sugiyama, Y. (eds) *The chimpanzees of Bossou and Nimba. Primatology monographs*. Tokyo: Springer, pp. 191–199.

Bruineberg, J., Chemero, A. and Rietveld, E. (2019) 'General ecological information supports engagement with affordances for "higher" cognition', *Synthese*, 196(12), pp. 5231–5251. doi: 10.1007/s11229-018-1716-9.

Bryson-Morrison, N. *et al.* (2017) 'Activity and habitat use of chimpanzees (Pan troglodytes verus) in the anthropogenic landscape of Bossou, Guinea, West Africa', *International Journal of Primatology*, 38, pp. 282–302. doi: 10.1007/s10764-01609947-4.

Bunnin, N. and Yu, J. (2004) *The Blackwell dictionary of western philosophy*. Oxford: Blackwell.

Butynski, T. M. (1982) 'Vertebrate predation by primates: A review of hunting patterns and prey', *Journal of Human Evolution*, 11(5), pp. 421–430. doi: 10.1016/S0047-2484(82)80095-X.

Byers, J. A. and Walker, C. (1995) 'Refining the motor training hypothesis for the evolution of play', *American Naturalist*, 146(1), pp. 25–40. doi: 10.1086/285785.

Byrne, R. W. (1997) 'The Technical Intelligence hypothesis: An additional evolutionary stimulus to intelligence?', in Whiten, A. and Byrne, R. W. (eds) *Machiavellian intelligence II*. Cambridge: Cambridge University Press, pp. 289–311.

Byrne, R. W. *et al.* (2017) 'Great ape gestures: Intentional communication with a rich set of innate signals', *Animal Cognition*, 20, pp. 755–769. doi: 10.1007/s10071-017-1096-4.

Byrne, R. W. and Byrne, J. M. E. (1993) 'Complex leaf-gathering skills of mountain gorillas (Gorilla g. beringei): Variability and standardization', *American Journal of Primatology*, 31(4), pp. 241–261. doi: 10.1002/ajp.1350310402.

Byrne, R. W., Corp, N. and Byrne, J. M. E. (2001) 'Estimating the complexity of animal behaviour: How mountain gorillas eat thistles', *Behaviour*, 138(4), pp. 525–557. doi: 10.1163/156853901750382142.

Byrne, R. W. and Whiten, A. (1988) *A machiavellian intelligence: Social expertise and the evolution of intellect in monkeys, apes, and humans*. Oxford: Clarendon Press.

Call, J. *et al.* (2003) 'Domestic Dogs (Canis familiaris) Are Sensitive to the Attentional State of Humans', *Journal of Comparative Psychology*, 117(3), pp. 257–263. doi: 10.1037/0735-7036.117.3.257.

Call, J. (2013) 'Three ingredients for becoming a creative tool user', in Sanz, C. M., Call, J., and Boesch, C. (eds) *Tool Use in Animals Cognition and Ecology*. Cambridge: Cambridge University Press, pp. 3–20. doi: 10.1017/CBO9780511894800.

Call, J., Carpenter, M. and Tomasello, M. (2005) 'Copying results and copying actions in the process of social learning: Chimpanzees (Pan troglodytes) and human children (Homo sapiens)', *Animal*

Cognition, 8(3), pp. 151–163. doi: 10.1007/s10071-004-0237-8.

Call, J. and Tomasello, M. (2007) *The gestural communication of apes and monkeys*. Mahwah: Psychology Press.

Cantalupo, C. and Hopkins, W. (2010) 'The cerebellum and its contribution to complex tasks in higher primates: A comparative perspective', *Cortex*, 46(7), pp. 821–830. doi: 10.1016/j.cortex.2009.10.004.

Cardoso, R. M. and Ottoni, E. B. (2016) 'The effects of tradition on problem solving by two wild populations of bearded capuchin monkeys in a probing task', *Biology letters*, 12, p. 20160604. doi: 10.1098/rsbl.2016.0604.

Caro, T. M. and Hauser, D. (1992) 'Is there teaching in nonhuman animals?', *The Quarterly Review of Biology*, 67(2), pp. 151–174. doi: 10.1086/417553.

Carosi, M., Linn, G. S. and Visalberghi, E. (2005) 'The Sexual Behavior and Breeding System of Tufted Capuchin Monkeys (Cebus apella)', *Advances in the Study of Behavior*, pp. 105–149. doi: 10.1016/S0065-3454(05)35003-0.

Carosi, M. and Visalberghi, E. (2002) 'Analysis of tufted capuchin (Cebus apella) courtship and sexual behaviour repertoire: Changes throughout the female cycle and female interindividual differences', *American Journal of Primatology*, 118, pp. 11–24. doi: 10.1002/ajpa.10083.

Carpenter, A. (1887) 'Monkeys opening oysters.', *Nature*, 36, p. 53. doi: 10.1038/036053d0.

Carvalho, S. *et al.* (2008) 'Chaînes opératoires and resource-exploitation strategies in chimpanzee (Pan troglodytes) nut cracking', *Journal of Human Evolution*, 55(1), pp. 148–163. doi: 10.1016/j.jhevol.2008.02.005.

Carvalho, S. *et al.* (2009) 'Tool-composite reuse in wild chimpanzees (Pan troglodytes): Archaeologically invisible steps in the technological evolution of early hominins?', *Animal Cognition*, 12(S1), pp. S103–S114. doi: 10.1007/s10071-009-0271-7.

Carvalho, S. *et al.* (2010) 'Bird in the hand: Bossou chimpanzees (Pan troglodytes) capture West African wood-owls (Ciccaba woodfordi) but not to eat', *Pan Africa News*, 17(1), pp. 6–9. doi: 10.5134/143514.

Carvalho, S. (2011) 'Extensive surveys of chimpanzee stone tools: From the telescope to the magnifying glass', in Matsuzawa, T., Humle, T., and Sugiyama, Y. (eds) *The chimpanzees of Bossou and Nimba. Primatology monographs*. Tokyo: Springer, pp. 145–155.

Carvalho, S., Sousa, C. and Matsuzawa, T. (2007) 'New nut-cracking sites in Diecké Forest, Guinea: An overview of the surveys', *Pan Africa News*, 14(1), pp. 11–13. doi: 10.5134/143472.

Castles, D. L., Whiten, A. and Aureli, F. (1999) 'Social anxiety, relationships and self-directed behaviour among wild female olive baboons', *Animal Behaviour*, 58(6), pp. 1207–1215. doi: 10.1006/anbe.1999.1250.

Cavalli-Sforza, L. L. and Feldman, M. W. (1981) *Cultural transmission and evolution: A quantitative approach*. Princeton, NJ: Princeton University Press.

Chaitin, G. J. (1966) 'On the Length of Programs for Computing Finite Binary Sequences', *Journal of the ACM (JACM)*, 13(4), pp. 547–569. doi: 10.1145/321356.321363.

Chaitin, G. J. (1975) 'A Theory of Program Size Formally Identical to Information Theory', *Journal of the ACM (JACM)*, 22(3), pp. 329–340. doi: 10.1145/321892.321894.

Chakrabaty, M. (2018) 'How stone tools shaped us: Post-phenomenology and material engagement theory', *Philosophy and Technology*, 32(2), pp. 243–264. doi: https://doi.org/10.1007/s13347-018-0310-x.

Chase, P. G. (2016) 'Form, function, and mental templates in Paleolithic Archaeology', in Sullivan III, A. P. and Olszewski, D. I. (eds) *Archaeological variability and interpretation in global perspective*. Boulder, CO: University Press of Colorado, pp. 291–305.

Chemero, A. (2009) *Radical embodied cognition*. Cambridge, MA: MIT Press.

Chevalier-Skolnikoff, S. (1990) 'Tool use by wild cebus monkeys at Santa Rosa National Park, Costa Rica', *Primates*, 31, pp. 375–383. doi: 10.1007/bf02381108.

Childe, G. (1933) *Man makes himself*. London: Watts.

Christensen, C. B. *et al.* (2012) 'Hearing with an atympanic ear: Good vibration and poor sound-pressure detection in the royal python, Python regius', *Experimental Biology*, 215(2), pp. 331–342. doi: 10.1242/jeb.062539.

Cladiere, N. and Whiten, A. (2012) 'Integrating the study of conformity and culture in humans and nonhuman animals', *Psychological Bulletin*, 138(1), pp. 126–145. doi: 10.1037/a0025868.

Clark, A. (1997) *Being There: Bringing Brain, Body and World Together Again*. Cambridge: MIT Press.

Clark, A. (1999) 'An embodied cognitive science?', *Trends in Cognitive Sciences*, pp. 345–351. doi: 10.1016/S1364-6613(99)01361-3.

Clark, A. (2008) *Supersizing the mind: Embodiment, action, and cognitive extension*. New York: Oxford University Press.

Clark, A. (2010) 'Coupling, constitution, and the cognitive kind: A reply to Adams and Aizawa', in Menary, R. (ed.) *The extended mind*. Cambridge, MA: MIT Press, pp. 81–89.

Clark, A. and Chalmers, D. (1998) 'The extended mind', *Analysis*, pp. 7–19. doi: 10.1093/analys/58.1.7.

Cleveland, A. *et al.* (2003) 'Throwing behaviour and mass distribution of stone selection in tufted capuchin monkeys (Cebus apella)', *American Journal of Primatology*, 61(4), pp. 159–172. doi: 10.1002/ajp.10120.

Coelho, C. G. *et al.* (2015) 'Social learning strategies for nut-cracking by tufted capuchin monkeys

(Sapajus spp.)', *Animal Cognition*, 18(4), pp. 911–919. doi: 10.1007/s10071-015-0861-5.

Coolidge, F. L. and Wynn, T. (2005) 'Working memory, its executive functions, and the emergence of modern thinking', *Cambridge Archaeological Journal*, 15(1), pp. 5–26. doi: 10.1017/S0959774305000016.

Coolidge, F. L. and Wynn, T. (2007) 'The working memory account of Neandertal cognition-How phonological storage capacity may be related to recursion and the pragmatics of modern speech', *Journal of Human Evolution*, 52(6), pp. 707–710. doi: 10.1016/j.jhevol.2007.01.003.

Cooper, L. H. and Harlow, H. F. (1961) 'Note on a Cebus monkey's use of a stick as a weapon', *Psychological Reports*, 8(3), p. 418. doi: 10.2466/pr0.1961.8.3.418.

Costall, A. (1995) 'Socializing affordances', *Theory & Psychology*, 5(4), pp. 467–481. doi: 10.1177/0959354395054001.

Costall, A. (2004) 'From Darwin to Watson (and cognitivism) and back again: The principle of animal-environment mutuality', *Behaviour and Philosophy*, 32(1), pp. 179–195. doi: Retrieved from http://www.jstor.org/stable/27759477.

Costall, A. (2008) 'Bringing the body back to life: James Gibson's ecology of agency', in Ziemke, T. and Frank, R. . (eds) *Cognitive Linguistics Research, 35.1: Body, Language and Mind, vol.1*. Berlin: Mouton de Gruyter, pp. 1–16.

Costall, A. (2012) 'Canonical affordances in context', *Avant: Trends in Interdisciplnary Studies*, 3(2), pp. 85–93.

Costall, A. (2014) 'Canonical affordances and creative agency', in Glaveanu, V. P., Gillespie, A., and Valsiner, J. (eds) *Rethinking Creativity: Contributions from Social and Cultural Psychology*. London: Routledge, pp. 69–81. doi: 10.4324/9781315866949.

Cottingham, J. (1978) '"A brute to the brutes?": Descartes' treatment of animals', *Philosophy*,

53(206), pp. 551–559. doi: 10.1017/s0031819100026371.

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

Cowan, N. (2001) 'The magical number 4 in short-term memory: A reconsideration of mental storage capacity', *Behavioral and Brain Sciences*, 24, pp. 87–114. doi: 10.1017/S0140525X01003922.

Crofoot, M. C. (2012) 'Why mob? Reassessing the costs and benefits of primate predator harassment', *Folia Primatologica*, 83(3–6), pp. 252–273. doi: 10.1159/000343072.

Curio, E. (1978) 'Adaptive significance of avian mobbing. I.', *Zeitschrift fur Tierpsychologie*, 48(2), pp. 175–183. doi: 10.1111/j.1439-0310.1978.tb00254.x.

Darwin, C. (1880) *Descent of man and selection in relation to sex*. New York: D. Appleton & Company.

Dean, L. G. *et al.* (2014) 'Human cumulative culture: A comparative perspective', *Biological Reviews*, 89(2), pp. 284–301. doi: 10.1111/brv.12053.

Deetz, J. (1967) *Invitation to archaeology*. Garden City, NJ: American Science Books. Natural History Press.

Deleuze, G. and Strauss, J. (1991) 'The fold', *Yale French Studies*, 80, pp. 227–247. doi: 10.2307/2930269.

Devos, C., Gatti, S. and Levreo, F. (2002) 'New record of algae feeding and scooping by Pan t. troglodytes at Lokoue Bai in Odzala National Park, Republic of Congo', *Pan Africa News*, 9(2), pp. 19–21. doi: 10.5134/143415.

Dibble, H. L. (1987) 'The interpretation of Middle Paleolithic scraper morphology', *American Antiquity*, 52(1), pp. 109–117. doi: 10.2307/281062.

van Dijk, L. and Rietveld, E. (2017) 'Foregrounding sociomaterial practice in our understanding of affordances: The skilled intentionality framework', *Frontiers in Psychology*. doi: 10.3389/fpsyg.2016.01969.

Domínguez-Rodrigo, M., et al. (2014). On meat eating and human evolution: A taphonomic analysis of BK4b (Upper Bed II, Olduvai Gorge, Tanzania), and its bearing on hominin megafaunal consumption. *Quaternary International*, *322–323*, 129–152. https://doi.org/10.1016/j.quaint.2013.08.015

Dougherty, J. W. D. and Kellar, C. M. (1982) 'Taskonomy: A practical approach to knowledge structures', *American Ethnologist*, 9(4), pp. 763–774. doi: 10.1525/ae.1982.9.4.02a00090.

Duboscq, J. *et al.* (2016) 'Scatch that itch: Revisiting links between self-directed behaviour and parasitological, social and environmental factors in a free-ranging primate', *Royal Society Open Science*, 3, p. 160571. doi: 10.1098/rsos.160571.

Dugatkin, L. A. and Godin, J. J. (1992) 'Prey approaching predators: A cost-benefit perspective', *Annales Zoologici Fennici*, 29(4), pp. 233–252. Available at: http://www.jstor.org/stable/23735625.

Dunbar, R. I. M. (1991) 'Functional significance of social grooming in primates', *Folia Primatologica*, 57, pp. 121–131. doi: 10.1159/000156574.

Dunbar, R. I. M. (1998) 'The social brain hypothesis', *Evolutionary Anthropology*, 6(5), pp. 178–190. doi: 10.1002/(SICI)1520-6505(1998)6:5<178::AID-EVAN5>3.0.CO;2-8.

Dunbar, R. I. M. (2010) 'The social role of touch in humans and primates: behavioural function and neurobiological mechanisms.', *Neuroscience and biobehavioral reviews*. United States, 34(2), pp. 260–268. doi: 10.1016/j.neubiorev.2008.07.001.

Dunbar, R. I. M., Gamble, C. and Gowlett, J. (2010) 'The social brain and distributed mind', in Dunbar, R., Gamble, C., and Gowlett, J. (eds) *Social Brain, Distributed Mind2*. Oxford: Oxford University Press,

pp. 3–13.

Dunbar, R. I. M. and Shultz, S. (2007) ‘Evolution in the social brain’, *Science*, 317(5843), pp. 1344–1347. doi: 10.1126/science.1145463.

Elton, S. (2006) ‘Forty years on and still going strong: The use of hominin-cercopithecid comparisons in palaeoanthropology’, *Journal of the Royal Anthropological Institute*, pp. 19–38. doi: 10.1111/j.1467-9655.2006.00279.x.

Emidio, R. A. and Ferreira, R. G. (2012) ‘Energetic Payoff of Tool Use for Capuchin Monkeys in the Caatinga: Variation by Season and Habitat Type’, *American Journal of Primatology*, 74(4), pp. 332–43. doi: 10.1002/ajp.22009.

Eshchar, Y. *et al.* (2016) ‘When and where to practice: social influences on the development of nut-cracking in bearded capuchins (Sapajus libidinosus)’, *Animal Cognition*, 19(3), pp. 605–618. doi: 10.1007/s10071-016-0965-6.

Essler, J. L. *et al.* (2017) ‘Capuchin monkeys’ use of human and conspecific cues to solve a hidden object-choice task.’, *Animal Cognition*, pp. 985–998. doi: 10.1007/s10071-017-1118-2.

Estienne, V. *et al.* (2019) ‘Acquisition of a complex extractive technique by the immature chimpanzees of Loango National Park, Gabon’, *Animal Behaviour*, 147, pp. 61–76. doi: 10.1016/j.anbehav.2018.11.002.

Evans, T. and Westergaard, G. C. (2004) ‘Discrimination of functionally appropriate and inappropriate throwing tools by captive tufted capuchins (Cebus apella)’, *Animal Cognition*, 7(4), pp. 255–262. doi: 10.1007/s10071-004-0220-4.

Falótico, T. (2011) *Uso de ferramentas por macacas-prego (Sapajus libidinosus) do Parque Nacional Serra da Capivara*. Universidade de Sao Paulo.

Falótico, T., Spagnoletti, N., *et al.* (2017) ‘Analysis of sea almond (Terminalia catappa) cracking sites

used by wild Burmese long-tailed macaques (Macaca fascicularis aurea)', *American Journal of Primatology*, 79, p. e22629. doi: 10.1002/ajp.22629.

Falótico, T., Luncz, L. V., *et al.* (2017) 'Cashew Nut Positioning during Stone Tool Use by Wild Bearded Capuchin Monkeys (Sapajus libidinosus)', *Folia Primatologica*, 76(6), pp. 392–397. doi: 10.1159/000459621.

Falótico, T., Verderane, M. P., *et al.* (2018) 'Food or threat? Wild capuchin monkeys (Sapajus libidinosus) as both predators and prey of snakes', *Primates*, 59, pp. 99–106. doi: 10.1007/s10329-017-0631-x.

Falótico, T., Coutinho, P. H. M., *et al.* (2018) 'Stone tool use by wild capuchin monkeys (Sapajus libidinosus) at Serra das Confusões National Park, Brazil', *Primates*, 59(4), pp. 385–394. doi: 10.1007/s10329-018-0660-0.

Falótico, T. *et al.* (2019) 'Three thousand years of wild capuchin stone tool use', *Nature Ecology and Evolution*, 3, pp. 1034–1038. doi: 10.1038/s41559-019-0904-4.

Falótico, T. and Ottoni, E. B. (2013) 'Stone throwing as a sexual display in wild female bearded capuchin monkeys, Sapajus libidinosus', *PLoS ONE*, 8(11), p. e79535. doi: 10.1371/journal.pone.0079535.

Falótico, T. and Ottoni, E. B. (2014) 'Sexual bias in probe tool manufacture and use by wild bearded capuchin monkeys', *Behavioural Processes*, 108, pp. 117–122. doi: 10.1016/j.beproc.2014.09.036.

Falótico, T. and Ottoni, E. B. (2016) 'The manifold use of pounding stone tools by wild capuchin monkeys of Serra da Capivara National Park, Brazil', *Behaviour*, 153(4), pp. 421–442. doi: 10.1163/1568539X-00003357.

Falótico, T., Siqueira, J. O. and Ottoni, E. B. (2017) 'Digging up food: Excavation stone tool use by wild capuchin monkeys', *Scientific Reports*, 7(1), p. 6278. doi: 10.1038/s41598-017-06541-0.

Fay, J. M. and Carroll, R. W. (1994) ‘Chimpanzee tool use for honey and termite extraction in central AfricaF’, *American Journal of Primatology*, 33, pp. 309–317. doi: 10.1002/ajp.1350340403.

Fedigan, L. M. (1990) ‘Vertebrate predation in Cebus capucinus: Meat eating in a neotropical monkey’, *Folia Primatologica*, 54(3–4), pp. 196–205. doi: 10.1159/000156444.

Feldman, J. (2000) ‘Minimization of Boolean complexity in human concept learning’, *Nature*, 407(6804), pp. 630–633. doi: 10.1038/35036586.

Feldman, J. (2006) ‘An algebra of human concept learning’, *Journal of Mathematical Psychology*, 50(4), pp. 339–368. doi: 10.1016/j.jmp.2006.03.002.

Ferreira, R. G., Emidio, R. A. and Jerusalinsky, L. (2010) ‘Three stones for three seeds: Natural occurrence of selective tool use by capuchins (Cebus libidinosus) based on an analysis of the weight of stones found at nutting sites’, *American Journal of Primatology*, 72(3), pp. 270–275. doi: 10.1002/ajp.20771.

Figma (2019) ‘Figma’. Available at: www.figma.com.

Fisher, N. (2017) ‘Kant on animal minds’, *Ergo*, 4(15), pp. 441–462. doi: 10.3998/ergo.12405314.0004.015.

FitzGibbon, C. D. (1994) ‘The costs and benefits of predator inspection behaviour in Thomson’s gazelles’, *Behavioural Ecology and Sociobiology*, 34(2), pp. 139–148. doi: 10.1007/BF00164184.

Fooden, J. (1995) *Systematic review of southeast asian longtail macaques, Macaca fasciculatis (Raffles, (1821))*, *Fieldiana Zoology new series*. Chicago, IL.

Foucart, J. *et al.* (2005) ‘A preliminary analysis of nut-cracking movement in a captive chimpanzee: Adaptation to the properties of tools and nuts’, in Roux, V. and Bril, B. (eds) *Stone knapping: The necessary conditions for a uniquely hominid behaviour*. Cambridge: McDonald Institure of Archaeological Research, pp. 147–157.

Fowler, A. and Sommer, V. (2007) 'Subsistence technology of Nigerian chimpanzees', *International Journal of Primatology*, 28, pp. 997–1023. doi: 10.1007/s10764-007-9166-0.

Fox, E. A., Sitompul, A. F. and van Schaik, C. P. (1999) 'Intelligent tool use in wild Sumatran orangutans', in Parker, S. T., Mitchell, R. W., and Miles, H. L. (eds) *The mentality of gorillas and orangutans*. Cambridge: Cambridge University Press, pp. 99–166.

Fox, E. B. A. *et al.* (2004) 'Intra-and interpopulational differences in orangutan (Pongo pygmaeus) activity and diet: Implications for the invention of tool use', *American Journal of Physical Anthropology*, 125(2), pp. 162–174. doi: 10.1002/ajpa.10386.

Fragaszy, D. M. *et al.* (2004) 'Wild capuchin monkeys (Cebus libidinosus) use anvils and stone pounding tools', *American Journal of Primatology*, 64(4), pp. 359–366. doi: 10.1002/ajp.20085.

Fragaszy, D. M. *et al.* (2010) 'How wild bearded capuchin monkeys select stones and nuts to minimize the number of strikes per nut cracked', *Animal Behaviour*, 80, pp. 205–214. doi: 10.1016/j.anbehav.2010.04.018.

Fragaszy, D. M. (2011) 'Community resources for learning: How capuchin monkeys construct technical traditions', *Biological Theory*, 6, pp. 231–240. doi: 10.1007/s13752-012-0032-8.

Fragaszy, D. M., Biro, D., *et al.* (2013) 'The fourth dimension of tool use: Temporally enduring artefacts aid primates learning to use tools', *Philosophical Transactions of the Royal Society B: Biological Sciences*, 368, p. 20120410. doi: 10.1098/rstb.2012.0410.

Fragaszy, D. M., Lui, Q., *et al.* (2013) 'Wild bearded capuchin monkeys (Sapajus libidinosus) strategically place nuts in a stable position during nut-cracking', *PLoS ONE*, 8, p. e56182.

Fragaszy, D. M. *et al.* (2017) 'Synchronized practice helps bearded capuchin monkeys learn to extend attention while learning a tradition', *Proceedings of the National Academy of Sciences of the United States of America*, 114(30), pp. 7798–7805. doi: 10.1073/pnas.1621071114.

Fragaszy, D. M. *et al.* (2019) 'How bearded capuchin monkeys (Sapajus libidinosus) prepare to use a stone to crack nuts', *American Journal of Primatology*, 81(3), p. e22958. doi: 10.1002/ajp.22958.

Fragaszy, D. M. *et al.* (2020) 'Adult and juvenile bearded capuchin monkeys handle stone hammers differently during nut-cracking', *American Journal of Primatology*, 82(7), p. e23156. doi: 10.1002/ajp.23156.

Fragaszy, D. M. and Adams-Curtis, L. E. (1991) 'Generative aspects of manipulation in tufted capuchin monkeys (Cebus apella)', *Journal of Comparative Psychology*, 105(4), pp. 387–397. doi: 10.1037/0735-7036.105.4.387.

Fragaszy, D. M. and Visalberghi, E. (2004) 'Socially biased learning in monkeys', *Learning and Behavior*, 32, pp. 24–35. doi: 10.3758/bf03196004.

Fragaszy, D. M., Visalberghi, E. and Fedigan, L. M. (2004) *The complete capuchin: The biology of the genus Cebus*. Cambridge: Cambridge University Press.

Froese, T. (2015) 'Enactive neuroscience, the direct perception hypothesis, and the socially extended mind', *Behavioral and Brain Sciences*, 38, p. e75. doi: 10.1017/S0140525X14000892.

Froese, T. and Leavens, D. A. (2014) 'The direct perception hypothesis: Perceiving the intention of another's action hinders its precise imitation', *Frontiers in Psychology*, 5, p. 65. doi: 10.3389/fpsyg.2014.00065.

Frohlich, M., Wittig, R. M. and Pika, S. (2016) 'Play-solicitation gestures in chimpanzees in the wild: Flexible adjustment to social circumstances and individual matrices', *Royal Society Open Science*, 3(8), p. 160278. doi: 10.1098/rsos.160278.

Furuichi, T. *et al.* (2015) 'Why do wild bonobos not use tools like chimpanzees do?', *Behaviour*, 152(3–4), pp. 425–460. doi: 10.1163/1568539X-00003226.

Fushimi, T. *et al.* (1991) 'Nut-cracking behaviour of wild chimpanzees (Pan troglodytes) in Bossou,

Guinea (West Africa)', in Ehara, A. et al. (eds) *Primatology Today*. Amsterdam: Elsevier Science B.V., pp. 695–696.

Gallagher, S. (2005) *How the body shapes the mind*. New York: Oxford University Press.

Gallagher, S. (2015) 'The new hybrids: Continuing debates on social perception', *Consciousness and Cognition*, 36, pp. 452–465. doi: 10.1016/j.concog.2015.04.002.

Gärdenfors, P. and Lombard, M. (2018) 'Causal cognition, force dynamics and early hunting technologies', *Frontiers in Psychology*, 9, p. 87. doi: 10.3389/fpsyg.2018.00087.

Garzón, P. C. and Keijzer, F. (2011) 'Plants: Adaptive behavior, root-brains, and minimal cognition', *Adaptive Behavior*, 19, pp. 155–171. doi: 10.1177/1059712311409446.

van Gelder, T. (1995) 'What might cognition be, if not computation', *The Journal of Philosophy*, 92(7), pp. 345–381.

Gell, A. (1998) *Art and agency: an anthropological theory*. Oxford: Clarendon Press.

Gibson, E. J. (1963) 'Perceptual learning', *Annual Review of Psychology*, 14, pp. 29–56. doi: 10.1146/annurev.ps.14.020163.000333.

Gibson, E. J. (1994) 'Has psychology a future?', *Psychological Science*, 5, pp. 69–76. doi: https://doi.org/10.1111/j.1467-9280.1994.tb00633.x.

Gibson, E. J. and Pick, A. D. (2000) *An ecological approach to perceptual learning and development*. New York, NY: Oxford University Press.

Gibson, J. J. (1979) *The Ecological Approach to Visual Perception*. Boston: Houghton Mifflin.

Gibson, K. R. (1986) 'Cognition, brain size, and the extraction of embedded resources', in Lee, P. C. and Else, J. G. (eds) *Primate ontogeny, cognition, and social behaviour*. Cambridge: Cambridge University Press, pp. 93–104.

Gilbert, S. F., Bosch, T. C. G. and Ledón-Rettig, C. (2015) 'Eco-Evo-Devo: Developmental symbiosis and developmental plasticity as evolutionary agents', *Nature Reviews Genetics*, 16(10), pp. 611–622. doi: 10.1038/nrg3982.

Glock, H. (2017) 'Wittgenstein and Davidson on animal minds', in Verheggen, C. (ed.) *Wittgenstein and Davidson on language, thought, and action*. Cambridge: Cambridge University Press, pp. 159–185.

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

Goodall, J. (1968) 'The behaviour of free-living chimpanzees of the Gombe Stream area', *Animal Behaviour Monographs*, 201(1), pp. 163–311. doi: 10.1016/s0066-1856(68)80003-2.

Goodall, J. (1986) *The chimpanzees of Gombe*. Cambridge: Belknap Press.

Gottlieb, G. (2002) 'Probabalistic epigenesis of development', in Valsiner, J. and Connolly, K. J. (eds) *Handbook of Developmental Psychology*. London: Sage, pp. 3–17. doi: 10.4135/9781848608306.n1.

Gottlieb, G. (2007) 'Probabalistic epigenesis', *Developmental Science2*, 10(1), pp. 1–11. doi: 10.1111/j.1467-7687.2007.00556.x.

Govier, E. (2019) 'Do you follow? Rethinking causality in archaeology', *Archaeological Dialogoues*, 26(1), pp. 51–55. doi: 10.1017/s1380203819000047.

Gowlett, J. A. J. (1979) 'Complexities of cultural evidence in the Lower and Middle Pleistocene', *Nature*, 278(5699), pp. 14–17. doi: 10.1038/278014b0.

Gowlett, J. A. J. (1984) 'Mental abilities of early man: A look at some hard evidence', *Higher Education Quarterly*, 38(3), pp. 199–220. doi: 10.1111/j.1468-2273.1984.tb01387.x.

Gowlland, G. (2019) 'The sociality of enskilment', *Ethnos*, 84(3), pp. 508–524. doi:

10.1080/00141844.2018.1455726.

Greuter, C. C. *et al.* (2013) 'Possible tool use in a mountain gorilla', *Behavioural Processes2*, 100, pp. 160–162. doi: 10.1016/j.beproc.2013.09.006.

Griffiths, P. E. *et al.* (2010) 'Probabilistic models of cognition: Exploring representations and inductive biases', *Trends in Cognitive Sciences*, 14(8), pp. 357–364. doi: 10.1016/j.tics.2010.05.004.

Griffiths, P. E. and Stotz, K. (2000) 'How the mind grows: A developmental perspective on the biology of cognition', *Synthese*, 122(1/2), pp. 29–51. doi: 10.1023/a:1005215909498.

Gruber, T. *et al.* (2011) 'Community-specific evaluation of tool affordances in wild chimpanzees', *Scientific Reports*, 1, p. 128. doi: 10.1038/srep00128.

Gruber, T. *et al.* (2012) 'The influence of ecology on chimpanzee (Pan troglodytes) cultural behavior: A case study of five ugandan chimpanzee communities', *Journal of Comparative Psychology*, 126(4), pp. 446–457. doi: 10.1037/a0028702.

Gruber, T. (2013) 'Historical hypotheses of chimpanzee tool use behaviour in relation to natural and human-induced changes in an East African rain forest', *Revue de primatologie*, 5, p. document 66. doi: 10.4000/primatologie.1690.

Gruber, T. *et al.* (2015) 'The spread of a novel behavior in wild chimpanzees: New insights into the ape cultural mind', *Communicative and Integrative Biology*, 8(2), p. e1017164. doi: 10.1080/19420889.2015.1017164.

Gruber, T., Clay, Z. and Zuberbühler, K. (2010) 'A comparison of bonobo and chimpanzee tool use: Evidence for a female bias in the Pan lineage', *Animal Behaviour*, 80(6), pp. 1023–1033. doi: 10.1016/j.anbehav.2010.09.005.

Gruber, T., Zuberbühler, K. and Neumann, C. (2016) 'Travel fosters tool use in wild chimpanzees', *eLife*, 5, p. e16371. doi: 10.7554/eLife.16371.

Grund, C. *et al.* (2019) 'Necessity creates opportunities for chimpanzee tool use', *Behavioral Ecology*, 30(4), pp. 1136–1144. doi: 10.1093/beheco/arz062.

Gumert, M. D. *et al.* (2019) 'Prevalence of tool behaviour is associated with pelage phenotype in intraspecific hybrid long-tailed macaques (Macaca fascicularis aurea × M. f. fascicularis)', *Behaviour*, 156(11), pp. 1083–1125. doi: 10.1163/1568539X-00003557.

Gumert, M. D., Hamada, Y. and Malaivijitnond, S. (2013) 'Human activity negatively affects stone tool-using Burmese long-tailed macaques Macaca fascicularis aurea in Laem Son National Park, Thailand', *ORYX*, 47(4), pp. 535–543. doi: 10.1017/S0030605312000130.

Gumert, M. D., Hoong, L. K. and Malaivijitnond, S. (2011) 'Sex differences in the stone tool-use behavior of a wild population of burmese long-tailed macaques (Macaca fascicularis aurea)', *American Journal of Primatology*, 73(12), pp. 1239–1249. doi: 10.1002/ajp.20996.

Gumert, M. D., Kluck, M. and Malaivijitnond, S. (2009) 'The physical characteristics and usage patterns of stone axe and pounding hammers used by long-tailed macaques in the Andaman sea region of Thailand', *American Journal of Primatology*, 71(7), pp. 594–608. doi: 10.1002/ajp.20694.

Gumert, M. D. and Malaivijitnond, S. (2012) 'Marine prey processed with stone tools by burmese long-tailed macaques (Macaca fascicularis aurea) in intertidal habitats', *American Journal of Physical Anthropology*, 149(3), pp. 447–457. doi: 10.1002/ajpa.22143.

Gumert, M. D. and Malaivijitnond, S. (2013) 'Long-tailed macaques select mass of stone tools according to food type', *Philosophical Transactions of the Royal Society B: Biological Sciences*, 368(1630), p. 20120413. doi: 10.1098/rstb.2012.0413.

Gumert, M. D., Tan, A. Y. and Malaivijitnond, S. (2019) 'Long-tailed macaque stone tool use in intertidal habitats', in Nowak, K., Barnett, A. A., and Matsuda, I. (eds) *Primates in flooded habitats*. Cambridge: Cambridge University Press, pp. 144–147.

Gunther, M. and Boesch, C. (1993) 'Energetic cost of nut-cracking behaviour in wild chimpanzees', in Preuschoft, H. and Chivers, D. (eds) *Hands of the primates*. Vienna: Springer, pp. 109–129.

Haidle, M. N. (2009) 'How to think a simple spear', in de Beaune, S. A., Coolidge, F. L., and Wynn, T. (eds) *Cognitive Archaeology and human evolution*. Cambridge: Cambridge University Press, pp. 57–73.

Haidle, M. N. (2010) 'Working-Memory Capacity and the Evolution of Modern Cognitive Potential', *Current Anthropology*, 51(S1), pp. S149–S166. doi: 10.1086/650295.

Haidle, M. N. (2014) 'Building a bridge: An archeologist's perspective on the evolution of causal cognition', *Frontiers in Psychology*, 5, p. 1472. doi: 10.3389/fpsyg.2014.01472.

Hall, K. R. L. (1963) 'Tool-using performances as indicators of behavioural adaptivity', *Current Anthropology*, 4(5), pp. 479–494. doi: 10.1086/200419.

Hamilton, C. and Fragaszy, D. M. (2014) 'Observation of weapon use in a group of semi-free tufted capuchins (Sapajus spp)', *Neotropical Primates*, 21(2), pp. 198–200. doi: 10.1896/044.021.0208.

Haslam, M. *et al.* (2009) 'Primate archaeology', *Nature*, 460, pp. 339–344. doi: 10.1038/nature08188.

Haslam, M. *et al.* (2013) 'Use-Wear Patterns on Wild Macaque Stone Tools Reveal Their Behavioural History', *PLoS ONE*, 8(8), p. e72872. doi: 10.1371/journal.pone.0072872.

Haslam, M. *et al.* (2014) 'Stone anvil damage by wild bearded capuchins (Sapajus libidinosus) during pounding tool use: A field experiment', *PLoS ONE*, 9(11), p. e111273. doi: 10.1371/journal.pone.0111273.

Haslam, M., Luncz, L. V, *et al.* (2016) 'Archaeological excavation of wild macaque stone tools', *Journal of Human Evolution*, 96, pp. 134–138. doi: 10.1016/j.jhevol.2016.05.002.

Haslam, M., Pascual-Garrido, A., *et al.* (2016) 'Stone tool transport by wild Burmese long-tailed macaques (Macaca fascicularis aurea)', *Journal of Archaeological Science: Reports*, 7, pp. 408–413. doi: 10.1016/j.jasrep.2016.05.040.

Haslam, M. *et al.* (2017) 'Primate archaeology evolves', *Nature Ecology and Evolution*, 1, pp. 1431–1437. doi: 10.1038/s41559-017-0286-4.

Haslam, M. and Falótico, T. (2015) 'Nasal probe and toothpick tool use by a wild female bearded capuchin (Sapajus libidinosus)', *Primates*, 56(3), pp. 211–214. doi: 10.1007/s10329-015-0470-6.

Hattori, Y., Kuroshima, H. and Fujita, K. (2006) 'I know you are not looking at me: capuchin monkeys' (Cebus apella) sensitivity to human attentional states', *Animal Cognition*, 10(2), p. 141. doi: 10.1007/s10071-006-0049-0.

Hattori, Y., Kuroshima, H. and Fujita, K. (2010) 'Tufted capuchin monkeys (Cebus apella) show understanding of human attentional states when requesting food held by a human.', *Animal cognition*. Germany, 13(1), pp. 87–92. doi: 10.1007/s10071-009-0248-6.

Hayashi, M. and Inoue-Nakamura, N. (2011) 'From handling stones and nuts to tool-use', in Matsuzawa, T., Humle, T., and Sugiyama, Y. (eds) *The chimpanzees of Bossou and Nimba. Primatology monographs*. Tokyo: Springer, pp. 175–182.

Heidegger, M. (1927/1996) *Being and time. A translation of Sein und Zeit*. Edited by J. Stambaugh. New York: State University of New York Press.

Henare, A., Holbraad, M. and Wastell, S. (2007) 'Introduction', in Henare, A., Holbraad, M., and Wastell, S. (eds) *Thinking through things: theorising artefacts ethnographically*. London: Routledge. doi: 10.4324/97080203088791.

Henrich, J. (2004) 'Demography and Cultural Evolution: How Adaptive Cultural Processes Can Produce Maladaptive Losses—The Tasmanian Case', *American Antiquity*, 69(2), pp. 197–214. doi:

10.2307/4128416.

Henshilwood, C. S. *et al.* (2002) 'Emergence of modern human behavior: Middle stone age engravings from South Africa', *Science*, 295(5558), pp. 1278–1280. doi: 10.1126/science.1067575.

Henshilwood, C. S., D'Errico, F. and Watts, I. (2009) 'Engraved ochres from the Middle Stone Age levels at Blombos Cave, South Africa', *Journal of Human Evolution*, 57(1), pp. 27–47. doi: 10.1016/j.jhevol.2009.01.005.

Hernandez-Aguilar, R. A., Moore, J. and Pickering, T. R. (2007) 'Savanna chimpanzees use tools to harvest the underground storage organs of plants', *Proceedings of the National Academy of Sciences*, 104(49), pp. 19210–19213. doi: 10.1073/pnas.0707929104.

Heyes, C. M. (1993) 'Imitation, culture and cognition', *Animal Behaviour*, 46(5), pp. 999–1010. doi: 10.1006/anbe.1993.1281.

Heylighen, F., Cilliers, P. and Gershenson, C. (2007) 'Complexity and philosophy', in Bogg, J. and Geyer, R. (eds) *Complexity, science and society*. Oxford: Radcliffe Publishing, pp. 117–134.

Hicks, T. C. *et al.* (2019) 'Bili-Uéré: A Chimpanzee Behavioural Realm in Northern Democratic Republic of Congo', *Folia Primatologica*, 26(2), pp. 19–20. doi: 10.1159/000492998.

Hicks, T. C. *et al.* (2020) 'The relationship between tool use and prey availability in chimpanzees (Pan troglodytes schweinfurthii) of Northern Democratic Republic of Congo', *International Journal of Primatology*, 41, pp. 936–959. doi: 10.1007/s10764-020-00149-4.

Hirata, S. *et al.* (2001) 'Capturing and toying with hyraxes (Dendrohyrax dorsalis) by wild chimpanzees (Pan troglodytes) at Bossou, Guinea', *American Journal of Primatology*, 53(2), pp. 93–97. doi: 10.1002/1098-2345(200102)53:2<93::aid-ajp5>3.0.co;2-x.

Hirata, S., Myowa, M. and Matsuzawa, T. (1998) 'Use of leaves as cushions to sit on wet ground by wild chimpanzees', *American Journal of Primatology*, 44, pp. 215–220. doi: 10.1002/(SICI)1098-

2345(1998)44:3<215::AID-AJP4>3.0.CO;2-Z.

Hobaiter, C. *et al.* (2014) 'Social network analysis shows direct evidence for social transmission of tool use in wild chimpanzees', *PLoS Biology*, 12(9), p. e1001960. doi: 10.1371/journal.pbio.1001960.

Hobaiter, C. and Byrne, R. W. (2011) 'The gestural repertoire of the wild chimpanzee', *Animal Cognition*, 14(5), pp. 745–767. doi: 10.1007/s10071-011-0409-2.

Hobaiter, C. and Byrne, R. W. (2014) 'The meanings of chimpanzee gestures', *Current Biology*, 24(14), pp. 1596–1600. doi: 10.1016/j.cub.2014.05.066.

Hockings, K. J. *et al.* (2015) 'Tools to tipple: Ethanol ingestion by wild chimpanzees using leaf-sponges', *Royal Society Open Science*, 2(6), p. 150150. doi: 10.1098/rsos.150150.

Hockings, K. J., Anderson, J. and Matsuzawa, T. (2009) 'Use of wild and cultivated foods by chimpanzees at Bossou, Republic of Guinea: Feeding dynamics in a human-influenced environment', *American Journal of Primatology*, 71(8), pp. 636–646. doi: 10.1002/ajp.20698.

Hodder, I. (2011) 'Human-thing entanglement: towards an integrated archaeological perspective', *Journal of the Royal Anthropological Institute*, 17(1), pp. 154–177. doi: 10.1111/j.1467-9655.2010.01674.x.

Hodder, I. (2012) *Entangled: An Archaeology of the Relationships between Humans and Things*, *Entangled: An archaeology of the relationships between humans and things*. Chichester: John Wiley and Sons, Inc. doi: 10.1002/9781118241912.

Hohmann, G. and Fruth, B. (2003) 'Culture in Bonobos? Between-species and within-species variation in behavior', *Current Anthropology*, 44(4), pp. 563–571. doi: 10.1086/377649.

Holzhaider, J. C., Hunt, G. R. and Gray, R. D. (2010) 'The development of pandanus tool manufacture in wild New Caledonian crows', *Behaviour*, 147(5–6), pp. 553–586. doi: 10.1163/000579510X12629536366284.

Hopkins, W. D., Russell, J. L. and Schaeffer, J. A. (2012) 'The neural and cognitive correlates of aimed throwing in chimpanzees: A magnetic resonnce image and behavioural study on a unique form of social tool use', *Phil Trans R Soc B*, 367(1585), pp. 37–47. doi: 10.1098/rstb.2011.0195.

Hoppitt, W. *et al.* (2008) 'Lessons from animal teaching', *Trends in Ecology and Evolution*, 23(9), pp. 486–493. doi: 10.1016/j.tree.2008.05.008.

Hoppitt, W. and Laland, K. N. (2013) *Social learning: an introduction to mechanisms, methods, and models*. Princeton, NJ: Princeton University Press.

Horner, V. *et al.* (2010) 'Prestige affects cultural learning in chimpanzees', *PLoS ONE*, 5(5), p. e10625. doi: 10.1371/journal.pone.0010625.

Hovers, E. (2009) 'Learning from mistakes: Flaking accidents and knapping skills in the assemblage of A.L 894, Hadar, Ethiopia', in Schick, K. and Toth, N. (eds) *The cutting edge: New approaches to the archaeology of human origins.* Gosport, Indiana: Stone Age Institute.

Hrubesch, C., Preuschoft, S. and van Schaik, C. P. (2009) 'Skill mastery inhibits adoption of observed alternative solutions among chimpanzees (Pan troglodytes)', *Animal Cognition*, 12, p. 209. doi: 10.1007/s10071-008-0183-y.

Huber, L. *et al.* (2009) 'The evolution of imitation: What do the capacities of non-human animals tell us about the mechanisms of imitation?', *Philosophical Transactions of the Royal Society B: Biological Sciences*, 364(1528), pp. 2299–2309. doi: 10.1098/rstb.2009.0060.

Huffman, M. A. and Kalunde, M. S. (1993) 'Tool-assisted predation on a squirrel by a female chimpanzee in the Mahale Mountains, Tanzania', *Primates*, 34(1), pp. 93–98. doi: 10.1007/bf02381285.

Huffman, M. A. and Quiatt, D. (1986) 'Stone handling by Japanese macaques (Macaca fuscata): Implications for tool use of stone', *Primates*, 27(4), pp. 413–423. doi: 10.1007/BF02381887.

Humle, T. (1999) ‘New record of fishing for termites (Macrotermes) by the chimpanzees of Bossou (Pan troglodytes verus), Guinea.’, *Pan Africa News*, 6(1), pp. 3–4. doi: 10.5134/143394.

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

Humle, T. (2006) ‘Ant dipping in chimpanzees: An example of how microecological variables, tool use, and culture reflect the cognitive abilities of chimpanzees’, in Matsuzawa, T., Tomonaga, M., and Tanaka, M. (eds) *Cognitive Development in Chimpanzees*. Tokyo: Springer, pp. 452–475. doi: 10.1007/4-431-30248-4_27.

Humle, T. (2010) ‘How are army ants shedding new light on culture in chimpanzees?’, in Lonsdorf, E. V, Ross, S., and Matsuzawa, T. (eds) *The mind of the chimpanzee: Ecological and experimental perspectives*. Chicago, IL: Chicago University Press, pp. 116–126.

Humle, T. (2011a) ‘Ant-dipping: How ants have shed light on culture’, in Matsuzawa, T., Humle, T., and Sugiyama, Y. (eds) *The chimpanzees of Bossou and Nimba. Primatology monographs*. Tokyo: Springer, pp. 97–106. doi: 10.1007/978-4-431-53921-6_10.

Humle, T. (2011b) ‘Location and ecology’, in Matsuzawa, T., Humle, T., and Sugiyama, Y. (eds) *The chimpanzees of Bossou and Nimba. Primatology monographs*. Tokyo: Springer, pp. 13–21.

Humle, T. (2011c) ‘The Tool Repertoire of Bossou Chimpanzees’, in Matsuzawa, T., Humle, T., and Sugiyama, Y. (eds) *The chimpanzees of Bossou and Nimba: Primatology monographs*. Tokyo: Springer, pp. 61–71. doi: 10.1007/978-4-431-53921-6_7.

Humle, T. and Matsuzawa, T. (2002) ‘Ant-dipping among the chimpanzees of Bossou, Guinea, and some comparisons with other sites’, *American Journal of Primatology*, 58(3), pp. 133–148. doi: 10.1002/ajp.10055.

Humle, T. and Matsuzawa, T. (2004) ‘Oil palm use by adjacent communities of chimpanzees at

Bossou and Nimba Mountains, West Africa', *International Journal of Primatology*, 25(3), pp. 551–581. doi: 10.1023/b:ijop.0000023575.93644.f4.

Humle, T., Snowdon, C. T. and Matsuzawa, T. (2009) 'Social influences on ant-dipping acquisition in the wild chimpanzees (Pan troglodytes verus) of Bossou, Guinea, West Africa', *Animal Cognition*, 12(S1), pp. 37–48. doi: 10.1007/s10071-009-0272-6.

Humle, T., Yamakoshi, G. and Matsuzawa, T. (2011) 'Algae Scooping Remains a Puzzle', in Matsuzawa, T., Humle, T., and Sugiyama, Y. (eds) *The chimpanzees of Bossou and Nimba: Primatology monographs*. Tokyo: Springer, pp. 117–122.

Humphrey, N. (1976) 'The social function of intellect', in Bateson, P. P. G. and Hinde, R. A. (eds) *Growing points in ethology*. Cambridge: Cambridge University Press, pp. 303–317.

Hunt, G. R. (1996) 'Manufacture and use of hook-tools by New Caledonian crows', *Nature*, pp. 249–251. doi: 10.1038/379249a0.

Hunt, G. R. and Gray, R. D. (2004) 'Direct observations of pandanus-tool manufacture and use by a New Caledonian crow (Corvus moneduloides)', *Animal Cognition*, 7(2), pp. 114–120. doi: 10.1007/s10071-003-0200-0.

Hunt, G. R., Gray, R. D. and Taylor, A. H. (2013) 'Why is tool use rare in animals?', in Sanz, C. M., Call, J., and Boesch, C. (eds) *Tool Use in Animals Cognition and Ecology*. Cambridge: Cambridge University Press, pp. 89–118. doi: 10.1017/CBO9780511894800.007.

Husserl, E. (1931/2012) *Ideas: General introduction to pure phenomenology*, *Ideas: General introduction to pure phenomenology*. London: Routledge. doi: 10.4324/9780203120330.

Hutchins, E. (1995) *Cognition in the wild*. Cambridge, MA: MIT Press.

Hutchins, E. (2005) 'Distributed cognition', *Cognition, Technology & Work*, 7(1), pp. 5–5. doi: 10.1007/s10111-004-0172-0.

Hutto, D. and Myin, E. (2013) *Radicalizing enactivism: Basic minds without content*. Cambridge MA: MIT Press.

Hutto, D. and Myin, E. (2017) *Evolving enactivism: Basic minds meet content*. Cambridge, MA: MIT Press.

Ihde, D. (1979) *Technics and praxis*. Dordrecht, Holland ; Boston: D. Reidel Pub. Co.

Ihde, D. (1990) *Technology and the lifeworld: from garden to earth*. Bloomington: Indiana University Press.

Ihde, D. and Malafouris, L. (2019) 'Homo faber Revisited: Postphenomenology and Material Engagement Theory', *Philosophy and Technology*, 32, pp. 195–214. doi: 10.1007/s13347-018-0321-7.

Iliopoulos, A. and Garofoli, D. (2016) 'The material dimensions of cognition: Reexamining the nature and emergence of the human mind', *Quaternary International*, 405(A), pp. 1–136. doi: 10.1016/j.quaint.2016.04.031.

Ingold, T. (1993) 'Tool-use, sociality and intelligence', in Gibson, K. and Ingold, T. (eds) *Tools, Language and Cognition in Human Evolution*. Cambridge: Cambridge University Press, pp. 429–446.

Ingold, T. (2000) *The perception of the environment: Essays on livelihood, dwelling, and skill*. London: Routledge. doi: 10.1207/S15327884MCA0902.

Ingold, T. (2010a) *Bringing Things to life: Creative entanglements in a world of materials*, *Realities Working Paper 15*. Available at: https://eprints.ncrm.ac.uk/id/eprint/1306/1/0510_creative_entanglements.pdf.

Ingold, T. (2010b) *Making: anthropology, archaeology, art and architecture*. London: Routledge.

Ingold, T. (2012) 'Toward an ecology of materials', *Annual Review of Anthropology*, 41(1), pp. 427–442. doi: 10.1146/annurev-anthro-081309-145920.

Inoue-Nakamura, N. and Matsuzawa, T. (1997) 'Development of Stone Tool Use by Wild Chimpanzees (Pan troglodytes)', *Journal of Comparative Psychology*, 111(2), pp. 159–173. doi: 10.1037/0735-7036.111.2.159.

Isaac, G. L. L. (1972) 'Chronology and tempo of cultural change during the Pleistocene', in Bishop, W. W. and Miller, J. A. (eds) *Calibration of hominoid evolution*. New York: Wenner-Gren Foundation and Scottish Academic Press, pp. 381–430.

Izawa, K. (1978) 'Frog-eating behaviour of wild black-capped capuchin (Cebus apella)', *Primates*, 19(4), pp. 633–642. doi: 10.1007/bf02373631.

Izawa, K. (1979) 'Foods and feeding behaviour of wild black-capped capuchin (Cebus apella)', *Primates*, 20, pp. 57–76. doi: 10.1007/BF02373828.

Janson, C. H. (1984) 'Female choice and mating system of the brown capuchin monkey Cebus apella (Primates: Cebidae)', *Zeitschrift fur Tierpsychologie*, 65(3), pp. 177–200. doi: 10.1111/j.1439-0310.1984.tb00098.x.

Janson, C. H. (1986) 'The mating system as a determinant of social evolution in capuchin monkeys (Cebus)', in Else, J. G. and Lee, P. C. (eds) *Primate ecology and conservation*. New York, NY: Cambridge University Press, pp. 169–179.

Jerison, H. J. (1976) *Evolution of the brain and intelligence*. New York: Academic Press.

Johnson, C. M. (2000) 'Distributed primate cognition: A review', *Animal Cognition*, pp. 167–183. doi: 10.1007/s100710100077.

Johnson, C. M. and Oswald, T. M. (2001) 'Distributed cognition in apes', in *Proceedings of the Annual Meeting of the Cognitive Science Society*, pp. 167–183.

Johnson, S. E. and Bock, J. (2004) 'Trade-offs in skill acquisition and time allocation among juvenile chacma baboons', *Human Nature*, 15(1), pp. 45–62. doi: 10.1007/s12110-004-1003-y.

Jolly, A. (1966) ‘Lemurs social behaviour and primate intelligence’, *Science*, 153(3735), pp. 501–506. doi: 10.1126/science.153.3735.501.

Kagan, A. and Lassiter, C. (2013) ‘The coupling-constitution fallacy: Much ado about nothing’, *Pragmatics and Cognitioni*, 21(1), pp. 178–192. doi: https://doi.org/10.1075/pc.21.1.08kag.

Kahlenberg, S. M. *et al.* (2008) ‘Immigration costs for females chimpanzees and male protection as an immigrant counterstrategy to intrasexual aggression’, *Animal Behaviour*, 76(5), pp. 1479–1509. doi: 10.1016/j.anbehav.2008.05.029.

Kahlenberg, S. M. and Wrangham, R. W. (2010) ‘Sex differences in chimpanzees’ use of sticks as play objects resemble those of children’, *Current Biology*. doi: 10.1016/j.cub.2010.11.024.

Kalan, A. K. and Boesch, C. (2018) ‘Re-emergence of the leaf clip gesture during an alpha takeover affects variation in male chimpanzee loud calls’, *PeerJ*, 6, p. e5079. doi: 10.7717/peerj.5079.

Kant, I. (2001) *Lectures on metaphysics*. Edited by K. Americks and S. Naragon. Cambridge: Cambridge University Press.

Kassel, G. (2010) ‘A formal ontology of artefacts’, *Applied Ontology*, 5(3–4), pp. 223–246. doi: 10.3233/AO-2010-0078.

Keller, C. M. and Keller, J. D. (1996) *Cognition and tool-use: The blacksmith at work*. Cambridge: Cambridge University Press. doi: 10.2307/1215850.

Keller, J. D. and Keller, C. M. (1991) *Thinking and acting with iron*, *Beckman Institute Cognitive Science Technical Reports*. Urbana.

Kempf, E. (2009) ‘Patterns of water use in primates’, *Folia Primatologica*, 80(4), pp. 275–294. doi: 10.1159/000252586.

Kendal, J., Giraldeau, L. A. and Laland, K. (2009) ‘The evolution of social learning rules: Payoff-biased

and frequency-dependent biased transmission', *Journal of Theoretical Biology*, 260(2), pp. 210–219. doi: 10.1016/j.jtbi.2009.05.029.

Keverne, E. B., Martensz, N. D. and Tuite, B. (1989) 'Beta-endorphin concentrations in cerebrospinal fluid of monkeys are influenced by grooming relationships.', *Psychoneuroendocrinology*. England, 14(1–2), pp. 155–161. doi: 10.1016/0306-4530(89)90065-6.

Kinani, J. and Zimmerman, D. (2014) 'Tool use for food acquisition in a wild mountain gorilla', *American Journal of Primatology2*, 77(3), pp. 353–357. doi: 10.1002/ajp.22351.

Kirsh, D. (2006) 'Distributed cognition: A methodological note', *Pragmatics and Cognition*, 14(2), pp. 249–262. doi: 10.1075/pc.14.2.06kir.

Kiverstein, J. D. and Rietveld, E. (2015) 'The primacy of skilled intentionality: On Hutto & Satne's the Natural Origins of Content', *Philosophia*, 43(3), pp. 701–721. doi: 10.1007/s11406-015-9645-z.

Kiverstein, J. D. and Rietveld, E. (2018) 'Reconceiving representation-hungry cognition: an ecological-enactive proposal', *Adaptive Behavior*, 26(4), pp. 147–163. doi: 10.1177/1059712318772778.

Knappett, C. and Malafouris, L. (2008) *Material agency: towards a non-anthropocentric approach*. New York: Springer.

Kolmogorov, A. N. (1968) 'Three approaches to the definition of the concept of quantity of information', *International Journal of Computer Mathematics*, 2(1–4), pp. 157–168. doi: 10.1080/00207166808803030.

Kolodny, O., Creanza, N. and Feldman, M. W. (2015) 'Evolution in leaps: The punctuated accumulation and loss of cultural innovations', *Proceedings of the National Academy of Sciences of the United States of America*, 112(49), pp. E6762–E6769. doi: 10.1073/pnas.1520492112.

Koops, K., Schöning, C., Mcgrew, W. C., *et al.* (2015) 'Chimpanzees prey on army ants at Seringbara, Nimba Mountains, Guinea: Predation patterns and tool use characteristics', *American Journal of*

Primatology, 77(3), pp. 319–329. doi: 10.1002/ajp.22347.

Koops, K., Schöning, C., Isaji, M., *et al.* (2015) 'Cultural differences in ant-dipping tool length between neighbouring chimpanzee communities at Kalinzu, Uganda', *Scientific Reports*, 5, p. 12456. doi: 10.1038/srep12456.

Koops, K., Furuichi, T., *et al.* (2015) 'Sex differences in object manipulation in wild immature chimpanzees (Pan troglodytes schweinfurthii) and bonobos (Pan paniscus): Preparation for tool use?', *PLoS ONE*, 10(10), p. e0139909. doi: 10.1371/journal.pone.0139909.

Koops, K., Visalberghi, E. and Van Schaik, C. P. (2014) 'The ecology of primate material culture', *Biology Letters*, 11, p. 20140508. doi: 10.1098/rsbl.2014.0508.

Kortlandt, A. and Holzhaus, E. (1987) 'New data on the use of stone tools by chimpanzees in Guinea and Liberia', *Primates*, 28, pp. 473–496. doi: 10.1007/BF02380862.

Kronenfeld, D. B. (2014) 'What "causal cognition" might mean', *Frontiers in Psychology*, 5, p. 1204. doi: 10.3389/fpsyg.2014.01204.

Krützen, M., Willems, E. P. and Van Schaik, C. P. (2011) 'Culture and geographic variation in orangutan behavior', *Current Biology*, 21(21), pp. P1808-1812. doi: 10.1016/j.cub.2011.09.017.

Lakoff, G. and Johnson, M. (1999) *Philosophy in the flesh: the embodied mind and its challenge to Western thought*. New York: Basic Books.

Laland, K. N. and Galef, B. G. (2009) *The question of animal culture*. Cambridge, MA: Harvard University Press.

Laland, K. N., Odling-Smee, F. J. and Feldman, M. W. (2001) 'Niche construction, ecological inheritance, and cycles of contingency in evolution', in Omaya, S., Griffiths, P. E., and Gray, R. D. (eds) *Cycles of contingency: Developmental systems and evolution*. Cambridge, MA, pp. 117–126.

Lamon, N. *et al.* (2017) 'Kin-based cultural transmission of tool use in whild chimpanzees', *Science Advances*, 3(4), p. e1602750. doi: 10.1126/sciadv.1602750.

Lamon, N. *et al.* (2018) 'Wild chimpanzees select tool material based on efficiency and knowledge', *Proceedings of the Royal Society B: Biological Sciences*, 285, p. 20181715. doi: 10.1098/rspb.2018.1715.

Lashley, K. (1951) 'The problem of serial order in behavior', in Jeffress, L. A. (ed.) *Cerebral mechanisms in behavior*. New York, NY: Wiley, pp. 112–131.

Latour, B. (1993) *We have never been modern*. Cambridge MA: Harvard University Press.

Latour, B. (2014) 'Technical does not mean material. Comment on Lemmonnier, Pierre, 2012. Mundane objects: Materiality and non-verbal communication. Walnut Creek, CA: Left Coast Press, Hau', *Journal of Ethnographic Theory*, 4(1), pp. 507–510.

Latour, B. and Lemmonier, P. (1994) *De la prehistoire aux missiles balistiques: L'intelligence sociale des techniques*. Paris: Le Decouverte.

Lave, J. and Wenger, E. (1991) *Situated learning: legitimate peripheral participation*. Cambridge: Cambridge University Press.

van Lawick-Goodall, J. (1968) 'The behaviour of free-living chimpanzees in the Gombe Stream Reserve', *Animal Behaviour Monographs*, 1(3), pp. 161–311, IN1–IN12. doi: 10.1016/S0066-1856(68)80003-2.

Van Lawick-Goodall, J. (1971) 'Tool-Using in Primates and Other Vertebrates', *Advances in the Study of Behavior*, 3(C), pp. 195–249. doi: 10.1016/S0065-3454(08)60157-6.

Leca, J. B. *et al.* (2007) 'Japanese macaque cultures: Inter- and intra-troop behavioural variability of stone handling patterns across 10 troops', *Behaviour*, 144, pp. 251–281. doi: 10.1163/156853907780425712.

Leca, J. B. *et al.* (2008) 'Stone-throwing by Japanese macaques: form and functional aspects of a group-specific behavioral tradition', *Journal of Human Evolution*, 55(6), pp. 989–998. doi: 10.1016/j.jhevol.2008.06.004.

Leca, J. B., Gunst, N. and Huffman, M. (2011) 'Complexity in object manipulation by japanese macaques (Macaca fuscata): A cross-sectional analysis of manual coordination in stone handling patterns', *Journal of Comparative Psychology*, 125(1), pp. 61–71. doi: 10.1037/a0020868.

Leder, D. (1990) *The absent body*. London: University of Chicago Press.

van Leeuwen, L., Smitsman, A. and van Leeuwen, C. (1994) 'Affordances, Perceptual Complexity, and the Development of Tool Use', *Journal of Experimental Psychology: Human Perception and Performance*, 20(1), pp. 174–191. doi: 10.1037/0096-1523.20.1.174.

Lehmann, J., Korstjens, A. H. and Dunbar, R. I. M. (2007) 'Group size, grooming and social cohesion in primates', *Animal Behaviour*, 74(6), pp. 1617–1629. doi: https://doi.org/10.1016/j.anbehav.2006.10.025.

Lemmonier, P. (1992) *Technological choices. Transformation in material cultures since the Neolothic*. London: Routledge.

Lemmonier, P. (1993) *Technological choices : transformation in material cultures since the Neolithic*.

Leont'ev, a N. (1981) *Problems of the development of mind*. Moscow: Progress.

Leroi-Gouran (1964) *La Geste et la parole: technique et langage*. Paris: Editions Albin Michel.

Leroi-Gourhan, A. (1943) *Evolution et techniques. L'homme et la matiere*. (reprinted. Paris: Albin Michel.

Lestel, D. and Grundmann, E. (1999) 'Tools, techniques and animals: The role of mediations of actions in the dynamics of social behaviours', *Social Science Information*, 38(3), pp. 367–407. doi:

10.1177/053901899038003002.

Liu, Q. *et al.* (2009) 'Kinematics and energetics of nut-cracking in wild capuchin monkeys (Cebus libidinosus) in Piauí, Brazil', *American Journal of Physical Anthropology*, 138(2), pp. 210–220. doi: 10.1002/ajpa.20920.

Liu, Q., Fragaszy, D. M. and Visalberghi, E. (2016) 'Wild capuchin monkeys spontaneously adjust actions when using hammer stones of different mass to crack nuts of different resistance', *American Journal of Physical Anthropology*, 161(1), pp. 53–61. doi: 10.1002/ajpa.23006.

Lombard, M. and Gärdenfors, P. (2017) 'Tracking the evolution of causal cognition in humans', *Journal of Anthropological Sciences*, 95, pp. 219–234. doi: 10.4436/jass.95006.

Lombard, M. and Haidle, M. N. (2012) 'Thinking a bow-and-arrow set: Cognitive implications of middle stone age bow and stone-tipped arrow technology', *Cambridge Archaeological Journal*, 22(2), pp. 237–264. doi: 10.1017/S095977431200025X.

Lombard, M., Högberg, A. and Haidle, M. N. (2019) 'Cognition: From capuchin rock pounding to Lomekwian flake production', *Cambridge Archaeological Journal*, 29(2), pp. 201–231. doi: 10.1017/S0959774318000550.

Lonsdorf, E. V. (2005) 'Sex differences in the development of termite-fishing skills in the wild chimpanzees, Pan troglodytes schweinfurthii, of Gombe National Park, Tanzania', *Animal Behaviour*, 70(3), pp. 673–683. doi: 10.1016/j.anbehav.2004.12.014.

Lorenz, K. (1952) *King Solomon's Ring*. New York: Thomas Y Crowell.

Lorenz, K. (1965) *Evolution and modification of behaviour*. Chicago, IL: University of Chicago Press.

Luncz, L V. *et al.* (2016) 'Distance-decay effect in stone tool transport by wild chimpanzees', *Proceedings of the Royal Society B: Biological Sciences*, 283, p. 20161607. doi: 10.1098/rspb.2016.1607.

Luncz, L.V. *et al.* (2016) 'Wild capuchin monkeys adjust stone tools according to changing nut properties', *Scientific Reports*, 6, p. 33089. doi: 10.1038/srep33089.

Luncz, L. V., Tan, A., *et al.* (2017) 'Resource depletion through primate stone technology', *eLife*, 6, p. e23647. doi: 10.7554/eLife.23647.

Luncz, L. V., Svensson, M. S., *et al.* (2017) 'Technological Response of Wild Macaques (Macaca fascicularis) to Anthropogenic Change', *International Journal of Primatology*, 38, pp. 872–880. doi: 10.1007/s10764-017-9985-6.

Luncz, L. V. *et al.* (2019) 'Group-specific archaeological signatures of stone tool use in wild macaques', *eLife*, 8, p. e46961. doi: 10.7554/eLife.46961.

Luncz, L. V. and Boesch, C. (2014) 'Tradition over trend: Neighboring chimpanzee communities maintain differences in cultural behavior despite frequent immigration of adult females', *American Journal of Primatology*, 76(7), pp. 649–57. doi: 10.1002/ajp.22259.

Luncz, L. V, Mundry, R. and Boesch, C. (2012) 'Evidence for cultural differences between neighboring chimpanzee communities', *Current Biology*, 22(10), pp. 922–926. doi: 10.1016/j.cub.2012.03.031.

Maestripieri, D. *et al.* (1992) 'A modest proposal: displacement activities as an indicator of emotions in primates', *Animal Behaviour*, 44(5), pp. 967–979. doi: https://doi.org/10.1016/S0003-3472(05)80592-5.

Malafouris, L. (2004) 'The Cognitive Basis of Material Engagement: Where Brain, Body and Culture Conflate', *Rethinking Materiality: The Engagement of Mind with the Material World*, pp. 53–62.

Malafouris, L. (2008) 'At the Potter's Wheel: An Argument for Material Agency', in *Material Agency*, pp. 19–36. doi: 10.1007/978-0-387-74711-8.

Malafouris, L. (2010) 'Metaplasticity and the human becoming: Principles of neuroarchaeology', *Journal of Anthropological Sciences*, 88, pp. 49–72.

Malafouris, L. (2013a) *How Things Shape the Mind: A Theory of Material Engagement*. Cambridge MA: MIT Press.

Malafouris, L. (2013b) 'The Enactive Sign', in *How Things Shape the Mind*. Cambridge, MA: MIT Press. doi: 10.7551/mitpress/9476.003.0009.

Malafouris, L. (2014) 'Creative thinging: The feeling of and for clay', *Pragmatics and Cognition*, 22(1), pp. 140–158. doi: 10.1075/pc.22.1.08mal.

Malafouris, L. (2015) 'Metaplasticity and the Primacy of Material Engagement', *Time and Mind*, 8(4), pp. 351–371. doi: 10.1080/1751696x.2015.1111564.

Malafouris, L. (2016) 'On human becoming and incompleteness: A Material Engagement approach to the study of embodiment in evolution and culture', in Etzelmuller, G. and Tewes, C. (eds) *Embodiment in Evolution and Culture*. Mohr Siebeck GmbH and Co, pp. 289–306.

Malafouris, L. (2019) 'Mind and material engagement', *Phenomenology and the Cognitive Sciences*, 18, pp. 1–17. doi: 10.1007/s11097-018-9606-7.

Malafouris, L. and Renfrew, C. (2010) *Cognitive life of things: recasting the boundaries of the mind*. Cambridge: McDonald Institute.

Malaivijitnond, S. *et al.* (2007) 'Stone-tool usage by Thai long-tailed macaques (Macaca fascicularis)', *American Journal of Primatology*, 69, pp. 227–233. doi: 10.1002/ajp.20342.

Mangalam, M. *et al.* (2018) 'Unique perceptuomotor control of stone hammers in wild monkeys', *Biology Letters*, 14, p. 20170587. doi: 10.1098/rsbl.2017.0587.

Mangalam, M. and Fragaszy, D. M. (2015) 'Wild bearded capuchin monkeys crack nuts dexterously', *Current Biology*, 25, pp. 1334–1339. doi: 10.1016/j.cub.2015.03.035.

Mangalam, M. and Fragaszy, D. M. (2016) 'Transforming the body-only system into the body-plus-

tool system', *Animal Behaviour*, 117, pp. 115–122. doi: 10.1016/j.anbehav.2016.04.016.

Mangalam, M., Rein, R. and Fragaszy, D. M. (2018) 'Bearded capuchin monkeys use joint synergies to stabilize the hammer trajectory while cracking nuts in bipedal stance', *Proceedings of the Royal Society B: Biological Sciences*, 285(1889), p. 20181797. doi: 10.1098/rspb.2018.1797.

Mannu, M. and Ottoni, E. B. (2009) 'The enhanced tool-kit of two groups of wild bearded capuchin monkeys in the caatinga: Tool making, associative use, and secondary tools', *American Journal of Primatology*, 71(3), pp. 242–251. doi: 10.1002/ajp.20642.

Marchant, L. F. and McGrew, W. C. (2007) 'Ant fishing by wild chimpanzees is not lateralised', *Primates*, 48, pp. 22–26. doi: 10.1007/s10329-006-0020-3.

Mareschal, D. *et al.* (2007) *Neuroconstructivism: How the brain constructs cognition*. Oxford: Oxford University Press.

Martel, M. *et al.* (2017) 'Tool use unravels body morphology representation in the brain', in de Vignemont, F. and Smith, A. J. . (eds) *The Subject's matter. Self-consciousness and the body*. Cambridge MA: MIT Press, pp. 51–74.

Martin, R. D., Solico, C. and Tavare, S. (2007) 'Primate origins: Implications of a Cretaceous ancestry', *Folia Primatologica*, 78(5–6), pp. 277–296. doi: 10.1159/000105145.

Matás, G. J. L., & Yravedra, J. (2022). 'We hunt to share': Social dynamics and very large mammal butchery during the Oldowan–Acheulean transition. *World Archaeology*, 1–31. https://doi.org/10.1080/00438243.2022.2030793

Mathy, F. and Feldman, J. (2012) 'What's magic about magic numbers? Chunking and data compression in short-term memory', *Cognition*, 122(3), pp. 346–362. doi: 10.1016/j.cognition.2011.11.003.

Matsusaka, T. *et al.* (2006) 'Tool-use for drinking water by immature chimpanzees of Mahale:

Prevalence of an unessential behavior', *Primates*, 47, pp. 113–122. doi: 10.1007/s10329-005-0158-4.

Matsuzawa, T. (1991a) *Chimpanzee mind*. Tokyo: Iwanami (in Japanese).

Matsuzawa, T. (1991b) 'Nesting cups and metatools in chimpanzees', *Behavioral and Brain Sciences*, 14(4), pp. 570–571. doi: 10.1017/S0140525X00071417.

Matsuzawa, T. (1994) 'Field experiments on use of stone tools by chimpanzees in the wild', in Wrangham, R. W. et al. (eds) *Chimpanzee cultures*. Cambridge, MA: Harvard University Press, pp. 351–370.

Matsuzawa, T. (1996) 'Chimpanzee intelligence in nature and in captivity: isomorphism of symbol use and tool use', in McGrew, W. C., Marchant, L. F., and Nishida, T. (eds) *Great Ape Societies*. Cambridge: Cambridge University Press, pp. 196–209. doi: 10.1017/cbo9780511752414.017.

Matsuzawa, T. (1997) 'The death of an infant chimpanzee at Bossou, Guinea', *Pan Africa News*, 4(1), pp. 4–6. doi: 10.5134/143350.

Matsuzawa, T. (1999) 'Communication and tool-use in chimpanzees: Cultural and social contexts', in Hauser, M. D. and Konishi, M. (eds) *The design of animal communication*. Cambridge MA: MIT Press, pp. 645–671.

Matsuzawa, T. *et al.* (2001) 'Emergence of culture in wild chimpanzees: education by master-apprenticeship', in Matsuzawa, T. (ed.) *Primate origins of human cognition and behaviour*. Tokyo: Springer, pp. 557–574.

Matsuzawa, T. (2019) 'Chimpanzees foraging on aquatic foods: Algae scooping in Bossou', *Primates*, 60, pp. 317–319. doi: 10.1007/s10329-019-00733-0.

Matsuzawa, T., Yamakoshi, G. and Humle, T. (1996) 'A newly found tool use by wild chimpanzees: Algae scooping (abstract)', *Primate Research*, 12, p. 283.

Mauss, M. (1936) ‘Les techniques du corps’, *Journal de Psychologie*, 32(3–4), pp. 365–386. doi: 10.1522/cla.mam.tec.

McBreaty, S. and Brooks, A. (2000) ‘The revolution that wasn’t: A new interpretation of the origin of modern human behaviour’, *Journal of Human Evolution*, 39(5), pp. 453–563. doi: 10.1006/jhev.2000.0435.

McGrew, W. C. (1974) ‘Tool use by wild chimpanzees in feeding upon driver ants’, *Journal of Human Evolution*, 3(6), pp. 501–508. doi: 10.1016/0047-2484(74)90010-4.

McGrew, W. C. (1977) ‘Socialization and object manupulation of wild chimpanzees’, in Chevalier-Skolnikoff, S. and Poirier, F. (eds) *Primate biosocial development*. New York, NY: Garland, pp. 261–288.

McGrew, W. C. (1985) ‘The chimpanzee and the oil palm: Patterns of culture’, *Social Biology and Human Affairs*, 50(1), pp. 7–23.

McGrew, W. C. (1987) ‘Tools to Get Food: The Subsistants of Tasmanian Aborigines and Tanzanian Chimpanzees Compared’, *Journal of Anthropological Research*, 43(3), pp. 247–258. doi: 10.1086/jar.43.3.3630525.

McGrew, W. C. (1992) *Chimpanzee material culture: implications for human evolution*. Cambridge: Cambridge University Press.

McGrew, W. C. (1993a) ‘Brains, hands, and minds’, in Berthelet, A. and Chavaillon, J. (eds) *The use of tools by human and non-human primates*. Oxford: Clarendon Press, pp. 143–153.

McGrew, W. C. (1993b) ‘The intelligent use of tools: Twenty propositions’, in Gibson, K. R. and Ingold, T. (eds) *Tools, Language and Cognition in Human Evolution*. Cambridge: Cambridge University Press, pp. 151–170.

McGrew, W. C. *et al.* (1997) ‘Why don’t chimpanzees in Gabon crack nuts?’, *International Journal of*

Primatology, 18(3), pp. 353–374. doi: 10.1023/A:1026382316131.

McGrew, W. C. *et al.* (2003) 'Ethoarchaeology and elementary technology of unhabituated wild chimpanzees at Assirik , Senegal , West Africa', *PaleoAnthropology*, 1, pp. 1–20.

McGrew, W. C. (2004) 'Primatology: Advanced ape technology', *Current Biology*, 14(24), pp. R1046–R1047. doi: 10.1016/j.cub.2004.11.042.

McGrew, W. C. (2010) 'In search of the last common ancestor: New findings on wild chimpanzees', *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365(1556), pp. 3267–3276. doi: 10.1098/rstb.2010.0067.

McGrew, W. C. (2013) 'Is primate tool use special? Chimpanzee and new caledonian crow compared', *Philosophical Transactions of the Royal Society B: Biological Sciences*, 368(1630), p. 20120422. doi: 10.1098/rstb.2012.0422.

McGrew, W. C. (2017) 'Field studies of Pan troglodytes reviewed and comprehensively mapped, focussing on Japan's contribution to cultural primatology', *Primates*, 58(1), pp. 237–258. doi: 10.1007/s10329-016-0554-y.

McGrew, W. C. *et al.* (2019) 'A simian view of the Oldowan', in Overmann, K. A. and Coolidge, F. L. (eds) *Squeezing minds from stones: Cognitive archaeology and the evolution of the human mind*. New York, NY: Oxford University Press, pp. 13–41. doi: 10.1093/oso/9780190854614.003.0002.

McGrew, W. C. and Collins, D. A. (1985) 'Tool use by wild chimpnzees (Pan troglodytes) to obtain termites (Macrotermes herus) in the Mahale Mountains, Tanzania', *American Journal of Primatology*, 9(1), pp. 47–62. doi: 10.1002/ajp.1350090106.

McGrew, W. C., Pruetz, J. D. and Fulton, S. J. (2005) 'Chimpanzees use tools to harvest social insects at Fongoli, Senegal', *Folia Primatologica*, 76(4), pp. 222–226. doi: 10.1159/000086023.

McGrew, W. C. and Tutin, C. E. G. (1972) 'Chimpanzee Dentistry', *The Journal of the American Dental*

Association, 85(6), pp. 1198–1204. doi: https://doi.org/10.14219/jada.archive.1972.0540.

McLennan, M., Rohen, J., *et al.* (2019) '"Customary" use of stick tools by chimpanzees in Bulindi, Uganda: update and analysis of digging techniques from behavioural observations', *Revue de primatologie*, 10. doi: 10.4000/primatologie.6706.

McLennan, M., Lorenti, G., *et al.* (2019) 'Digging for clues: Stick tools used for honey digging in a second community of "forest fragment chimpanzees" outside the Budongo and Bugoma Forests, Uganda', *Revue de primatologie*, 10. doi: 10.4000/primatologie.6718.

McNabb, J., Binyon, F. and Hazelwood, L. (2004) 'The large cutting tools from the South African Acheulean and the question of social traditions', *Current Anthropology*, 45(5), pp. 653–677. doi: 10.1086/423973.

Mendes, F. D. C. *et al.* (2015) 'Diversity of nutcracking tool sites used by Sapajus libidinosus in Brazilian Cerrado', *American Journal of Primatology*, 77(5), pp. 535–546. doi: 10.1002/ajp.22373.

Mendonça-Furtado, O. *et al.* (2014) 'Does hierarchy stability influence testosterone and cortisol levels of bearded capuchin monkeys (Sapajus libidinosus) adult males? A comparison between two wild groups', *Behavioural Processes*, 109(A), pp. 79–88. doi: 10.1016/j.beproc.2014.09.010.

Meno, W., Coss, R. G. and Perry, S. (2013) 'Development of snake-directed antipredator behaviour by white-faced capuchin monkeys: I. Snake-species discrimination', *American Journal of Primatology*, 75, pp. 281–291. doi: 10.1002/ajp.22106.

Mercader, J. (2002) 'Excavation of a chimpanzee stone tool site in the African rainforest', *Science*, 296(5572), pp. 1425–1455. doi: 10.1126/science.1070268.

Mercader, J. *et al.* (2007) '4,300-year-old chimpanzee sites and the origins of percussive stone technology', *Proceedings of the National Academy of Sciences*, 104(9), pp. 3034–3048. doi: 10.1073/pnas.0607909104.

Merleau-Ponty, M. (1962) *Phenomenology of perception*, *Phenomenology of Perception*. Edited by D. A. Landes. London: Kegan Paul. doi: 10.4324/9780203720714.

Meulman, E. J. M. *et al.* (2012) 'The Role of terrestriality in promoting primate technology', *Evolutionary Anthropology*, 21(2), pp. 58–68. doi: 10.1002/evan.21304.

Meulman, E. J. M. and Van Schaik, C. P. (2013) 'Orangutan tool use and the evolution of technology', in Sanz, C. M., Call, J., and Boesch, C. (eds) *Tool Use in Animals Cognition and Ecology*. Cambridge: Cambridge University Press, pp. 176–202. doi: 10.1017/CBO9780511894800.012.

Meulman, E. J. M., Seed, A. M. and Mann, J. (2013) 'If at first you don't succeed... Studies of ontogeny shed light on the cognitive demands of habitual tool use', *Philosophical Transactions of the Royal Society B: Biological Sciences*, 368(1630), p. 20130050. doi: 10.1098/rstb.2013.0050.

Miller, G. A. (1956) 'The magical number seven, plus or minus two: some limits on our capacity for processing information', *Psychological Review*, 63(2), pp. 81–97. doi: 10.1037/h0043158.

Mineka, S. and Cook, M. (1988) 'Social learning and the acquisition of snake fear in monkeys', in Zentall, T. R. and Galef, B. G. (eds) *Social learning: Psychological and biological perspectives*. Hillsdale, NJ: Erlbaum, pp. 51–73.

Mitchell, J. D. and Mori, S. A. (1987) 'The cashew and its relatives (Anacardium: Anacardiaceae)', *Memoirs of the New York Botanical Garden*, 42, pp. 1–76.

Möbius, Y. *et al.* (2008) 'Cultural differences in army ant predation by West African chimpanzees? A comparative study of microecological variables', *Animal Behaviour*, 76(1), pp. 37–45. doi: 10.1016/j.anbehav.2008.01.008.

Molesti, S., Meguerditchian, A. and Bourjade, M. (2020) 'Gestural communication in olive baboons (Papio anubis): repertoire and intentionality', *Animal Cognition*, 23(1), pp. 19–40. doi: 10.1007/s10071-019-01312-y.

Montgomery, S. H. (2014) 'The relationship between play, brain growth and behavioural flexibility in primates', *Animal Behaviour*, 90, pp. 281–286. doi: 10.1016/j.anbehav.2014.02.004.

Morgan, B. J. and Abwe, E. E. (2006) 'Chimpanzees use stone hammers in Cameroon', *Current Biology*, 26(26), pp. R632–R633. doi: 10.1016/j.cub.2006.07.045.

Morgan, C. L. (1894) *An introduction to comparative psychology*. London: Walter Scott.

Mosley, H. (2020) 'Primate tool use and the socio-ecology of thinging: how non-humans think through tools', *Adaptive Behavior*, 29(2), pp. 153–167. doi: 10.1177/1059712320943623.

Mosley, H. and Haslam, M. (2015) 'Extending material cognition to primate tool use', *Quaternary International*, 405, pp. 70–77. doi: 10.1016/j.quaint.2015.11.020.

Motes-Rodrigo, A. *et al.* (2019) 'Chimpanzee extractive foraging with excavating tools: Experimental modeling of the origins of human technology', *PloS one*, 14(5), p. e0215644. doi: 10.1371/journal.pone.0215644.

Moura, A. C. (2004) *The capuchin monkey and the caatinga dry forest: a hard life in a harsh habitat*. University of Cambridge.

Moura, A. C. (2006) 'Stone banging by wild capuchin monkeys: An unusual auditory display', *Folia Primatologica*, 78(1), pp. 36–45. doi: 10.1159/000095684.

Moura, A. C. and Lee, P. C. (2004) 'Capuchin stone tool use in Caatinga dry forest', *Science*, 306(5703), p. 1909. doi: 10.1126/science.1102558.

Moura, A. C. and Lee, P. C. (2010) 'Wild capuchins show male-biased feeding tool use', *International Journal of Primatology*, 31, pp. 457–470. doi: 10.1007/s10764-010-9406-6.

Mugisha, S., Zuberbühler, K. and Hobaiter, C. (2016) 'First observation of Dorylus ant feeding in Budongo chimpanzees supports absence of stick-tool culture', *Primates*, 57, pp. 389–394. doi:

10.1007/s10329-016-0533-3.

Musgrave, S. *et al.* (2016) 'Tool transfers are a form of teaching among chimpanzees', *Scientific Reports*, 6, p. 34783. doi: 10.1038/srep34783.

Musgrave, S. *et al.* (2020) 'Teaching varies with task complexity in wild chimpanzees', *Proceedings of the National Academy of Sciences of the United States of America*, 117(2), pp. 969–976. doi: 10.1073/pnas.1907476116.

Musgrave, S. *et al.* (2021) 'The ontogeny of termite gathering among chimpanzees in the Goualougo Triangle, Republic of Congo', *American Journal of Physical Anthropology*, 174(2), pp. 187–200. doi: 10.1002/ajpa.24125.

Myowa-Yamakoshi, M. and Yamakoshi, G. (2011) 'Play Behaviors Involving the Use of Objects in Young Chimpanzees at Bossou', in Matsuzawa, T., Humle, T., and Sugiyama, Y. (eds) *The chimpanzees of Bossou and Nimba. Primatology monographs*. Tokyo: Springer, pp. 231–240. doi: 10.1007/978-4-431-53921-6_25.

Nahallage, C. A. D. and Huffman, M. A. (2012) 'Stone handling behavior in rhesus macaques (Macaca mulatta), a behavioral propensity for solitary object play shared with Japanese macaques', *Primates*, 53(1), pp. 71–78. doi: 10.1007/s10329-011-0279-x.

Nakamura, M. and Itoh, N. (2008) 'Hunting with tools by Mahale chimpanzees', *Pan Africa News*, 15(1), pp. 3–6. doi: 10.5134/143489.

Nishida, T. (1973) 'The ant-gathering behaviour by the use of tools among wild chimpanzees of the Mahali Mountains', *Journal of Human Evolution*, 2, pp. 357–370. doi: 10.1016/0047-2484(73)90016-X.

Nishida, T. (1980a) 'Local differences in responses to water among wild chimpanzees', *Folia Primatologica*, 33(3), pp. 189–209. doi: 10.1159/000155934.

Nishida, T. (1980b) ‘The leaf-clipping display: A newly discovered expressive gesture in wild chimpanzees’, *Journal of Human Evolution*, 9(2), pp. 117–128. doi: 10.1016/0047-2484(80)90068-8.

Nishida, T. *et al.* (1999) ‘Ethogram and ethnography of Mahale chimpanzees’, *Anthropological Science*, 107, pp. 141–188. doi: 10.1537/ase.107.141.

Nishida, T. and Hiraiwa, M. (1982) ‘Natural history of a tool-using behavior by wild chimpanzees in feeding upon wood-boring ants’, *Journal of Human Evolution*, 11(1), pp. 73–99. doi: 10.1016/S0047-2484(82)80033-X.

Nishida, T., Matsusaka, T. and McGrew, W. C. (2009) ‘Emergence, propagation, or disappearance of novel behavioural patterns in the habituated chimpanzees of Mahale’, *Primates*, 50(1), pp. 23–36. doi: 10.1007/s10329-008-0109-y.

Nishie, H. (2011) ‘Natural history of Camponotus ant-fishing by the M group chimpanzees at the Mahale Mountains National Park, Tanzania’, *Primates*, 52(4), pp. 329–342. doi: 10.1007/s10329-011-0270-6.

O’Grady, R. T. (1984) ‘Evolutionary theory and teleology’, *Journal of Theoretical Biology*, 107(4), pp. 563–578. doi: 10.1016/S0022-5193(84)80133-2.

O’Malley, R. C. *et al.* (2012) ‘The appearance and spread of ant fishing among the Kasekala chimpanzees of Gombe: A possible case of intercommunity cultural transmission’, *Current Anthropology*, 53(5), pp. 650–663. doi: 10.1086/666943.

O’Regan, J. K. and Noë, A. (2001) ‘A sensorimotor account of vision and visual consciousness’, *Behavioral and Brain Sciences*, 24(5), pp. 939–973. doi: 10.1017/S0140525X01000115.

Oakley, K. P. (1956) *Man the tool-maker*. 3rd edn. London: Printed by order of the Trustees of the British Museum.

Odling-Smee, P. J., Laland, K. N. and Feldman, M. W. (1996) ‘Niche construction’, *American*

Naturalist, 147(4), pp. 641–648. doi: 10.1086/285870.

Odling-Smee, P. J., Laland, K. N. and Feldman, M. W. (2003) *Niche Construction: The neglected process in evolution.* Princeton: Princeton University Press.

Ohashi, G. (2006) 'Behavioral repertoire of tool use in the wild chimpanzees at Bossou', in Matsuzawa, T., Tomonaga, M., and Tanaka, M. (eds) *Cognitive Development in Chimpanzees*. Tokyo: Springer, pp. 439–451. doi: 10.1007/4-431-30248-4_26.

Oswalt, W. H. (1976) *An anthropological analysis of food-getting technology*. New York: Wiley-Interscience.

Ottoni, E. B. (2015) 'Tool Use Traditions in Nonhuman Primates: The Case of Tufted Capuchin Monkeys', *Human Ethology Bulletin*, Proc. of t, pp. 22–40.

Ottoni, E. B. and Izar, P. (2008) 'Capuchin monkey tool use: Overview and implications', *Evolutionary Anthropology*, 17(4), pp. 171–178. doi: 10.1002/evan.20185.

Ottoni, E. B. and Mannu, M. (2001) 'Semifree-ranging tufted capuchins (Cebus apella) spontaneously use tools to crack open nuts', *International Journal of Primatology*, 22, pp. 347–358. doi: 10.1023/A:1010747426841.

Ottoni, E. B., de Resende, B. D. and Izar, P. (2005) 'Watching the best nutcrackers: What capuchin monkeys (Cebus apella) know about others' tool-using skills', *Animal Cognition*, 8(4), pp. 215–219. doi: 10.1007/s10071-004-0245-8.

Overmann, K. A. and Wynn, T. (2019a) 'Materiality and Human Cognition', *Journal of Archaeological Method and Theory*, 26, pp. 457–478. doi: 10.1007/s10816-018-9378-y.

Overmann, K. A. and Wynn, T. (2019b) 'On tools making minds: An archaeological perspective on human cognitive evolution', *Journal of Cognition and Culture*, 19(1–2), pp. 39–58. doi: 10.1163/15685373-12340047.

Oyama, S. (2000) *The ontogeny of information: Developmental systems and evolution*. 2nd edn. Durham, NC: Duke University Press. doi: 10.1215/9780822380665.

Oyama, S., Griffiths, P. E. and Gray, R. D. (2001) *Cycles of contingency: Developmental systems and evolution*. Cambridge, MA: Cambridge University Press.

Panger, M. A. *et al.* (2002) 'Cross-site differences in foraging behavior of white-faced capuchins (Cebus capucinus)', *American Journal of Physical Anthropology*, 119(1), pp. 52–66. doi: 10.1002/ajpa.10103.

Parisi, F. (2019) 'Temporality and metaplasticity. Facing extension and incorporation through material engagement theory', *Phenomenology and the Cognitive Sciences*, 18(1), pp. 205–221. doi: 10.1007/s11097-018-9599-2.

Parker, S. T. (2015) 'Re-evaluating the extractive foraging hypothesis', *New Ideas in Psychology*, 37, pp. 1–12. doi: 10.1016/j.newideapsych.2014.11.001.

Parker, S. T. and Gibson, K. R. (1977) 'Object manipulation, tool use and sensorimotor intelligence as feeding adaptations in cebus monkeys and great apes', *Journal of Human Evolution*, 6(7), pp. 623–641. doi: 10.1016/S0047-2484(77)80135-8.

Parr, L. A. *et al.* (1997) 'Grooming down the hierarchy: Allogrooming in captive brown capuchin monkeys, Cebus apella', *Animal Behaviour*, 54, pp. 361–367. doi: 10.1006/anbe.1996.0419.

Pascual-Garrido, A. (2018) 'Scars on plants sourced for termite fishing tools by chimpanzees: Towards an archaeology of the perishable', *American Journal of Primatology*, 80(9), p. e22921. doi: 10.1002/ajp.22921.

Pascual-Garrido, A. (2019) 'Cultural variation between neighbouring communities of chimpanzees at Gombe, Tanzania', *Scientific Reports*, 9, p. 8260. doi: 10.1038/s41598-019-44703-4.

Pavlov, I. P. (1927) *Conditioned reflexes*. Oxford: Oxford University Press.

Pelegrin, J. (2005) ‘Remarks about archaeological techniques and methods of knapping: Elements of a Cognitive approach to stone knapping’, in Roux, V. and Bril, B. (eds) *Stone knapping, the necessary conditions for a uniquely hominin behaviour*. Cambridge: McDonald Institure of Archaeological Research, pp. 23–34.

Pelegrin, J., Karlin, C. and Bodu, P. (1988) ‘Chaines operatoires: Un outil pour le prehistorien. Notes et Monographies Techniques (no.25)’, in Tixier, J. (ed.) *Technologie Prehistorique*. Paris: CNRS, pp. 55–62.

Penn, D. C. and Povinelli, D. J. (2007) ‘On the lack of evidence that non-human animals possess anything remotely resembling a “theory of mind”’, *Philosophical Transactions of the Royal Society B: Biological Sciences*, 362, pp. 731–744. doi: 10.1098/rstb.2006.2023.

Perelman, P. *et al.* (2011) ‘A molecular phylogeny of living primates’, *PLoS Genetics*, 7(3), p. e1001342. doi: 10.1371/journal.pgen.1001342.

Perez-Barberia, F. J., Shultz, S. and Dunbar, R. I. M. (2007) ‘Evidence for coevolution of sociality and relative brain size in three orders of mammals’, *Evolution*, 61, pp. 2811–2821. doi: 10.1111/j.1558-5646.2007.00229.x.

Perreault, C. *et al.* (2013) ‘Measuring the complexity of lithic technology’, *Current Anthropology*, 54(S8), pp. S397–S406. doi: 10.1086/673264.

Perry, S. E., Barrett, B. J. and Godoy, I. (2017) ‘Older, sociable capuchins (Cebus capucinus) invent more social behaviours, but younger monkeys innovate more in other contexts’, *PNAS*, 114(30), pp. 7806–7813. doi: 10.1073/pnas.1620739114.

Pfaffenberger, B. (1992) ‘Social Anthropology of Technology’, *Annual Review of Anthropology*, 21, pp. 491–516. doi: 10.1146/annurev.anthro.21.1.491.

Phillips, K. A. *et al.* (2004) ‘Use of visual, acoustic, and olfactory information during embedded

invertebrate foraging in brown capuchins (Cebus apella)', *Journal of Comparative Psychology*, 118(2), pp. 200–205. doi: 10.1037/0735-7036.118.2.200.

Phillips, K. A., Grafton, B. W. and Haas, M. E. (2003) 'Tap-scanning for invertebrates by capuchins (Cebus apella)', *Folia Primatologica*, 74(3), pp. 162–164. doi: 10.1159/000070650.

Pierce, J. D. (1986) 'A Review of Tool Use in Insects', *The Florida Entomologist*, 69(1), p. 95. doi: 10.2307/3494748.

Pika, S. and Frolich, M. (2019) 'Gestural acquisition in great apes: The social negotiation hypothesis', *Animal Cognition*, 22, pp. 551–565. doi: 10.1007/s10071-017-1159-6.

Piredda, G. (2017) 'The mark of the cognitive and the coupling-constitution fallacy: A defense of the extended mind hypothesis', *Frontiers in Psychology*, 8, p. 2061. doi: 10.3389/fpsyg.2017.02061.

Plooij, F. X. (1978) 'Some basic traits of language in wild chimpanzees?', in Lock, A. (ed.) *Action, gesture, and symbol: the emergence of language*. New York, NY: Academic Press, pp. 111–131.

Pollick, A. S. and de Waal, F. B. M. (2007) 'Ape gestures and language evolution', *PNAS*, 104(19), pp. 8184–8189. doi: 10.1073/pnas.0702624104.

Povinelli, D. J. (2000) *Folk Physics for Apes*. New York: Oxford University Press.

Povinelli, D. J. (2010) *Folk physics for apes: The chimpanzee's theory of how the world works*. Oxford: Oxford University Press. doi: 10.1093/acprof:oso/9780198572190.001.0001.

Premack, D. and Woodruff, G. (1978) 'Does the chimpanzee have a theory of mind?', *Behavioral and Brain Sciences*, 1(4), pp. 515–526. doi: 10.1017/S0140525X00076512.

Preston, B. (1998) 'Cognition and tool use', *Mind & Language*, 13(4), pp. 513–547. doi: 10.1111/1468-0017.00090.

Proffitt, T. *et al.* (2016) 'Wild monkeys flake stone tools', *Nature*, 539(7627), pp. 85–88. doi:

10.1038/nature20112.

Pruetz, J. D. *et al.* (2015) 'New evidence on the tool-assisted hunting exhibited by chimpanzees (Pan troglodytes verus) in a savannah habitat at Fongoli, Sénégal', *Royal Society Open Science*, 2(4), p. 140507. doi: 10.1098/rsos.140507.

Pruetz, J. D. and Bertolani, P. (2007) 'Savannah chimpanzees, Pan troglodytes verys, hunt with tools', *Current Biology*, 17(5), pp. 412–417. doi: 10.1016/j.cub.2006.12.042.

Putnam, H. (1981) 'Brains in a vat', in *Reason, truth and history*. Cambridge: Cambridge University Press, pp. 1–21.

Quartz, S. and Sejnowksi, T. (1997) 'The neural basis of cognitive development: A constructivist manifesto', *Behavioral and Brain Sciences*, 20(4), pp. 537–596. doi: 10.1017/s0140525x97001581.

Reader, S. M., Hager, Y. and Laland, K. N. (2011) 'The evolution of primate general and cultural intelligence', *Philosophical Transactions of the Royal Society B: Biological Sciences*, 2(4), p. 140507. doi: 10.1098/rstb.2010.0342.

Renfrew, C. (2001) 'Symbol before concept: material engagement and the early development of society', in Hodder, I. (ed.) *Archaeological Theory Today*. Cambridge: Polity Press, pp. 122–40.

Renfrew, C. (2004) 'Towards a Theory of Material Engagement', in DeMarrais, E., Gosden, C., and Renfrew, C. (eds) *Rethinking materiality the engagement of mind with the material world*. Cambridge: McDonald Institute, pp. 23–32.

Resende, B. *et al.* (2021) 'Revisiting the fourth dimension of tool use: how objects become tools for capuchin monkeys', *Evolutionary Human Sciences*. 2021/03/05. Cambridge University Press, 3, p. e18. doi: DOI: 10.1017/ehs.2021.16.

de Resende, B. D., Ottoni, E. B. and Fragaszy, D. M. (2008) 'Ontogeny of manipulative behavior and nut-cracking in young tufted capuchin monkeys (Cebus apella): A perception-action perspective',

Developmental Science, 11(6), pp. 828–840. doi: 10.1111/j.1467-7687.2008.00731.x.

Reynolds, V. (2005) *The chimpanzees of the Budongo forest: Ecology, behaviour and conservation*. Oxford: Oxford University Press.

Riedel, J. *et al.* (2008) 'The early ontogeny of human-dog communication', *Animal Behaviour*, 75(3), pp. 1003–1014. doi: 10.1016/j.anbehav.2007.08.010.

Rietveld, E. and Kiverstein, J. (2014) 'A rich landscape of affordances', *Ecological Psychology*, 26(4), pp. 325–352. doi: 10.1080/10407413.2014.958035.

Roberts, G. and Sherratt, T. N. (1998) 'Development of cooperative relationships through increasing investment.', *Nature*. England, 394(6689), pp. 175–179. doi: 10.1038/28160.

Roberts, P. (2016) '"We have never been behaviourally modern": The implications of Material Engagement Theory and Metaplasticity for understanding the Late Pleistocene record of human behaviour', *Quaternary International*, 405, pp. 8–20. doi: 10.1016/j.quaint.2015.03.011.

Romanes, G. (1912) *Animal intelligence*. New York: Appleton.

Rosati, A. G. (2017) 'Foraging cognition: Reviving the ecological intelligence hypothesis', *Trends in Cognitive Sciences*, 21(9), pp. 691–702. doi: 10.1016/j.tics.2017.05.011.

Rowlands, M. (2009) 'Extended cognition and the mark of the cognitive', *Philosophical Psychology*, 22(1), pp. 1–19. doi: 10.1080/09515080802703620.

Rowlands, M. (2010) 'What is cognition? Extended cognition and the criterion of the cognitive', in Dunbar, R., Gamble, C., and Gowlett, J. (eds) *Social Brain, Distributed Mind*. Oxford: Oxford University Press, pp. 317–335.

Russon, A. E. *et al.* (2014) 'Orangutan fish eating, primate aquatic fauna eating, and their implications for the origins of ancestral hominin fish eating', *Journal of Human Evolution*, 77, pp. 50–

63. doi: 10.1016/j.jhevol.2014.06.007.

Rutz, C. and St Clair, J. J. H. (2012) 'The evolutionary origins and ecological context of tool use in New Caledonian crows', *Behavioural Processes*, 89(2), pp. 153–165. doi: 10.1016/j.beproc.2011.11.005.

Sahlins, M, D. (1972) *Stone Age Economics*. London: Tavistock.

Sakamaki, T. (1998) 'First record of algae-feeding by a female chimpanzee at Mahale', *Pan Africa News*, 5(1), pp. 1–3. doi: 10.5134/143366.

Sakura, O. and Matsuzawa, T. (1991) 'Flexibility of wild chimpanzee nut-cracking behaviour using stone hammers and anvils: An experimental analysis', *Ethology*, 87(3–4), pp. 237–248. doi: 10.1111/j.1439-0310.1991.tb00249.x.

Sambrook, T. and Whiten, A. (1997) 'On the nature of complexity in cognitive and behavioural science', *Theory & Psychology*, 7(2), pp. 191–213. doi: 10.1177/0959354397072004.

Sanz, C. M. *et al.* (2014) 'Insect prey characteristics affecting regional variation in chimpanzee tool use', *Journal of Human Evolution*, 71, pp. 28–37. doi: 10.1016/j.jhevol.2013.07.017.

Sanz, C. M. and Morgan, D. B. (2007) 'Chimpanzee tool technology in the Goualougo Triangle, Republic of Congo', *Journal of Human Evolution*, 52(4), pp. 420–433. doi: 10.1016/j.jhevol.2006.11.001.

Sanz, C. M. and Morgan, D. B. (2009) 'Flexible and persistent tool-using strategies in honey-gathering by wild chimpanzees', *International Journal of Primatology*, 30, pp. 411–427. doi: 10.1007/s10764-009-9350-5.

Sanz, C. M. and Morgan, D. B. (2010) *The complexity of chimpanzee tool-use behaviours*. Edited by E. V Lonsdorf, S. R. Ross, and T. Matsuzawa. Chicago, IL: University of Chicago Press.

Sanz, C. M. and Morgan, D. B. (2013) 'Ecological and social correlates of chimpanzee tool use',

Philosophical Transactions of the Royal Society B: Biological Sciences, 368(1630), p. 20120416. doi: 10.1098/rstb.2012.0416.

Sayers, K. and Lovejoy, C. O. (2008) 'The chimpanzee has no clothes', *Current Anthropology2*, 49(1), pp. 87–114. doi: 10.1086/523675.

van Schaik, C. P., Deaner, R. O. and Merrill, M. Y. (1999) 'The conditions for tool use in primates: Implications for the evolution of material culture', *Journal of Human Evolution*, 36(6), pp. 719–741. doi: 10.1006/jhev.1999.0304.

van Schaik, C. P., Fox, E. A. and Sitompul, A. E. (1996) 'Manufacture and use of tools in wild Sumatran orangutans: Implications for human evolution', *Naturwissenschaften*, 83(4), pp. 186–188. doi: 10.1007/s001140050271.

van Schaik, C. P. and van Noordwijk, M. A. (1989) 'The special role of male Cebus monkeys in predation avoidance and its effect on group composition', *Behavioral Ecology and Sociobiology*, 24(5), pp. 265–276. doi: 10.1007/BF00290902.

Schick, K., & Toth, N. (1994). Early stone age technology in Africa: A review and a case study into the nature and function of spheroids and subspheroids. In R. Corruccini & R. Ciochon (Eds.), *Integrative paths to the past: Palaeoanthropological advances in honoe of F. Clark Howell* (pp. 429–449). Prentice-Hall.

Schiffer, M. B. (1976) *Behavioural Archaeology*. New York: Academic Press.

Schofield, D. P. *et al.* (2018) 'Cumulative culture in nonhumans: overlooked findings from Japanese monkeys?', *Primates*, 59(2), pp. 113–122. doi: 10.1007/s10329-017-0642-7.

Schöning, C. *et al.* (2008) 'The nature of culture: Technological variation in chimpanzee predation on army ants revisited', *Journal of Human Evolution*, 55(1), pp. 48–59. doi: 10.1016/j.jhevol.2007.12.002.

Schorkopf, D. L. P. (2016) ‘Male meliponine bees (Scaptotrigona aff. depilis) produce alarm pheromones to which workers respond with fight and males with fight’, *Journal of Comparative Psychology. A, Neuroethology, Sensory, Neural and Behavioural Physiology*, 202(9–10), pp. 667–78. doi: 10.1007/s00359-016-1109-9.

Seed, A. M. and Byrne, R. W. (2010) ‘Animal tool-use’, *Current Biology*, 20(23), pp. R1032–R1039. doi: 10.1016/j.cub.2010.09.042.

Seed, A. M. and Call, J. (2019) ‘Problem-solving in tool-using and non-tool-using animals’, in Chun Choe, J. (ed.) *Encyclopedia of Animal Behavior. Volume 1*. 2nd edn. Amsterdam: Elsevier, pp. 408–415. doi: 10.1016/B978-0-12-813251-7.00090-0.

Sellet, F. (1993) ‘Chaine operatoire: The concept and its applications’, *Lithic Technology*, 18(1 & 2), pp. 106–112. doi: 10.1080/01977261.1993.11720900.

Shaw, R. E., Turvey, M. T. and Mace, W. M. (1982) ‘Ecological psychology. The consequence of a commitment to realism’, in Weimer, W. and Palermo, D. (eds) *Cognition and the symbolic processes. Vol. 2*. Hillsdale, NJ: Lawrence Erlbaum Associates, Inc., pp. 159–226.

Shennan, S. (2001) ‘Demography and cultural innovation: A model and its implications for the emergence of modern human culture’, *Cambridge Archaeological Journal*, 11(1), pp. 5–16. doi: 10.1017/s0959774301000014.

Sherrow, H. M. (2005) ‘Tool use in insect foraging by the chimpanzees of Ngogo, Kibale National Park, Uganda’, *American Journal of Primatology*, 65(4), pp. 377–383. doi: 10.1002/ajp.20122.

Shettleworth, S. J. (2010) *Cognition, Evolution, and Behaviour*. second ed. Oxford: Oxford University Press.

Shott, M. J. (2003) ‘Chaîne opératoire and reduction sequence’, *Lithic Technology*, 28(2), pp. 95–105. doi: 10.1080/01977261.2003.11721005.

Shott, M. J. (2010) 'Size dependence in assemblage measures: Essentialism, materialism, and "She" analysis in archaeology', *American Antiquity*, 75(4), pp. 886–906. doi: 10.7183/0002-7316.75.4.886.

Shumaker, R. W., Walkup, K. R. and Beck, B. B. (2011) *Animal Tool Behaviour*. Baltimore: The John Hopkins University Press.

Sillar, B. and Tite, M. S. (2000) 'The challenge of "Technological choices" for materials science approaches in archaeology', *Archaeometry*, 1, pp. 2–20. doi: 10.1111/j.1475-4754.2000.tb00863.x.

Sinclair, A. (2000) 'Constellations of knowledge: Human agency and material affordance in lithic technology', in Dobres, M. A. and Robb, J. (eds) *Agency in Archaeology*. London: Routledge, pp. 196–212.

Sirianni, G. *et al.* (2018) 'Do chimpanzees anticipate an object's weight? A field experiment on the kinematics of hammer-lifting movements in the nut-cracking Tai chimpanzees', *Animal Cognition*, 21(1), pp. 109–118. doi: 10.1007/s10071-017-1144-0.

Sirianni, G., Mundry, R. and Boesch, C. (2010) 'When to choose which tool: Multidimensional and conditional selection of nut-cracking hammers in wild chimpanzees', *Animal Behaviour*, 100, pp. 152–165. doi: 10.1016/j.anbehav.2014.11.022.

Sirianni, G. and Visalberghi, E. (2013) 'Wild bearded capuchins process cashew nuts without contacting caustic compounds', *American Journal of Primatology*, 75(4), pp. 387–393. doi: 10.1002/ajp.22119.

Skinner, B. F. (1938) *The behaviour of organisms*. New York: Appleton-Century-Crofts.

Smitsman, A. W. (1997) 'The development of tool use: changing boundaries between organism and environment', in Dent-Read, C. and Zukow-Goldring, P. (eds) *Evolving explanations of development*. Washington: American Psychological Association, pp. 301–329.

Smitsman, A. W. and Bongers, R. M. (2012) 'Tool use and tool making: A developmental action

perspective', in Valsiner, J. and Connolly, K. J. (eds) *Handbook of Developmental Psychology*. London: SAGE Publications Ltd, pp. 172–193. doi: 10.4135/9781848608306.n8.

Sousa, C. (2011) 'Use of leaves for drinking water', in Matsuzawa, T., Humle, T., and Sugiyama, Y. (eds) *The chimpanzees of Bossou and Nimba: Primatology monographs*. Tokyo: Springer, pp. 85–96.

Sousa, C., Biro, D. and Matsuzawa, T. (2009) 'Leaf-tool use for drinking water by wild chimpanzees (Pan troglodytes): Aquisition patterns and handedness', *Animal Cognition*, 12, pp. 115–125. doi: 10.1007/s10071-009-0278-0.

Souto, A. *et al.* (2001) 'Critically endangered blonde capuchins fish for termites and use new techniques to accomplish the task', *Biology Letters*, 7(4), pp. 532–535. doi: 10.1098/rsbl.2011.0034.

Spagnoletti, N. *et al.* (2011) 'Stone tool use by adult wild bearded capuchin monkeys (Cebus libidinosus). Frequency, efficiency and tool selectivity', *Journal of Human Evolution*, 61(1), pp. 97–107. doi: 10.1016/j.jhevol.2011.02.010.

Spagnoletti, N. *et al.* (2013) 'Vertebrate consumption by wild bearded capuchin monkeys (Sapajus libidinosus) from Fazenda Boa Vista (Piaui, Brazil)', in *II Congresso Latina Americano, XV Congresso Brasileiro de Primatologia, 4-9/8*. Recife (PE), Brazil.

Speth, J. (2010). *The Palaeoanthropology and archaeology of big game hunting: Protein, fat, or politics?* Springer.

St Amant, R. and Horton, T. E. (2008) 'Revisiting the definition of animal tool use', *Animal Behaviour*, 75(4), pp. 1199–1208. doi: 10.1016/j.anbehav.2007.09.028.

Stanford, C. B. *et al.* (2000) 'Chimpanzees in Bwindi-Impenetrable National Park, Uganda, use different tools to obtain different types of honey', *Primates*, 41(3), pp. 337–341. doi: 10.1007/BF02557602.

Stoffregen, T. A. (2003) 'Affordances as properties of the animal-environment system', *Ecological*

Psychology, 15(12), pp. 115–134. doi: 10.1207/S15326969ECO1502_2.

Stotz, K. (2014) 'Extended evolutionary psychology: The importance of transgenerational developmental plasticity', *Frontiers in Psychology*, 5, p. 908. doi: 10.3389/fpsyg.2014.00908.

Stotz, K. (2017) 'Why developmental niche construction is not selective niche construction: And why it matters', *Interface Focus*, 7(5), p. 20160157. doi: 10.1098/rsfs.2016.0157.

Stout, D. and Chaminade, T. (2009) 'Making tools and making sense: Complex, intentional behaviour in human evolution', *Cambridge Archaeological Journal*, 19(1), pp. 85–96. doi: 10.1017/S0959774309000055.

Sugiyama, Y. (1981) 'Observations on the population dynamics and behavior of wild chimpanzees at Bossou, Guinea, in 1979-1980', *Primates*, 22(4), pp. 435–444. doi: 10.1007/BF02381236.

Sugiyama, Y. (1989) 'Description of some characteristic behaviours and discussion on their propagation process among chimpanzees of Bossou, Guinea', in Sugiyama, Y. (ed.) *Behavioural studies of wild chimpanzees at Bossou, Guinea*. Inuyama: Primate Research Institute, Kyoto University, pp. 43–76.

Sugiyama, Y. (1994) 'Tool use by wild chimpanzees', *Nature*, 367(6461), pp. 327–327. doi: 10.1038/367327a0.

Sugiyama, Y. (1995a) 'Drinking tools of wild chimpanzees at Bossou', *American Journal of Primatology*, 37, pp. 263–269. doi: 10.1002/ajp.1350370308.

Sugiyama, Y. (1995b) 'Tool-use for catching ants by chimpanzees at Bossou and Monts Nimba, West Africa', *Primates*, 36(2), pp. 193–205. doi: 10.1007/BF02381345.

Sugiyama, Y. (1997) 'Social tradition and the use of tool-composites by wild chimpanzees', *Evolutionary Anthropology*, 6(1), pp. 23–27. doi: 10.1002/(SICI)1520-6505(1997)6:1<23::AID-EVAN7>3.0.CO;2-X.

Sugiyama, Y. (1998) ‘Local variation of tool-using repertoire in wild chimpanzees’, in Nishida, T. (ed.) *Comparative study of the behaviour of the genus Pan by compiling video ethogram*. Kyoto: Nissho Printer, pp. 82–91.

Sugiyama, Y. and Humle, T. (2011) ‘A wild chimpanzee uses a stick to disable a snare at Bossou, Guinea’, *Pan Africa News*, 18(1), pp. 3–4. doi: 10.5134/143530.

Sugiyama, Y. and Koman, J. (1979a) ‘Social structure and dynamics of wild chimpanzees at Bossou, Guinea’, *Primates*, 20(3), pp. 323–339. doi: 10.1007/BF02373387.

Sugiyama, Y. and Koman, J. (1979b) ‘Tool-using and -making behavior in wild chimpanzees at Bossou, Guinea’, *Primates*, 20(4), pp. 513–524. doi: 10.1007/BF02373433.

Sugiyama, Y. and Koman, J. (1987) ‘A preliminary list of chimpanzees’ alimentation at Bossou, Guinea’, *Primates*, 28, pp. 133–147. doi: 10.1007/bf02382192.

Sugiyama, Y., Koman, J. and Bhoye Sow, M. (1988) ‘Ant-catching wands of wild chimpanzees at bossou, guinea’, *Folia Primatologica*, 51, pp. 56–60. doi: 10.1159/000156357.

Susi, T. and Ziemke, T. (2005) ‘On the subject of objects: Four views on object perception and tool use’, *tripleC*, 3(2), pp. 6–19. doi: https://doi.org/10.31269/triplec.v3i2.19.

Sutton, J. (2006) ‘Distributed cognition: Domains and dimensions’, *Pragmatics and Cognition*, 14(2), pp. 235–247. doi: 10.1075/pc.14.2.05sut.

Suzuki, A. (1966) ‘On the insect-eating habits among wild chimpanzees living in the savanna woodland of western Tanzania’, *Primates*, 7(4), pp. 481–487. doi: 10.1007/bf01730244.

Szokolszky, A. *et al.* (2019) ‘Ecological approaches to perceptual learning: learning to perceive and perceiving as learning’, *Adaptive Behavior*, 27(6), pp. 363–388. doi: 10.1177/1059712319854687.

Takeshita, H. *et al.* (2005) ‘Exploring by doing: How young chimpanzees discover surfaces through

actions with objects', *Infant Behavior and Development*, 28(3), pp. 316–328. doi: 10.1016/j.infbeh.2005.05.009.

Tan, A. W. Y. *et al.* (2015) 'There is more than one way to crack an oyster: Identifying variation in burmese long-tailed macaque (Macaca fascicularis aurea) stone-tool use', *PLoS ONE*, 10(5), p. e0124733. doi: 10.1371/journal.pone.0124733.

Tan, A. W. Y. *et al.* (2016) 'Complex processing of prickly pear cactus (Opuntia sp.) by free-ranging long-tailed macaques: Preliminary analysis for hierarchical organisation', *Primates*, 57(2), pp. 141–147. doi: 10.1007/s10329-016-0525-3.

Tan, A. W. Y. (2017) 'From play to proficiency: The ontogeny of stone-tool use in coastal-foraging long-tailed macaques (Macaca fascicularis) from a comparative perception-action perspective', *Journal of Comparative Psychology*, 131(2), pp. 89–114. doi: 10.1037/com0000068.

Tan, A. W. Y. *et al.* (2018) 'Young macaques (Macaca fascicularis) preferentially bias attention towards closer, older, and better tool users', *Animal Cognition*, 21(4), pp. 551–563. doi: 10.1007/s10071-018-1188-9.

Teleki, G. (1973) 'Notes on chimpanzees interactions with small carnivores in Gombe National Park, Tanzania', *Primates*, 14(4), pp. 407–411. doi: 10.1007/bf01731361.

Tennie, C. *et al.* (2020) 'The zone of latent solutions and its relevance to understanding ape cultures', *Biology and Philosophy*, 35(5), p. 55. doi: 10.1007/s10539-020-0976-9.

Tennie, C., Call, J. and Tomasello, M. (2009) 'Ratcheting up the ratchet: On the evolution of cumulative culture', *Philosophical Transactions of the Royal Society B: Biological Sciences*, 364(1528), pp. 2405–2415. doi: 10.1098/rstb.2009.0052.

Terborgh, J. (1983) *Five new world primates: a study in comparative ecology*. Princeton, NJ: Princeton University Press.

Thompson, E. (2005) 'Sensorimotor subjectivity and the enactive approach to experience', *Phenomenology and the Cognitive Sciences*, 4, pp. 407–427. doi: 10.1007/s11097-005-9003-x.

Thorndike, E. L. (1911) *Animal intelligence*. Darien, CT: Hafner Publishing Company.

Tinbergen, N. (1951) *The study of instinct*. Oxford: Clarendon Press.

Tinbergen, N. (1963) 'On aims and methods of ethology', *Zeitschrift fur Tierpsychologie*, 20(4), pp. 410–433. doi: 10.1111/j.1439-0310.1963.tb01161.x.

Tomasello, M. (1994) 'The question of chimpanzee cultures', in Wrangham, R. W. et al. (eds) *Chimpanzee cultures*. Cambridge MA: Harvard University Press, pp. 301–377.

Tomasello, M. (1996) 'Do apes ape?', in Heyes, C. M. and Gaaled, B. G. (eds) *Social learning in animals: the roots of culture*. London: Academic Press, pp. 319–346.

Tomasello, M. and Call, J. (1997) *Primate Cognition*. New York: Oxford University Press.

Tomasello, M., Melis, A. P., Tennie, C., Wyman, E., & Herrmann, E. (2012). Two key steps in the evolution of human cooperation: The interdependence hypothesis. *Current Anthropology*, *53*(6), 673–692. https://doi.org/10.1086/668207

Tonooka, R. (2001) 'Leaf-folding behavior for drinking water by wild chimpanzees (Pan troglodytes verus) at Bossou, Guinea', *Animal Cognition*, 4, pp. 325–334. doi: 10.1007/s100710100110.

Tonooka, R., Inoue, R. and Matsuzawa, T. (1994) 'Leaf-folding behaviour for drinking water by wild chimpanzees at Bossou, Guinea: A field experiment and leaf selectivity (in Japanese with English summary)', *Primate Research*, 10(3), pp. 307–313.

Tonooka, R., Tomonaga, M. and Matsuzawa, T. (1997) 'Acquisition and transmission of tool making and use for drinking juice in a group of captive chimpanzees (Pan troglodytes)', *Japanese Psychological Research*, 4(4), pp. 407–427. doi: 10.1111/1468-5884.00058.

Torrence, R. (1989) *Retooling: towards a behavioral theory of stone tools*, *Time, Energy and Stone Tools*. Cambridge: Cambridge University Press.

Toth, N., & Schick, K. (2018). An overview of the cognitive implications of the Oldowan industrial complex. *Azania: Archaeological Research in Africa*, *53*(1), 3–39. https://doi.org/10.1080/0067270X.2018.1439558

Turcsán, B. *et al.* (2015) 'Fetching what the owner prefers? Dogs recognize disgust and happiness in human behaviour', *Animal Cognition*, 18, pp. 83–94. doi: 10.1007/s10071-014-0779-3.

Turvey, M. T. (1992) 'Affordances and prospective control: An outline of the ontology', *Ecological Psychology*, 4(3), pp. 173–187. doi: 10.1207/s15326969eco0403_3.

Turvey, M. T. and Shaw, R. (1979) 'The primacy of perceiving: An ecology reformation of perception for understanding memory', *Perspectives on memory research: Essays in honor of Uppsala University's 500th Anniversary*. doi: 10.4324/9781315774893.

Tutin, C. E. G. and Fernandez, M. (1992) 'Insect-eating by sympatric lowland gorillas (Gorilla g. gorilla) and chimpanzees (Pan t. troglodytes) in the Lope Reserve, Gabon', *American Journal of Primatology*, 28(1), pp. 29–40. doi: 10.1002/ajp.1350280103.

Tutin, C. E. G., Ham, R. and Wrogemann, D. (1995) 'Tool-use by chimpanzees (Pan t. troglodytes) in the Lope Reserve, Gabon', *Primates*, 36(2), pp. 181–192. doi: 10.1007/BF02381344.

Udell, M. A. R., Dorey, N. R. and Wynne, C. D. L. (2011) 'Can your dog read your mind? Understanding the causes of canine perspective taking', *Learning and Behavior*, 39(4), pp. 289–302. doi: 10.3758/s13420-011-0034-6.

Vaesen, K. (2012a) 'Cumulative cultural evolution and demography', *PLoS ONE*, 7(7), p. e40989. doi: 10.1371/journal.pone.0040989.

Vaesen, K. (2012b) 'The cognitive bases of human tool use', *Behavioral and Brain Sciences*, 35(4), pp.

203–218. doi: 10.1017/S0140525X11001452.

Varela, F. J. *et al.* (1991) *The embodied mind: Cognitive science and human experience*, *The Embodied Mind: Cognitive Science and Human Experience*. Cambridge, MA: MIT Press. doi: 10.29173/cmplct8718.

Varela, F. J. (1999) *Ethical know-how: Action, wisdom, and cognition*. Stanford, CA: Stanford University Press.

Verderane, M. P. *et al.* (2013) 'Socioecology of wild bearded capuchin monkeys (Sapajus libidinosus): An analysis of social relationships among female primates that use tools if feeding', *Behaviour*, 150, pp. 659–689. doi: 10.1163/1568539X-00003076.

de Vignemont, F (2017) 'Agency and bodily ownership: the bodyguard hypothesis', in de Vignemont, Frederique and Smith, A. J. . (eds) *The Subject's matter. Self-consciousness and the body*. Cambridge MA: MIT Press, pp. 217–236.

Visalberghi, E. *et al.* (2007) 'Characteristics of hammer stones and anvils used by wild bearded capuchin monkeys (Cebus libidinosus) to crack open palm nuts', *American Journal of Physical Anthropology*, 132(3), pp. 426–444. doi: 10.1002/ajpa.20546.

Visalberghi, E. *et al.* (2008) 'Physical properties of palm fruits processed with tools by wild bearded capuchins (Cebus libidinosus)', *American Journal of Primatology*, 70(9), pp. 884–891. doi: 10.1002/ajp.20578.

Visalberghi, E., Spagnoletti, N., *et al.* (2009) 'Distribution of potential suitable hammers and transport of hammer tools and nuts by wild capuchin monkeys', *Primates*, 50(2), pp. 95–104. doi: 10.1007/s10329-008-0127-9.

Visalberghi, E., Addessi, E., *et al.* (2009) 'Selection of effective stone tools by wild bearded capuchin monkeys', *Current Biology*, 19(3), pp. 213–217. doi: 10.1016/j.cub.2008.11.064.

Visalberghi, E. *et al.* (2013) 'Use of stone hammer tools and anvils by bearded capuchin monkeys over time and space: Construction of an archeological record of tool use', *Journal of Archaeological Science*, 40(8), pp. 3222–3232. doi: 10.1016/j.jas.2013.03.021.

Visalberghi, E. *et al.* (2015) 'Percussive tool use by Taï western chimpanzees and fazenda boa vista bearded capuchin monkeys: A comparison', *Philosophical Transactions of the Royal Society B: Biological Sciences*, 370, p. 20140351. doi: 10.1098/rstb.2014.0351.

Visalberghi, E. *et al.* (2016) 'Factors affecting cashew processing by wild bearded capuchin monkeys (Sapajus libidinosus, Kerr 1792)', *American journal of primatology*, 78(8), pp. 799–815. doi: 10.1002/ajp.22545.

Visalberghi, E. *et al.* (2017) 'Female bearded capuchin monkeys (Sapajus libidinosus) use objects to solicit the sexual partner', *Journal of Comparative Psychology*, 131(3), pp. 207–213. doi: 10.1037/com0000072.

Visalberghi, E. and Fragaszy, D. M. (2012) 'What Is Challenging About Tool Use? The Capuchin's Perspective', in Wasserman, E. A. and Zentall, T. R. (eds) *Comparative Cognition: Experimental Explorations of Animal Intelligence*. New York, NY: Oxford University Press, pp. 777–799. doi: 10.1093/acprof:oso/9780195377804.003.0028.

Visalberghi, E. and Fragaszy, D. M. (2013) 'The etho-cebus project: Stone-tool use by wild capuchin monkeys', in Sanz, C. M., Call, J., and Boesch, C. (eds) *Tool Use in Animals Cognition and Ecology*. New York, NY: Cambridge University Press, pp. 203–222. doi: 10.1017/CBO9780511894800.013.

Visalberghi, E. and Limongelli, L. (1994) 'Lack of comprehension of cause-effect relations in tool-using capuchin monkeys (Cebus apella).', *Journal of Comparative Psychology*, 108(1), pp. 15–22. doi: 10.1037//0735-7036.108.1.15.

Visalberghi, E. and Néel, C. (2003) 'Tufted capuchins (Cebus apella) use weight and sound to choose

between full and empty nuts', *Ecological Psychology*, 15(3), pp. 215–228. doi: 10.1207/S15326969ECO1503_2.

Visalberghi, E. and Trinca, L. (1989) 'Tool use in capuchin monkeys: Distinguishing between performing and understanding', *Primates*, 30, pp. 311–521. doi: 10.1007/BF02380877.

Vitale, A. F., Visalberghi, E. and De Lillo, C. (1991) 'Responses to a snake model in captive crab-eating macaques (Macaca fascicularis) and captive tufted capuchins (Cebus apella)', *International Journal of Primatology*, 12(3), pp. 277–286. doi: 10.1007/BF02547588.

van de Waal, E., Borgeaud, C. and Whiten, A. (2013) 'Potent social learning and conformity shape a wild primate's foraging decisions', *Science*, 340(6131), pp. 483–485. doi: 10.1126/science.1232769.

Waga, I. C. *et al.* (2006) 'Spontaneous tool use by wild capuchin monkeys (Cebus libidinosus) in the Cerrado', *Folia Primatologica*, 77(5), pp. 337–344. doi: 10.1159/000093698.

Walls, M. (2016) 'Making as a didactic process: Situated cognition and the chaîne opératoire', *Quaternary International*, 405(Part A), pp. 21–30. doi: 10.1016/j.quaint.2015.03.005.

Walls, M. and Malafouris, L. (2016) 'Creativity as a Developmental Ecology', in Glăveanu, V. (ed.) *The Palgrave Handbook of Creativity and Culture Research*. London: Palgrave Macmillan, pp. 623–638. doi: 10.1057/978-1-137-46344-9_30.

Watson, J. B. (1913) 'Psychology as the behaviourist views it', *Psychological Review*, 20(2), pp. 158–177. doi: 10.1037/h0074428.

Watts, D. P. (2008) 'Tool use by chimpanzees at Ngogo, Kibale National Park, Uganda', *International Journal of Primatology*, 29(1), pp. 83–94. doi: 10.1007/s10764-007-9227-4.

West, M., King, A. and Arberg, A. (1988) 'The inheritance of niches: the role of ecological legacies in ontogeny', in Blass, E. (ed.) *Developmental psychobiology and behavioural ecology*. New York: Plenum, pp. 41–62.

Westergaard, G. C. (1995) 'The subsistence technology of capuchins', *International Journal of Primatology*, 15(6), pp. 899–906. doi: 10.1007/BF02736075.

Westergaard, G. C. *et al.* (1998) 'Aimed throwing as a means of food transfer between tufted capuchins (Cebus apella)', *International Journal of Primatology*, 19, pp. 123–131. doi: 10.1023/A:1020315212310.

Westergaard, G. C. *et al.* (2000) 'A comparative study of aimed throwing by monkeys and humans', *Neuropsychologia*, 38(11), pp. 1511–1517. doi: 10.1016/s0028-3932(00)00056-7.

Westergaard, G. C. and Fragaszy, D. M. (1987) 'The manufacture and use of tools by capuchin monkeys (Cebus apella)', *Journal of Comparative Psychology*, 101(2), pp. 159–168. doi: 10.1037/0735-7036.101.2.159.

Westergaard, G. C. and Suomi, S. J. (1994) 'Aimed throwing of stones by tufted capuchin monkeys (Cebus apella)', *Human Evolution*, 9, pp. 323–329. doi: 10.1007/BF02435518.

Westergaard, G. C. and Suomi, S. J. (1995) 'The production and use of digging tools by monkeys: A nonhuman primate model of a hominid subsistence activity', *Journal of Anthropological Research*, 51(1), pp. 1–8. doi: 10.1086/jar.51.1.3630369.

Westergaard, G. C. and Suomi, S. J. (1997) 'Capuchin monkey (Cebus apella) grips for the use of stone tools', *American Journal of Physical Anthropology*, 103(1), pp. 131–5. doi: 10.1002/(SICI)1096-8644(199705)103:1<131::AID-AJPA9>3.0.CO;2-Z.

Whitehouse, J., Micheletta, J. and Waller, B. (2017) 'Stress behaviours buffer macaques from aggression', *Scientific Reports*, 7(1), p. 11083. doi: 10.1038/s41598-017-10754-8.

Whiten, A. *et al.* (1999) 'Cultures in chimpanzees', *Nature*, 399(6737), pp. 628–685. doi: 10.1038/21415.

Whiten, A. *et al.* (2001) 'Charting cultural variation in chimpanzees', *Behaviour*, 138(11–12), pp.

1481–1516. doi: 10.1163/156853901317367717.

Whiten, A. *et al.* (2009) 'Emulation, imitation, over-imitation and the scope of culture for child and chimpanzee', *Philosophical Transactions of the Royal Society B: Biological Sciences*, 364(1528), pp. 2417–2428. doi: 10.1098/rstb.2009.0069.

Whiten, A., Horner, V. and Marshall-Pescini, S. (2003) 'Cultural Panthropology', *Evolutionary Anthropology*, 12(2), pp. 92–105. doi: 10.1002/evan.10107.

Whitesides, G. H. (1985) 'Nut cracking by wild chimpanzees in Sierra Leone, West Africa', *Primates*, 26, pp. 91–94. doi: 10.1007/BF02389050.

Wilson, M. (2002) 'Six views of embodied cognition', *Psychonomic Bulletin and Review*, pp. 625–636. doi: 10.3758/BF03196322.

Witherington, D. C. (2019) 'Making sense of microdevelopment, macrodevelopment, and their interrelation', *Human Development*, 63, pp. 33–37. doi: 10.1159/000501635.

Wittgenstein, L. (1953) *Philosophical investigations*. Oxford: Blackwell.

Wolff, P. (2007) 'Representing causation', *Journal of Experimental Psychology: General*, 136(1), pp. 82–111. doi: 10.1037/0096-3445.136.1.82.

Wondra, E. M. *et al.* (2016) 'A new report of chimpanzee ant-fishing from the Issa Valley, Tanzania', *African Primates*, 11(1), pp. 1–18.

Wrangham, R. W. *et al.* (2016) 'Distribution of a chimpanzee social custom is explained by matrilineal relationship rather than conformity', *Current Biology*, 26, pp. 3033–3037. doi: 10.1016/j.cub.2016.09.2005.

Wu, J. and Baldwin, I. T. (2009) 'Herbivory-induced signalling in plants: Perception and action', *Plant, Cell and Environment*, 32(9), pp. 1161–1174. doi: 10.1111/j.1365-3040.2009.01943.x.

Wynn, T. (1993) 'Layers of thinking in tool behaviour', in Gibson, K. R. and Ingold, T. (eds) *Tools, language, and cognition in human evolution*. Cambridge: Cambridge University Press, pp. 389–406. doi: 10.1017/CBO9781107415324.004.

Wynn, T. (1995) 'Handaxe enigmas', *World Archaeology*, 27(1), pp. 10–24. doi: 10.1080/00438243.1995.9980290.

Wynn, T. (2004) 'Comment on McNabb, Binyon and Hazelwood, "The large cutting tools from the South African Acheulean and the question of social traditions"', *Current Anthropology*, 45(5), pp. 672–673. doi: 10.1086/423973.

Wynn, T. *et al.* (2011) '"An ape's view of the oldowan" revisited', *Evolutionary Anthropology*, 20(5), pp. 181–197. doi: 10.1002/evan.20323.

Wynn, T. and McGrew, W. C. (1989) 'An Ape's View of the Oldowan', *Man*, 24(3), pp. 383–398. doi: 10.2307/2802697.

Yamakoshi, G. (1998) 'Dietary responses to fruit scarcity of wild chimpanzees at Bossou, Guinea: Possible implications for ecological importance of tool use', *American Journal of Physical Anthropology*, 106(3), pp. 283–295. doi: 10.1002/(SICI)1096-8644(199807)106:3<283::AID-AJPA2>3.0.CO;2-O.

Yamakoshi, G. (2001) 'Ecology of tool use in wild chimpanzees: Toward reconstruction of early hominid evolution', in Matsuzawa, T. (ed.) *Primate origins of human cognition and behaviour*. Tokyo: Springer, pp. 537–556.

Yamakoshi, G. (2011) 'Pestle-pounding behaviour: the key to the coexistence of humans and chimpanzees', in Matsuzawa, T., Humle, T., and Sugiyama, Y. (eds) *The chimpanzees of Bossou and Nimba. Primatology monographs*. Tokyo: Springer, pp. 107–115.

Yamakoshi, G. and Matsuzawa, T. (1993) 'Preliminary surveys of the chimpanzees in the Nimba

Reserve, Cote d'Ivoire', *Primate Research*, 9, pp. 13–18. doi: 10.5134/143483.

Yamakoshi, G. and Myowa-Yamakoshi, M. (2004) 'New observations of ant-dipping techniques in wild chimpanzees at Bossou, Guinea', *Primates*, 45, pp. 25–32. doi: 10.1007/s10329-003-0056-6.

Yamakoshi, G. and Sugiyama, Y. (1995) 'Pestle-pounding behavior of wild chimpanzees at Bossou, Guinea: A newly observed tool-using behavior', *Primates*, 36(4), pp. 489–500. doi: 10.1007/BF02382871.

Yamamoto, S. *et al.* (2008) 'Invention and modification of a new tool use behavior: Ant-fishing in trees by a wild chimpanzee (Pan troglodytes verus) at Bossou, Guinea', *American Journal of Primatology*, 70(7), pp. 699–702. doi: 10.1002/ajp.20544.

Yamamoto, S. *et al.* (2011) 'Ant Fishing in Trees: Invention and Modification of a New Tool-Use Behavior', in Matsuzawa, T., Humle, T., and Suyigama, Y. (eds) *The chimpanzees of Bossou and Nimba. Primatology monographs*. Tokyo: Springer, pp. 123–130. doi: 10.1007/978-4-431-53921-6_13.

Zhu, Q. and Bingham, G. P. (2010) 'Learning to perceive the affordance for long-distance throwing: Smart mechanism or function learning?', *Journal of Experimental Psychology: Human Perception and Performance*, 36(4), pp. 862–875. doi: 10.1037/a0018738.

Appendix 1: Species variant catalogues

Table 24 List of all Chimpanzee variants included, with their functional modes and causal functions

Variant (sites at which present)	Functional mode (causal function)
Aimed throw (BOS, ASS, BUD, GOM, GOU, KIB, MAM, TAI)	Throw (create/augment the value of a social signal, extend the user's reach)
Algae scoop (BOS)	Reach (extend the user's reach)
Ant dip (BOS, ASS, GOM, GOU, TAI)	Insert and probe (extend the user's reach)
Ant fish (BOS, ASS, GOM, LOP, MAK, MAM)	Insert and probe (extend the user's reach)
Anvil prop (BOS)	Apply or drape (amplify the user's mechanical force)
Bee probe (MAK)	Insert and probe (extend the user's reach), hammer or pound (amplify the user's mechanical force)
Branch drag (BOS, BUD, GOM, GOU, KIB, LOP, MAK, MAM, TAI)	Drag (create/augment the value of a social signal)
Branch haul (BOS)	Reach (extend the user's reach)
Comb (BUD)	Scratch or rub (bodily comfort)
Dig and probe (BOS)	Dig (amplify the user's mechanical force), insert and probe (extend the user's reach)
Expel (BOS, GOM, MAK, MAM, TAI)	Insert and probe (extend the user's reach), prod or penetrate (amplify the user's mechanical force)
Flailing stick or club (BOS, GOM, MAM, TAI)	Club (create/augment the value of a social signal)
Fluid dip (BOS, ASS, GOM, GOU, KIB, LOP, MAK, MAM, TAI)	Insert and probe (extend the user's reach)
Fly whisk (BUD, GOM, TAI)	Wave (bodily comfort)
Insect pound (BOS, TAI)	Insert and probe (extend the user's reach), hammer or pound (amplify the user's mechanical force)
Investigatory probe (BOS, GOM, GOU, KIB, MAK, MAM, TAI)	Insert and probe (extend the user's reach)
Leaf brush (GOM)	Wipe (effective control of liquids and/or small solids)
Leaf clip (BOS, BUD, KIB, MAK, MAM, TAI)	Symbolise (create/augment the value of a social signal)
Leaf cushion (BOS, GOU, KIB, TAI)	Apply or drape (bodily comfort)
Leaf dab (GOM, GOU, KIB)	Absorb (bodily comfort)

Table 1 Cont. List of all Chimpanzee variants included, with their functional modes and causal functions

Variant (sites at which present)	Functional mode (causal function)
Leaf mop (GOM, MAK)	Wipe (effective control of liquids and/or small solids)
Leaf napkin (ASS, BUD, GOM, GOU, KIB, MAM, TAI)	Wipe (bodily comfort)
Leaf sponge/fold/spoon (BOS, BUD, GOM, GOU, KIB, LOP, MAM, TAI)	Absorb (effective control of liquids and/or small solids)
Leaf wipe (GOM, TAI)	Wipe (effective control of liquids and/or small solids)
Lever open (GOM, GOU, LOP, TAI)	Pry or apply leverage (amplify the user's mechanical force)
Marrow pick (GOU, TAI)	Insert and probe (extend the user's reach)
Nasal probe (MAM)	Insert and probe (bodily comfort)
Nut crack (BOS, TAI)	Hammer or pound (amplify the user's mechanical force)
Nut extraction (GOU, TAI)	Pry or apply leverage (amplify the user's mechanical force
Open and probe (GOU)	Hammer or pound (amplify the user's mechanical force), insert and probe (extend the user's reach)
Palm sap collect* (BOS)	Absorb (effective control of liquids and/or small solids)
Perforate termite nest (GOU)	Prod or penetrate (amplify the user's mechanical force)
Pestle-pound (BOS)	Hammer or pound (amplify the user's mechanical force)
Pound beehive (GOU)	Hammer or pound (amplify the user's mechanical force)
Push-pull (BOS, GOM, MAM, TAI)	Insert and probe (extend the user's reach), absorb (effective control of liquids and/or small solids)
Rain cover (GOU)	Apply or drape (bodily comfort)
Resin pound (BOS)	Insert and probe (extend the user's reach), hammer or pound (amplify the user's mechanical force)
Seat stick (GOU)	Apply or drape (bodily comfort)
Self-tickle (GOM, GOU)	Scratch or rub (bodily comfort)
Termite fish (BOSS, ASS, GOM, GOU, MAK)	Insert and probe (extend the user's reach)

Table 25 List of all Capuchin variants included, with their functional modes and causal functions

Variant (site)	Functional mode (causal function)
Aimed throw (SDC, FBV)	Throw (create/augment the value of a social signal, extend the user's reach)
Dig (SDC)	Hammer or pound (amplify the user's mechanical force), dig (amplify the user's mechanical force)
Expel (SDC)	Insert and probe (extend the user's reach), prod or penetrate (extend the user's reach)
Fluid dip (SDC)	Insert and probe (extend the user's reach)
Hatchet* (SDC)	Hammer or pound (amplify the user's reach)
Nasal probe (SDC)	Insert and probe, scratch or rub (bodily comfort)
Nut crack (SDC, FBV)	Hammer or pound (amplify the user's mechanical force)
Open and probe (SDC)	Hammer or pound (amplify the user's mechanical force), insert and probe (extend the user's reach)
Poking stick (spear) (SDC)	Prod or penetrate, club (create or augment the value of a social signal)
Pound open* (SDC)	Hammer or pound (amplify the user's mechanical force)
Rock pound* (SDC)	Hammer or pound (amplify the user's mechanical force)
Self-poke* (SDC)	Scratch or rub (bodily comfort)
Tooth pick* (SDC)	Scratch or rub (bodily comfort)

Table 26 List of all Macaque variants included, with their functional modes and causal functions

Variant (site)	Functional mode (causal function)
Axe hammer* (PNY, SRY)	Hammer or pound (amplify the user's mechanical force)
Nut crack (PNY, SRY)	Hammer or pound (amplify the user's mechanical force)
Hatchet* (PNY, SRY)	Hammer or pound (amplify the user's mechanical force)

Appendix 2: Values assigned and aspect complexity of NHP variants

Site code	Variant	Prevalence	Context	Mode	Secondary	Causal fun	Secondary	Max mods	Crit(min)	Crit(max)	Phases	Focal aspe	Modules	Static relat	Dynamic re	Total objec	Problem so	Techno-uni
BOS	Aimed thro	C	S	Throw	N/A	Create or a	Extend the	0	7	7	4	3	1	0	1	1	3	1
BOS	Algae scoo	C	F	Reach	N/A	Extend the	N/A	4	7	10	4	3	1	0	2	2	6	2
BOS	Ant dip	C	EF	Insert and	N/A	Extend the	N/A	4	7	11	4	3	1	1	1	2	7	2
BOS	Ant fish	R	EF	Insert and	N/A	Extend the	N/A	4	6	9	4	3	1	1	1	2	5	1
BOS	Branch dra	C	S	Drag	N/A	Create or a	N/A	0	6	6	4	3	1	0	1	1	2	1
BOS	Branch hau	R	F	Reach	N/A	Extend the	N/A	3	6	8	4	3	1	1	1	2	4	1
BOS	Dig and pro	R	EF	Dig	Insert and	Amplify the	Extend the	4	11	15	7	4	2	1	2	3	8	2
BOS	Expel	C	EF	Insert and	Poke or spe	Extend the	Amplify the	4	6	9	4	3	1	1	1	2	5	1
BOS	Flailing stic	C	S	Club	N/A	Create or a	N/A	0	5	5	4	3	1	0	1	1	1	1
BOS	Fluid dip	C	EF	Insert and	N/A	Extend the	N/A	3	6	9	4	3	1	1	1	2	5	1
BOS	Insect pour	R	EF	Insert and	Hammer or	Extend the	Amplify the	4	6	9	4	3	1	0	2	2	5	1
BOS	Investigato	C	O	Insert and	N/A	Extend the	N/A	3	6	8	4	3	1	1	1	2	4	1
BOS	Leaf clip	C	S	Symbolise	N/A	Create or a	N/A	1	5	5	4	3	1	0	1	1	1	2
BOS	Leaf cushio	R	H	Apply or dr	N/A	Bodily com	N/A	2	4	5	4	3	1	1	0	1	1	1
BOS	Leaf sponge	C	EF	Absorb	N/A	Effective co	N/A	2	7	8	4	3	1	1	1	2	4	1
BOS	Nut crack	C	EF	Hammer or	N/A	Amplify the	N/A	1	10	12	5	4	1	1	2	3	7	2
BOS	Nut crack (	R	EF	Apply or dr	Hammer or	Amplify the	N/A	2	13	15	7	5	2	2	2	4	8	3
BOS	Palm sap co	R	EF	Absorb	N/A	Effective co	N/A	4	14	20	8	4	3	1	1	2	12	2
BOS	Pestle pour	C	EF	Hammer or	N/A	Amplify the	N/A	3	10	16	6	3	2	0	1	1	10	1
BOS	Push-pull	R	EF	Insert and	Absorb	Extend the	Effective co	3	10	11	6	4	2	1	3	4	5	2
BOS	Resin poun	R	EF	Insert and	Hammer or	Extend the	Amplify the	4	6	9	4	3	1	0	2	2	5	1
BOS	Termite fis	R	EF	Insert and	N/A	Extend the	N/A	3	6	9	4	3	1	1	1	2	5	2
SDC	Aimed thro	C	S	Throw	N/A	Create or a	Extend the	0	7	7	4	3	1	0	1	1	3	1
SDC	Digging too	C	EF	Hammer or	Dig	Amplify the	N/A	0	8	10	4	3	1	0	1	1	6	1
SDC	Expel	C	EF	Insert and	Poke or spe	Extend the	Amplify the	3	7	10	4	3	1	1	1	2	6	1
SDC	Fluid dip	C	EF	Insert and	N/A	Extend the	N/A	3	7	10	4	3	1	1	1	2	6	1
SDC	Hatchet	C	EF	Hammer or	N/A	Amplify the	N/A	1	9	12	5	4	1	1	2	3	7	2
SDC	Nasal prob	R	H	Insert and	Scratch or	Bodily com	N/A	1	6	6	4	3	1	0	1	1	2	1
SDC	Nut crack	C	EF	Hammer or	N/A	Amplify the	N/A	1	9	12	5	4	1	1	2	3	7	2
SDC	Open and p	R	EF	Hammer or	Insert and	Amplify the	Extend the	3	12	16	7	4	2	1	2	3	9	2
SDC	Poking stic	R	S	Poke or spe	Club	Create or a	N/A	2	5	6	4	3	1	0	1	1	2	1
SDC	Pound ope	C	EF	Hammer or	N/A	Amplify the	N/A	0	8	11	4	3	1	0	1	1	7	1
SDC	Scratch	R	H	Scratch or	N/A	Bodily com	N/A	1	5	5	4	3	1	0	1	1	1	1
SDC	Stone pour	C	O	Hammer or	N/A	Amplify the	N/A	0	6	7	4	3	1	0	1	1	3	1
SDC	Tooth pick	R	H	Scratch or	N/A	Bodily com	N/A	1	6	6	4	3	1	1	1	2	2	1
PNY	Axe hamm	C	EF	Hammer or	N/A	Amplify the	N/A	1	6	7	4	3	1	0	1	1	3	1
PNY	Nut crack (	C	EF	Hammer or	N/A	Amplify the	N/A	1	8	12	5	4	1	1	2	3	7	2
PNY	Nut crack (	C	EF	Hammer or	N/A	Amplify the	N/A	1	8	12	5	4	1	1	2	3	7	2

Appendix 3: Cognigrams for Lomekwian variants

Table 27 List of variants derived from Lombard, Högberg and Haidle (2019)

Functional Context	***Variant***
Subsistence	*Carcass process*
	Passive anvil flake production and use
	Bipolar flake production and use
Secondary tool-use	*Passive anvil/hammer flake production*
	Open and probe

Table 28 Inferred Values assigned and aspect complexity of NHP variants, following Lombard, Högberd and Haidle (2019)

Site code	Prevalence	Context	Mode	Secondary	Causal fun	Secondary	Max mods	Crit(min)	Crit(max)	Phases	Focal aspe	Modules	Problem so	Techno-uni
LOM	Caracass pr	EF	Cut	N/A	Amplify the	N/A	0	7	7	4	3	1	3	1
LOM	Passive har	EF	Hammer or	N/A	Amplify the	N/A	0	10	10	4	4	1	6	1
LOM	Bipolar kna	EF	Hammer or	N/A	Amplify the	N/A	1	14	14	5	5	2	9	1
LOM	Passive har	EF	Hammer or	Cut	Amplify the	Amplify the	1	16	16	7	5	2	9	2
LOM	Bipolar kna	EF	Hammer or	Cut	Amplify the	Amplify the	2	20	20	8	6	3	12	2

Figure 55 Cognitive ecology for the behavioural variant 'Passive anvil/hammer flaking'

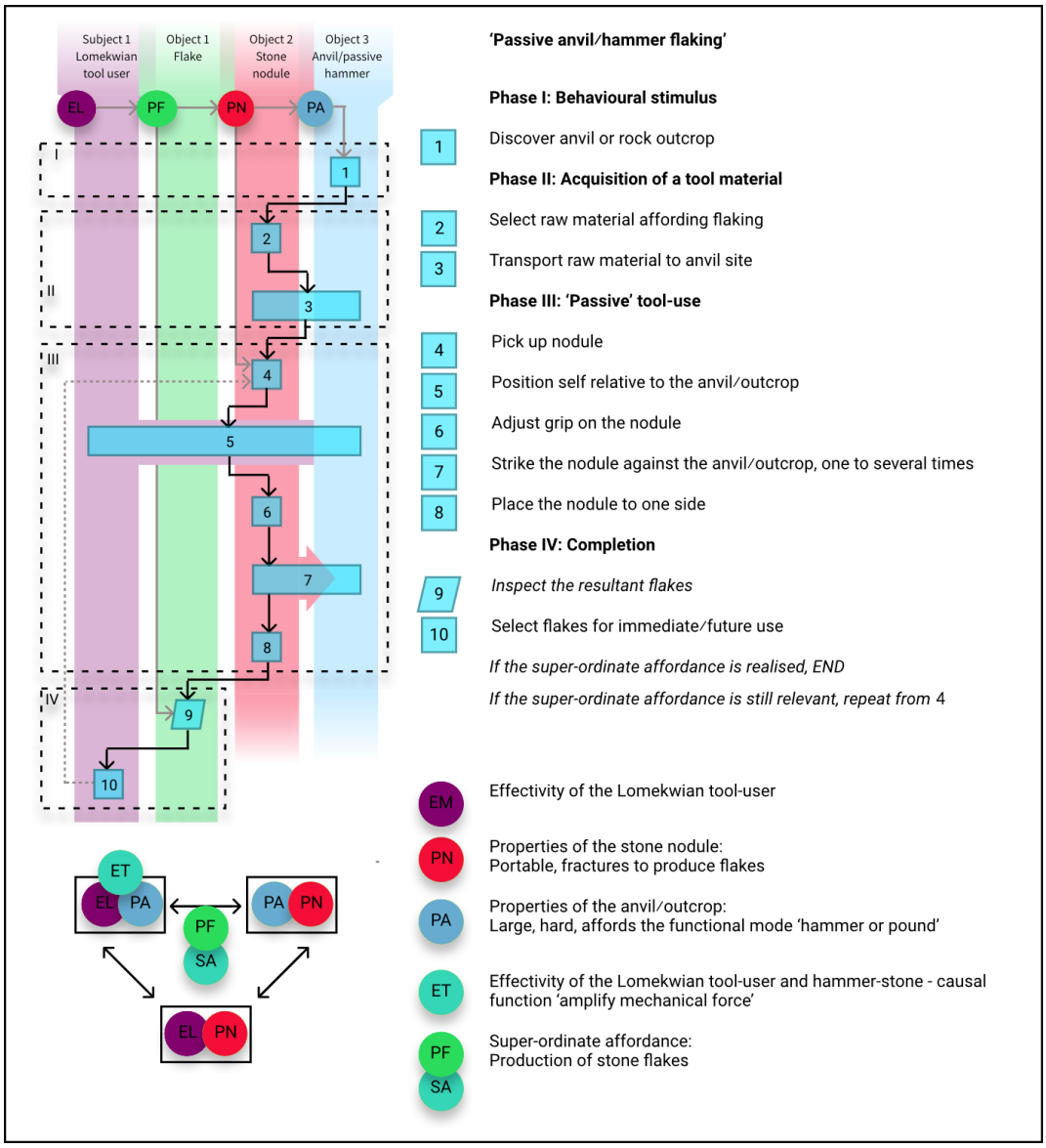


Figure 56 Cognitive ecology for the behavioural variant 'Carcass process'

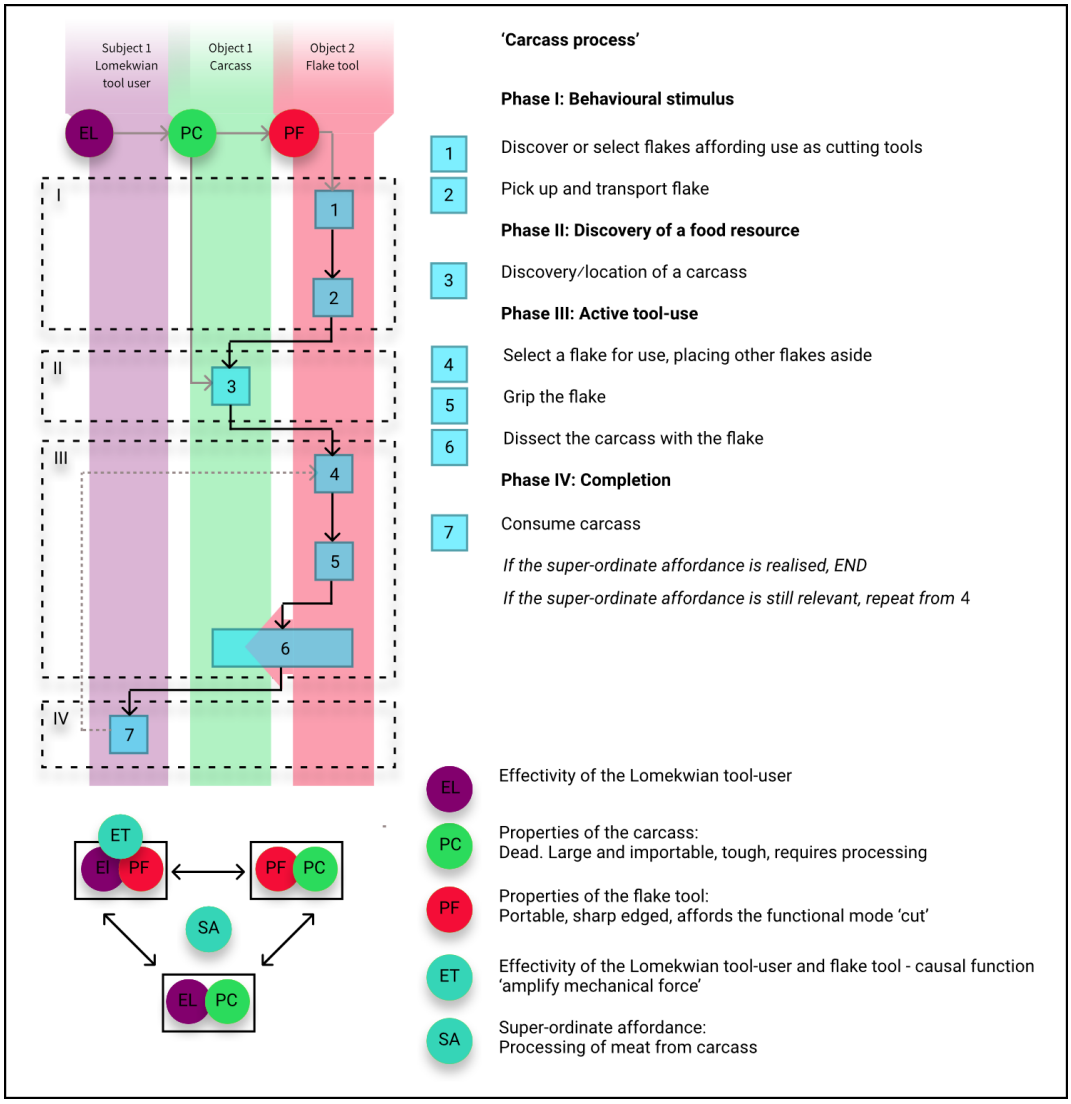


Figure 57 Cognitive ecology for the behavioural variant 'Bipolar flake production'

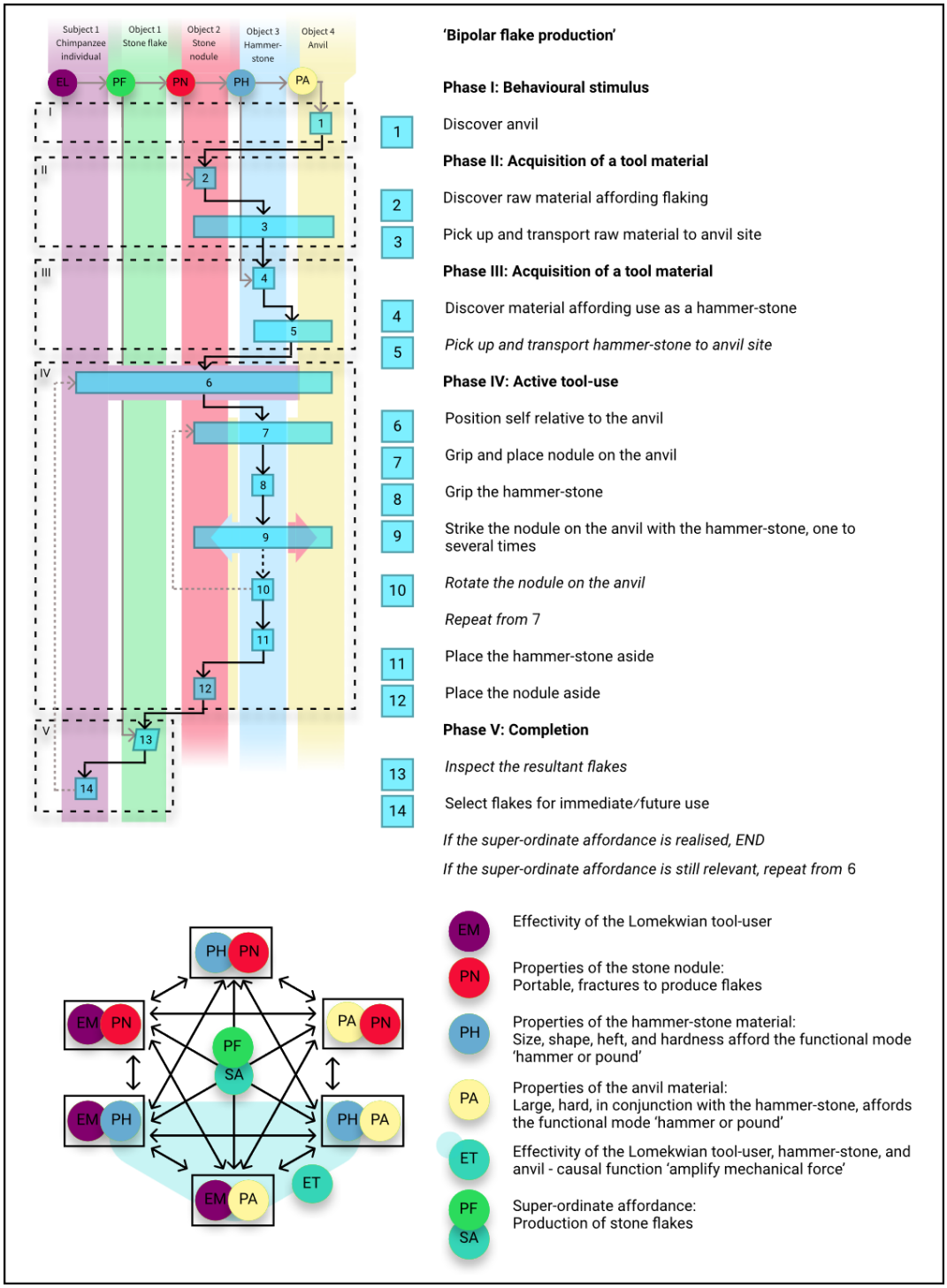


Figure 58 Cognitive ecology for the variant 'Passive anvil flake production and use'

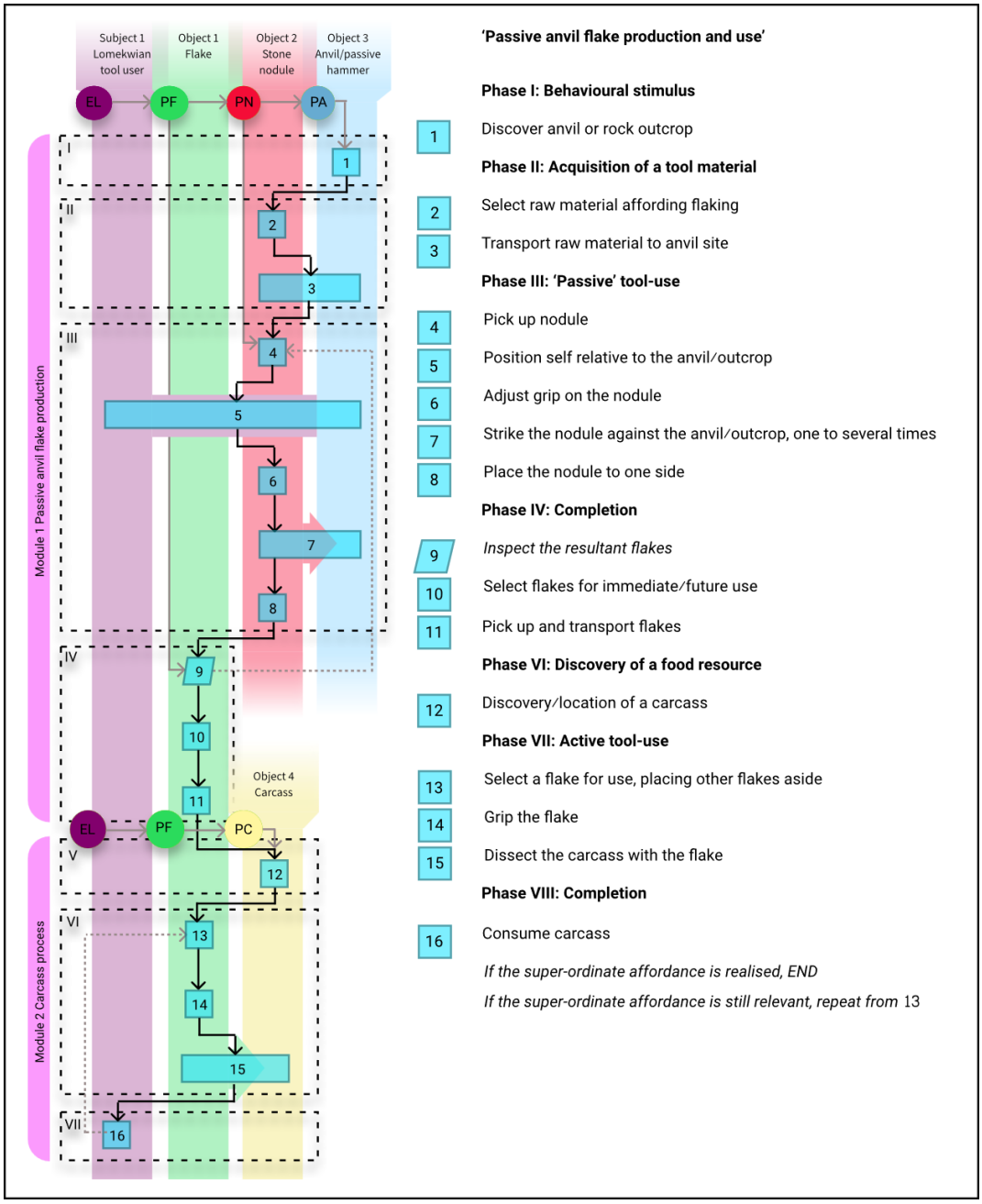


Figure 59 Affordance relationships for the variant 'Passive anvil flake production and use'

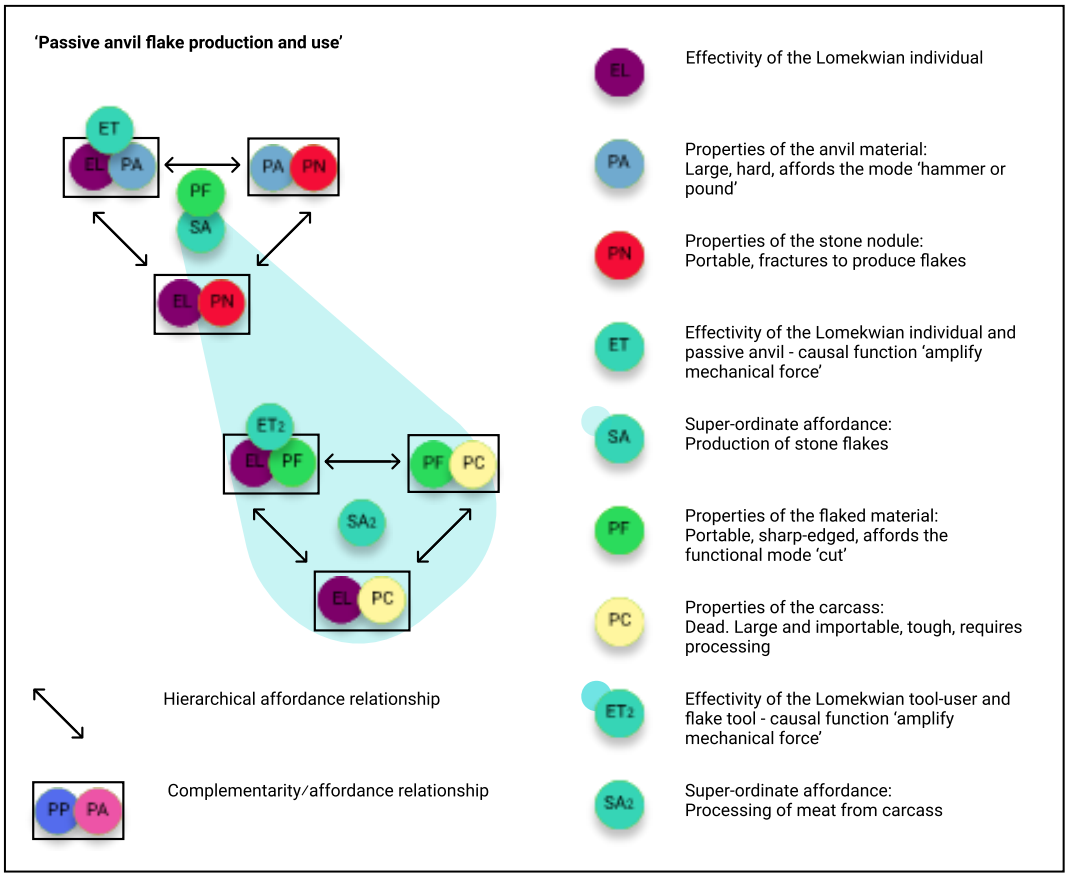


Figure 60 Cognitive ecology for the variant 'Bipolar flake production and use'

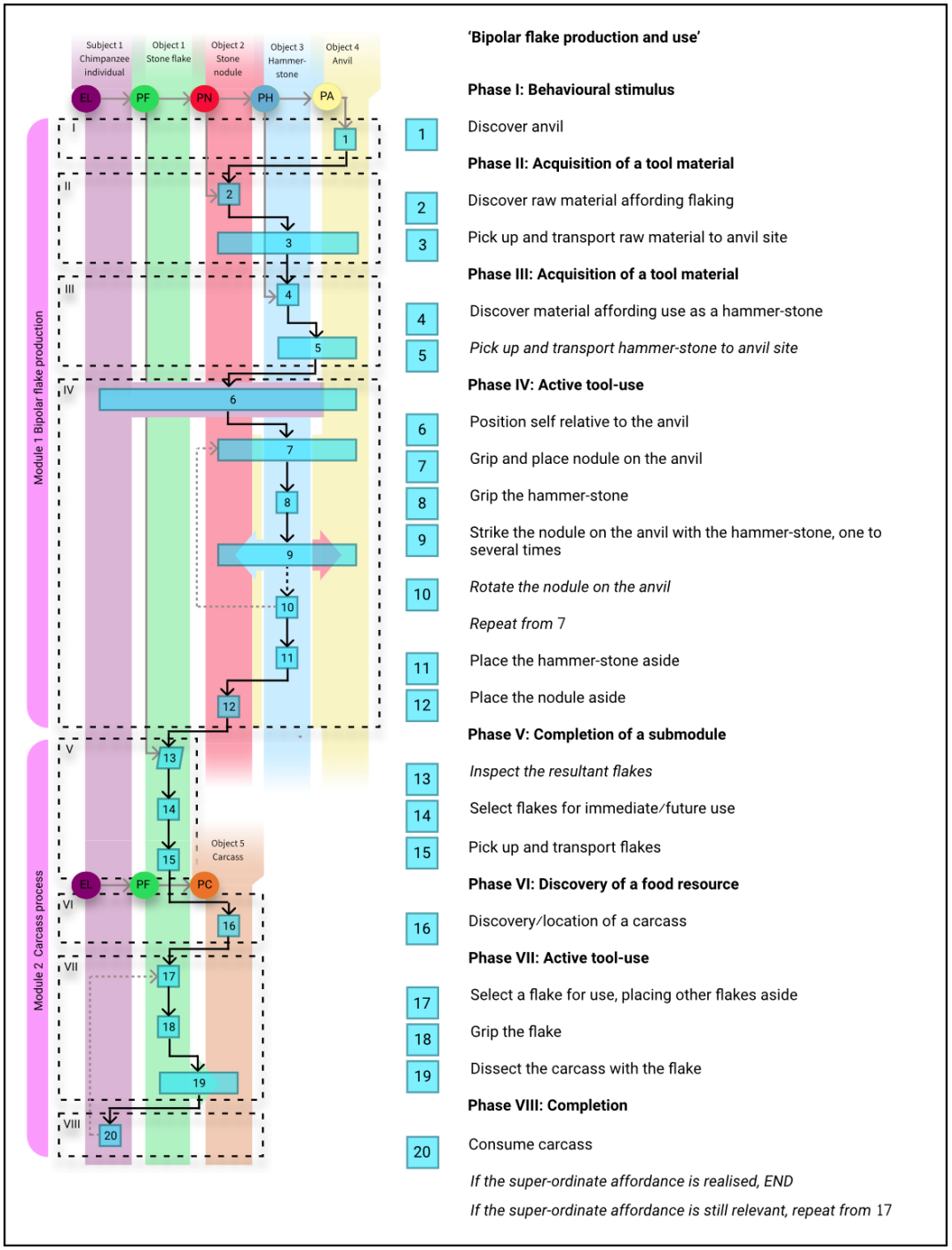


Figure 61 Affordance relationships for the variant 'Bipolar flake production and use'