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Extending material cognition to primate tool use

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ABSTRACT

The concept of extended or distributed cognition has been present in archaeology for some time, yet despite its inclusion of non-human hominin ancestors, it has remained distinctly anthropocentric in nature. Here, we suggest that the same concept may also be used to independently describe and interpret non-human animals within their own social and material networks. We illustrate this suggestion with examples from the tool use behaviour of wild monkeys and chimpanzees. Non-human primate social groups develop bodies of traditional knowledge, and we consider whether idiosyncratic expression of such knowledge may be viewed in terms of an individual's constructed social identity. At a micro-level, the performance of an individual tool use technique may be analogous to the idea of 'personhood' found in anthropological holistic or perspectivist theory; at a macro-level the physical and social distribution of primate technology is amenable to interpretation as an example of extended or distributed cognition. We conclude that combined consideration of extended cognition and niche construction offers a promising means for interpreting the material residues of non-human primate behaviour.

1. Introduction

Humans are cognitively complex creatures. By this, we mean that humans engage in abstract analogical reasoning, understand multiple levels of intentionality in others, can perceive and devise solutions to difficult physical and social problems, and on occasion demonstrate novel behaviour appropriate to resolving difficulties. We also mean that they do these things in ways that involve many components at once. Yet even these broad descriptions do not cover all the ways that the term 'cognition' may be applied to various behavioural, neurological, cultural, social, and material patterns found in and created by humans and other animals (Shettleworth, 2010; Malafouris, 2013). The concept is even discussed for plants (Garzon and Keijzer, 2011). Because of this bewildering variety, we are reluctant to use 'cognition' as anything but a generic umbrella term for information processing (Rowlands, 2009), and consider it a term that always requires qualification to be of any use as a tractable scientific concept.

In this paper, therefore, we do not attempt to address cognition in its nebulous entirety. Instead, we explore the material dimensions of cognition through the specific and narrow lens of tool use. Even more specifically, we examine the ways that wild primate tool use may be usefully understood and examined as an example of extended or distributed cognition. We assess the extent to which tool use as extended cognition may inform our understanding of such phenomena as social traditions and the need to solve foraging problems. We thereby hope to identify ways that we can study the tools themselves (including archaeologically recovered material) in order to reconstruct the processes that underlay their selection, modification and use by non-human primates (NHP). Further, because concepts of agency and personhood are related to cognition in some of its human manifestations, we believe that they are worth considering in tool-using NHP. Our paper presents one way of bringing a cognitive element into the new field of primate archaeology (Carvalho et al., 2008; Haslam et al., 2009; Stewart et al., 2011; Haslam, 2012, 2014a, 2014b; McGrew et al., 2014).

2. Cognition and the distributed mind

All definitions of cognition have a common thread that identifies a reflexive, interactive process, rather than a static character state (Rowlands, 2009). These interactions may in theory occur anywhere from the neuronal level up to and beyond intergenerational transmission of social customs. An important outcome is that cognition is something that changes the physical world as it

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happens, which makes it amenable to scientific observation and, in some cases, archaeological preservation. In the following, we consider the observable, external physical manifestations of cognition in terms of either physical or social domains (Shettleworth, 2010). These do overlap, but their separation helps identify more clearly the specific links between tool use and distributed cognition.

For us, physical cognition involves reasoning about, and solving technical problems through interaction with, the material world. Social cognition involves reasoning about, and solving problems through interaction with, other individuals. In terms of tool use, physical cognition includes such activities as selecting and modifying materials, orienting tools, using appropriate force, identifying targets for tool use and perceiving and assessing their affordances. Tool use affects social cognition by structuring social relationships, by bringing individuals together in ways that would not otherwise occur, and by facilitating social learning. In turn, social learning is essential for creating traditions, and cultural behaviours.

Interactions between individuals and objects (including tools), or between different individuals, may be considered to involve cognition when either the gathering or use of information requires both components. These interactions, and the characteristics of the interacting components, are what we understand to constitute extended or distributed cognition. Since all interactions involving a living entity are inherently relational, and must involve at least two entities, they must all include some aspect of cognition.

We consider all cognition relating to Primate tool-use to be embodied on the grounds that all perception and physical problem-solving processes are constrained by real-world and bodily context (Barrett and Henzi, 2005). Embodiment breaks down the distinction between stimulus, thought and action (Merleau-Ponty, 2002; Costall, 2008).

The notions of extended and distributed mind possess subtle variations in the literature of embodied cognition (Barrett and Henzi, 2005; Ziemke and Frank, 2008). Extended mind theory has drawn from Donald's work on external memory storage (Donald, 1998), to argue that the cognition of an individual lies beyond the internalised 'mind' and in the holistic integration of external objects, or things, with the human organism (Gamble, 2010; Rowlands, 2010). The concept of distributed mind builds on a broad interdisciplinary base – considering cognition to be not just embodied, but also embedded in the external world, and emergent. For some, cognition is situated not just external to the internal mind, but also beyond the individual agent (Clark, 1997; Clark and Chalmers, 1998; Clark, 1999).

With the notion of external cognition, we can assess the abilities or actions of specific individuals, at the time of their acting, but we cannot assess the extent to which their actions were fundamentally dependent on information coming from outside their own body. This situation limits our ability to see how individuals affect others in their social network, and we may miss critical steps in how observed behaviour emerged within and is maintained by certain environmental cues. In this scheme, inanimate objects such as tools are not independent actors, but they do mediate the behaviour of individuals and groups, by constraining the range of options available in time and space – they enable certain activities and prevent others. We note that in this formulation, extended cognition has much in common with niche construction, and we suggest that the latter may actually be a more useful concept than the former in cases where the environment is sufficiently stable for adaptive responses to emerge and succeed (Sterelny, 2010).

In accordance with Actor-Network Theory (Latour, 2003), a system of actors and environment may be viewed as a set of nodes, and cognition is then comprised of a process of nodal interaction and restructuring. The cognitive system involves an active and constant process of engagement, such that 'material culture becomes a physical correlate of that system and part of the extended phenotype of the individual agents that comprise it' (Dunbar et al., 2010, p. 12). There is a clear temporal element involved, as material products resulting from earlier action can transform the nature of later events.

3. Recognising external cognition

To identify cases of primate external cognition (distributed or extended) requires a working definition of the phenomena. We follow Clark and Chalmers (1998) in their use of the Parity Principle. This states that any and all external activity is to be considered cognitive which, were it to take place within the mind, would be considered a part of the cognitive process of a task. For example, the use of a pencil and paper to write out a long division problem would qualify as external cognition. The same process could take place internally as mental arithmetic but as the cognitive load is shared by the environment, in this case by the pencil and paper, cognition can be described as external.

Distributed cognition is broadly defined as the flow of information through a system, with the actor being only part of the information matrix. Cognition is co-constructed, with the constraints of action/interpretation acting as a dynamic mediative process. Distributed cognition is manifest in the shared customs and traditions of a group, as well as in collective decision making. An example is found in the movement patterns of baboons (Strandburg-Pushkin et al., 2015), where no one individual guides or dictates movement initiation or direction. This process is a decision distributed across the band as a whole, with each member only needing to respond to local factors or triggers (Hutchins, 1995), and either following a specific initiator or compromising by taking an intermediate path. Eventually, the troop as a whole will move, because a 'decision' has been made by the group and not by any individual, no matter what their social ranking (Strandburg-Pushkin et al., 2015).

Extended cognition takes things a step further. In an extended model, information can be held in the environment independent of an individual's interaction. Not only can the environment mediate information but it can also retain cognition as an external 'memory store'. In an extended model, material culture acts to make what is conceptually intangible real through physical representation (e.g. Day, 2004). Examples of this are information written in a notebook for future reference (Clark, 1999) or mental time-travel using calendars (Donald, 1998).

Cognition may therefore be embodied, distributed and/or extended (Ziemke and Frank, 2008), moving from the least to most contentious views on external cognitive processes. These categories are not mutually exclusive, and to help distinguish between the three, we adapt the six criteria laid out by Wilson (2002), as follows:

(1) Cognition must be situated: it is grounded by the environment;
(2) Cognition is time sensitive: it is concurrent with stimulus and action;
(3) Cognition is body-based: it is grounded in physical action;
(4) Cognition guides action: it contributes to and underlies behavioural responses;
(5) Cognitive work is offloaded onto the environment: individuals derive and collect causal cues from the environment and others to reduce the cognitive workload;
(6) The environment is part of the cognitive system: information flow between individual and environment is such that the 'mind' is too restrictive a unit for understanding cognition.

The environment can retain and mediate information as an external memory store.

For simplicity these criteria have been reordered hierarchically such that with each criterion, the strength of assumed external cognition increases. The lower criteria represent the lesser degree of material embodiment (Clark, 1999; Nunez, 1999) whilst the final criteria represent radical or full embodiment and distributed cognition (cf. Clark, 1999; Ziemke and Frank, 2008). To be categorised as embodied cognition, we suggest that criteria (1–4) must be fulfilled; to qualify as distributed cognition, (1–5); and as extended cognition, (1–6) are required.

The result of distributed/extended cognitive process is the *active* coupling of objects with the organism. In this coupled system both parts, animal and object, play a causal role in the cognitive process. A distinction is made between *active* and *passive* coupling to separate the phenomenon of extended cognition from historic associations or perceptions of the environment which might be entirely internalised (Clark and Chalmers, 1998). The perception of the sun as being bright is therefore not a case of external cognition as it only plays an explanatory role in cognition and does not mediate between actor and environment.

We note that this definition of external cognition closely mirrors that in some definitions of tool-use: '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*" (emphasis added, St. Amant and Horton, 2008:1203). We therefore hypothesise that all external cognition involves some aspect of tool-use, and the question then becomes, how much of tool-use involves external cognition?

For example, tool-use in chimpanzees is often planned. A chimpanzee may approach a feeding site with tools already in its mouth (Byrne et al., 2013). If the entirety of a tool-use behaviour is pre-planned, and is in fact a series of practical actions to achieve an end, then we suggest that at no stage is external cognition involved, although embodied physical cognition clearly is. To demonstrate distributed cognition it must be shown that the coupling process is *active* and involves a dynamic two-way process where agents are *causally* coupled to their environments. In this way, following Kirsh (2004), we move towards a system of agent and mediator, action and reaction as opposed to a system in which a 'pure-agent' operates and awaits a consequence (2004, p7).

To maintain our focus on the observable components of cognition, it is noted that by adopting criterion (6), we take a conservative view of externalism not wholly in keeping with that of Clarke and Chalmers' (1998) 'active externalism'. Since theory of mind already presents a hurdle for studies in Primate cognition (see Barrett et al., 2007), our approach to extended cognition places greater focus on the storage of external mental *content* rather than external mental *processing*. Whilst for some the sixth criterion is necessary in identifying cases of external cognition, we recognise that for others this does not hold true. Proponents of Material Engagement theory assert that 'things' are incapable of storing mental content that agents may tap into, and that information is instead brought forth in the interaction between mind & matter – i.e. meaning emerges through engagement (Renfrew and Malafouris, 2010; Malafouris, 2013).

4. Physical cognition in wild NHP

Tool-use in non-human primates is predominantly utilitarian, and takes place most often in an extractive foraging context. The most prolific NHP tool users – bearded capuchins (*Sapajus libidinosus*) (Ottoni and Izar, 2008; Mannu and Ottoni, 2009; Spagnoletti et al., 2011), Burmese long-tailed macaques (*Macaca fascicularis aurea*) (Gumert et al., 2009), orang-utans (*Pongo pygmaeus*) (van Schaik et al., 2003) and chimpanzees (*Pan troglodytes*) (McGrew, 1992) – all use either percussive or probe tools to process hidden or encased foods, including nuts, hard fruits, tubers, lizards, and small invertebrates. The sensorimotor-intelligence hypothesis suggests that to facilitate these extractive diets in the absence of a physical or anatomical adaptation, increased cranial capacity and greater manual dexterity have been evolutionarily selected for (Parker and Gibson, 1977; Melin et al., 2014). Yet despite evidence that foraging skills have played a role in primate cognitive evolution (Reader et al., 2011), there is no conclusive data showing primate tool use in itself to be an adaptive mechanism in the strict sense of differentially increasing reproductive fitness (Biro et al., 2013).

Tool manufacture and use mediates between environment and individual. Physical cognition is visible in the flexibility of alternative techniques expressed by an individual, and in the appropriate mapping of tool morphology onto ecological context. NHP tool use may be structurally simpler than in humans, yet in order to reach a goal via the specific actions of a particular technique, individual primates still need to establish a relationship between themselves, the tool they exploit, and a target item (Visalberghi and Fragaszy, 2006). To operate effectively, these relational representations involve perceiving and acting on the properties of objects in relation to other objects. For example, bearded capuchins and chimpanzees appear to recognise functional and non-functional tool features (Sabbatini et al., 2012), and tool selection has been shown to vary with ecological constraints, required mechanical properties (Massaro et al., 2012), and risks associated with target foods (Humle and Matsuzawa, 2002; Sirianni and Visalberghi, 2013).

Iterations and modification phases both before and during tool use bouts suggest a reflexive component to physical cognition and material interaction. As a NHP tool user engages with the environment they must continuously monitor the relationships between themselves and all other foci, adapting and altering their technique when necessary.

4.1. Capuchin nut-cracking at Fazenda Boa Vista, Brazil

Wild Brazilian bearded capuchin monkeys at the Fazenda Boa Vista (FBV) site regularly use stone tools to pound open hard palm nuts (Visalberghi and Fragaszy, 2013). *Astrocaryum* palm nuts have a thick, hard husk that bearded capuchins (*Sapajus libidinosus*) cannot remove without tools. To crack the nuts, the capuchin must first find (and often transport) a suitable hammer and suitable anvil with the appropriate mechanical properties (Visalberghi et al., 2007, 2013) (Fig. 1). The nut must be positioned correctly on the anvil, in order to prevent it rolling or flying off (Fragaszy et al., 2010; Fragaszy et al., 2013a); the capuchin must then coordinate itself, its grip of the hammer-stone, and strike in relation to the nut and anvil. Thus relational representations exist between actor, nut, hammer stone and anvil. These relations are visible in the tool-selection, positioning and sequence of actions, and emergent in the process of actor and environmental interaction.

This relational coding can be seen as a two way process. Evidence suggests that the mediating process of tool on environment can have an internalised effect on the actor's cognition at a neuronal level (Maravita and Iriki, 2004). Tool-use, as an extension of the body, causes a re-structuring of the plastic neuronal representation of the user's physical self. This means that through manipulation of a long stick to reach an object, for example, the individual's perception of their own body, posture, and distance

Fig. 1. Wild capuchin stone tool niche construction at Fazenda Boa Vista, Brazil. (a) An adult male capuchin bipedally transports a quartzite pounding tool to the small sandstone anvil (with a nut on it) at the right of picture. (b) An adult and juvenile capuchin (with its hand on a quartzite pounding tool) on a large sandstone anvil, surrounded by broken nut debris.

between themselves and other objects is altered as if the stick were incorporated within their 'body schema'.

The physicality of tool use satisfies criteria (1–4). In order for these relationships to be causal, which would satisfy criterion (5), there must be some indication that actions taken in the behavioural sequence are epistemic. For the FBV example, whilst the majority of actions appear purely practical, the placing of the nut on the anvil is a crucial part of the process. By tapping the nut on the anvil prior to its placement, and releasing the nut to see how it moves against the anvil surface, capuchins are able to ascertain the most efficient (or most stable) axis on which to rest the nut (Fragaszy et al., 2013a). This process involves the capuchin's brain, and haptic feedback, but also information about the affordances of external objects with which the monkey is not in direct contact. By satisfying criteria (1–5), capuchin nut-cracking at FBV can therefore be said to involve distributed cognition.

As for criterion (6), there is no clear evidence that the FBV environment stores memory beyond long-lasting (including archaeological) physical remains of anvils, hammers and nutshells, although these may form an ontogenetic niche (cf. Laland & O'Brien, 2012). For example, observations of juveniles at FBV suggest that object manipulation related to the processing of nuts occurs at greater rates with increased proximity to anvil sites, irrespective of concurrent cracking by others (Fragaszy et al., 2013b). The suggestion is that the accumulation of archaeological features related to tool use creates a landscape that encourages the development of tool use behaviours (Visalberghi et al., 2013). Large hammer stones, which at FBV are rare and are naturally unevenly distributed with respect to constructed tool use sites (Visalberghi et al., 2009), are present for young individuals to explore from an early age at those sites, and are used preferentially once the juveniles are strong enough. Since juveniles cannot transport large stones themselves, they are reliant on the accumulation from past adult use. As well as the accumulation of large hammer stones, nut-cracking also creates enduring artefacts in the form of pits on anvils (Visalberghi et al., 2013; Haslam et al., 2014), which are also preferentially re-used by juveniles. The characteristics of these pits enable youngsters to practice the correct placing of nuts, and aid the honing of striking precision (Fragaszy et al., 2013b).

We suggest that the shape of an anvil pit affects the optimum position of a placed nut and future tool-use (Visalberghi et al., 2013) in an analogous way to how a human painting will affect a future viewer. There is a recognisable physical trace but there can be no guarantee that any kind of stored meaning also will be either intentionally imbued or identically transmitted – consider for example the various components of Pleistocene cave paintings that regularly defy modern attempts at interpretation (Aubert et al., 2014). Since we can only observe the environment as mediating and not 'storing', mental content must be restricted to the perceived and therefore internal, leaving criterion (6) unfulfilled.

In terms of understanding past cognition, we can work backwards from tool to action in a primate archaeological context. For example, we can examine the tools that have been selected for use (identifying them via use-damage or depositional context) in order to reconstruct the qualities that the animal perceived as differentiating a given tool from the natural background. Those qualities, potentially including mass, shape, material and previous use, are a critical part of the influence the tool has on the animal's decision-making process. In other words, they are an analysable, external material component of the animal's cognition. This approach has already been successful in differentiating two types of stone tool used by long-tailed macaques in coastal Thailand, in terms of size, hardness and the position and type of use-damage present on the tools (Gumert et al., 2009; Haslam et al., 2013).

5. Social cognition in wild NHP

As noted, wild NHP nut-cracking and probe tool-use appear to primarily solve ecological problems, not social ones, although social tool use for activities such as play or courtship does exist in non-human primates (Shumaker et al., 2011; Haslam, 2014b; Falotico and Ottoni, 2013). Utilitarian material culture would therefore often appear to lack the immediate communicative function of other behaviours such as vocalisation or grooming. For this reason, social activities associated with and surrounding tool use are more tractable for investigating material cognition: social cognition may be viewed through the interactive learning contexts and social biases which affect and are affected by tool-use. For example, Boesch (2003) explored this approach when analysing how the meaning of leaf-clipping behaviour varied between chimpanzee populations. Shredding or 'clipping' leaves in a particular manner conveys courtship information to social partners among the Eastern chimpanzees at Mahale, while among the Western chimpanzees at Bossou, the same behaviour holds play connotations. It is not the use of the tool, but the way in which conspecifics perceive an individual's actions, that gives the behaviour its salience.

5.1. Chimpanzee nut-cracking at Taï National Park, Ivory Coast

Wild West African chimpanzees (*Pan troglodytes verus*) in the Taï Forest, Ivory Coast, use stone and wooden hammers to crack open *Coula edulis* nuts (Luncz et al., 2012). Recent findings have shown that neighbouring groups exploit cultural knowledge to respond in different ways to the same ecological problem posed by changing properties of *Coula* nuts (Luncz et al., 2012). Though two of three communities responded to a softening of the nut shell by switching to softer, but more abundant wooden hammers, one group maintained its preference for heavier stone tools.

Another study at the same site found that an immigrant female from a neighbouring group adjusted her own tool-use behaviour to match that of her new social group (Luncz and Boesch, 2014). Adjusting foraging strategy is important in establishing both informational and normative conformity (Claidiere and Whiten, 2012) when faced with new sets of ecological and social challenges. An immigrant female will not know her new territory, so learning from others how to find and process food resources will be of great advantage. At the same time, intra-sexual aggression towards incoming females may also be a driving factor (Kahlenberg et al., 2008), in that adopting the local behaviour of a new group reduces aggression directed towards a new individual, speeding up social integration (Luncz and Boesch, 2014).

The ability to aptly utilise socially-derived information can be a great advantage, and reduces individual cognitive workload (Galef, 1995). Tool use traditions are distributed by definition, since they require the transmission of information between individuals, and primatologists have documented the social basis for technological learning in wild chimpanzees (Biro et al., 2003; Luncz et al., 2012; Fragaszy et al., 2013b). Cross-population comparisons have revealed differences in tool kits and behaviours that cannot be accounted for by genetics or ecology (Whiten et al., 1999; van Schaik et al., 2003; Gruber et al., 2012; Luncz et al., 2012). Social biases are expressed through the preferential copying of particular individuals (Ottoni et al., 2005; Dindo et al., 2009; Horner et al., 2010), conformity to technical 'norms' (Whiten et al., 2005; Dindo et al., 2009; Gruber et al., 2011; Luncz and Boesch, 2014), and sex biases in the participation of specific tool-use behaviours (Lonsdorf, 2005; Mannu and Ottoni, 2009; Moura and Lee, 2010; Spagnoletti et al., 2011).

At the macro-level, social structure affects and is affected by tool use behaviour. The social brain hypothesis (Dunbar, 2009) postulates that neo-cortex size correlates with social complexity, with a logical implication that social relationships may therefore indirectly affect tool-use behaviour if technical abilities are linked to brain expansion (Reader et al., 2011). Chimpanzees form smaller subgroups during tool using activities than in other foraging contexts, which Sanz and Morgan (2013) suggest influences the frequency and nature of social interactions that drive the development of complex tool use. On the other side of the relationship, the linearity of hierarchical female relationships in capuchins is increased as tool use creates usurpable resources, leading to increased female competition (Verderane et al., 2013).

At a micro-level, the development of a particular tool use technique situates an individual within the wider technological matrix of the group to which they belong. Traditional functionalist arguments make a semantic distinction between technology and technique such that the latter is fundamentally limited to individual practice (Gatewood, 1985; Keller and Keller, 1991). Technology, in contrast, is expressive in nature, a body or collective classification held at the group level and above that of the individual. Technology may exist as multiple overlapping 'constellations' of knowledge, within which an individual develops an idiosyncratic technique (Ingold, 1993; Wynn, 1993). Whilst cognition at the group level may, as noted above, take place in the interaction between nodes, identity at a micro-level exists at the nodes themselves. Within this network, inanimate objects can be mediating agents, and where they mediate social relationships they may be vital to the continuous reconciliation of social networks (Lemonnier, 1993; Dunbar, 2009).

Since chimpanzee technological traditions are socially learned, the number of informant nodes and direction in which information is transmitted defines the style of technique that is available to and expressed by the individual. Thus, in the development of technique, an individual primate situates themselves and their technical identity (either deliberately or otherwise) with relation to the broader matrix of technological options available to the group. In reality, whilst technology may not be critical to personhood (being above the level of the individual), techniques are 'active ingredients of personal and social identity' (Ingold, 1993, p.438). NHP tool-use in both the micro and macro-sense can therefore be seen as an ongoing negotiation between social and physical cognitive problems, creating a specific behavioural identity in non-human primates analogous to personhood.

6. Discussion: niche construction and material cognition

The social nature of tool use places elements of primate social and physical cognition beyond the individual. Niche construction theory (Fragaszy, 2012; Laland and O'Brien, 2012) provides a means of exploring how the residual artefacts of tool use structure cognition and influence the propagation of technical traditions. The ontogenetic niche is the inherited social and physical environmental context in which juveniles develop. This environment is formed of social partners and the residual artefacts of past tool behaviour. While the former affects tool use through the limitation of available social learning sources, the latter alters the physical environment, artificially shaping the pool of available tool-materials and constructing 'enabling' sites (Gunst et al., 2008; Fragaszy et al., 2013b) (Fig. 2). The two factors combine to drive the development and distribution of tool use traditions over time, as material culture and technical tradition become increasingly inter-dependent (Hodder, 2011).

One part of the primate archaeological approach examines the ways in which the physical environment shapes tool use behaviours, as well as the ways tools may change the environment, to better understand the cognitive processes underlying tool-use. The complementary theories of niche construction and material agency (Malafouris, 2008) provide a useful context from which to approach these processes. As the clay and wheel in Malafouris' (2008) "potter's wheel" example constrain and enable the potter, so the pits on an anvil guide and influence the behaviour of capuchins. The niche thus represents the dynamic flow of mediative agency between the nut-crackers and the material physicality of the anvil over time.

The notion that the archaeological residues of tool use (e.g. broken nuts and shells, damaged plants, probes left in social insect nests) influence future tool behaviour, independent of concurrent tool use, brings a new dimension to long-term studies of animal behaviour and cognition. The patterning and density of activity sites on a landscape, their inter-visibility and relationship to features such as water courses and tool material sources are all archaeologically salient, and provide an opportunity to assess otherwise intractable social data such as group size and foraging routes. More concretely, the identification of persistent, stable primate technological traditions allows us to infer the presence and persistence of the social networks that sustain them.

Niche construction theory presents a complement to distributed or extended cognition. In both instances information, the currency of cognitive processes is extracted by primate individuals from their socio-material environments, although whether we may consider this information to have been 'stored' remains open to debate. The actions of past individuals change the information content of the environment, shaping later learning by other individuals and blurring the distinction between social and asocial learning (Laland and Galef, 2009; Sterelny, 2009). Testable

Fig. 2. Wild capuchin stick tool niche construction at Serra da Capivara National Park, Brazil. An adult male capuchin (a) modifies a long stick by trimming its length and side twigs, before (b) using it as a probe by inserting it into a tree stump. The capuchin then (c) further modifies the tool length by biting the end off, and again (d) uses it to probe the tree stump. Several other discarded probe tools and parts of tools are visible, leaning against the base of the stump.

correlates such as tool selection, skill acquisition and social aspects of tool use provide a solid grounding for the further exploration of primate material cognition.

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