Recognizing Culture in Wild Primate Tool Use

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Abstract Cultural differences between animal groups offer a means of tracing social relationships and cognition through time and across space. Where behaviours include tool use, we can observe the influence of available materials and role models on the development of tool-based activities. Here, we discuss the ways that we can study the social influence of tool-use behaviour in wild primates, focusing on two species that use durable stone tools: bearded capuchin monkeys (*Sapajus libidinosus*) and Western chimpanzees (*Pan troglodytes verus*). We concentrate on durable tools, as these provide an archaeologically recoverable record of activities. However, we also consider the influence of less durable tools when examining behavioural patterns in capuchins and chimpanzees. In order to study abstract concepts like culture and cognition, we identify socially learned behavioural diversity that is not influenced by environmental circumstances. This diversity, when compared among social units, allows us to detect cultural differences. Our bottom-up approach identifies some of the opportunities and challenges in studying social cognition through tool use in wild-ranging primates.

Keywords Social learning · Stone tools · Chimpanzee · Capuchin · Primate archaeology

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1 Introduction

This chapter discusses the notion of culture, with a focus on tool use in wild primate groups. Specifically, we look at methods that help us detect and understand the development and transmission of socially learned tool-use patterns. We concentrate on durable objects, namely, stones, used by wild primates, as these objects form a salient and long-lasting marker of tool use both for the animals involved and for us as researchers (Fragaszy et al. 2013; Haslam 2012; Haslam et al. 2009, 2016a, b, 2017; Luncz et al. 2015). This focus naturally restricts our discussion primarily to three primate species that are currently known to use stone tools in the wild: bearded capuchins (*Sapajus libidinosus*) in Brazil, Western chimpanzees (*Pan troglodytes verus*) in west Africa and long-tailed macaques (*Macaca fascicularis aurea*) in SE Asia (Boesch and Boesch-Achermann 2000; Gumert et al. 2009; Haslam et al. 2016c; Luncz et al. 2017; Matsuzawa et al. 2011; Ottoni and Izar 2008; Visalberghi and Fragaszy 2013). In the remainder of this chapter, we concentrate on the first two of these taxa, as they are longer studied in the wild at multiple field sites.

To begin with, we note that we work with wild animals and with the patchy archaeological record created by both wild animals and human ancestors (Falótico and Ottoni 2013; Haslam 2014; Haslam et al. 2014, 2013; Luncz and Boesch 2015; Luncz et al. 2015, b; Proffitt et al. 2016). Under natural conditions, behavioural observations are often difficult, and fully controlled experiments are impossible. Because of this, our data are always incomplete and our conclusions typically inferential. Further, because of our emphasis on recording natural behaviour under natural conditions, we must always begin with empirical observations and build upwards from those to more abstract concepts such as culture.

In the following, therefore, we base our discussion on the concrete notion of observed, socially influenced and shared behaviours. The inclusion of a social component inevitably implies regularly interacting individuals. We identify socially influenced behaviour by detecting and analysing behavioural diversity that is not solely influenced by environmental circumstances. We discount entirely a second criterion often applied to studies of animal culture, namely, ruling out genetic causation for a given behaviour. The reason for ignoring genetics is practical: there are currently no studies that reliably identify a specific genetic pathway for any tool-use activity, in humans or other animals. However, to minimize the potential effect of genetically underlying predispositions for certain behaviours, we focus in our work on animals of the same subspecies.

Beyond directly observable phenomena, *culture* is for us simply a label that can be applied to a set of widespread, socially influenced behaviours exhibited by interacting members of a particular group or community of individuals (McGrew 2004; Morin 2016; Whitehead and Rendell 2015). One individual can be part of many different and potentially overlapping cultures; in humans, for example, the same person may be labelled an academic, a conservative, a fan of death metal and a football supporter. Each of these labels defines a set of behaviours that such an individual is likely to exhibit. This perspective also emphasizes the two main

benefits of cultural labelling: (1) it is descriptive, it delineates for analytical purposes who are inside or outside of a particular cultural group as defined by a researcher, and (2) it is informative; a given individual part of a given cultural group informs on which behaviour they are likely to exhibit (and perhaps suggests that other as-yet unobserved but typically linked behaviours may also be followed).

The culture label may also inform on where and when an individual lived, although linking behaviour to geographic origin becomes more difficult the less is known about the behavioural repertoire of individuals. Where reliable observations have been collected during long-term studies of wild primates, we can use sets of co-occurring behaviours to distinguish location from behaviour alone. For example, if the behaviour of a given capuchin monkey includes use of stick probes, digging stones and stone throwing for sexual display, we know that it belongs to one of the extant *Sapajus libidinosus* groups in Serra da Capivara National Park, Northeast Brazil (Falótico and Ottoni 2013, 2014; Haslam and Falótico 2015; Ottoni and Izar 2008). If they include hand-sniffing and eye-poking, then they are almost certainly part of a *Cebus capucinus* group in Lomas Barbudal, Costa Rica (Perry 2011). The information in the cultural primatology dataset assembled by Whiten et al. (2001) can be used in a similar fashion for chimpanzees, and that of van Schaik et al. (2003) for orangutans.

In our empirical formulation, therefore, there is no such thing as a cultural process, only social transmission and learning processes. Documentation of behavioural variants, and assessment of social input to the learning and spread of those variants, comprises our fundamental research focus among wild primates. Everything else involves analytical distinctions made away from the field. In the remainder of this chapter, we will outline what we know of technological traditions within wild stone-tool-using capuchins and chimpanzees. We concentrate on tool-use behaviours and the factors that suggest that these behaviours are socially learned. We then give examples of how those behaviours may be assembled under cultural labels at different scales of analysis and for different purposes.

2 Chimpanzees

Observing wild chimpanzees in their natural habitat is a difficult and time-consuming challenge. Impenetrable tropical rain forests have many unpredictable obstacles and visibly can be very low. Nevertheless the rich behavioural repertoire of wild chimpanzees offers unique opportunities to answer lingering questions of culture and cognition of our highly sociable sister clade. Long-term field projects and detailed observations provide insightful information of complex social structures of our closest living relatives. Historically, identifying culture in wild chimpanzees has involved detecting diversity in behaviour where underlying ecological driving factors can be excluded (Whiten et al. 1999). The unique behavioural repertoire of each participating chimpanzee community was described as the culture of that community. However, the chimpanzee groups under study ranged over

thousands of kilometres, and therefore underlying ecological or genetic factors for behavioural diversity could not be entirely excluded.

A long-term research project in the Taï National Park in Ivory Coast has been ongoing for more than 30 years (Boesch and Boesch-Achermann 2000). Over time and with patience, three neighbouring communities were gradually habituated to the presence of humans. All three communities live in one continuous stretch of tropical rainforest with bordering territories, and ecological circumstances are similar throughout the forest. This setting enabled the search for socially influenced behaviours, and our recent research has shown that many aspects of chimpanzees' behaviour are influenced by their social group (Luncz and Boesch 2014; Luncz et al. 2012, 2018).

One of the most striking differences between neighbours involves their nut-cracking behaviour. Chimpanzees in the Taï forest are known to crack five different nut species. Some of them are only eaten opportunistically and observations are rare. However, from November to March the group spends hours each day cracking the highly nutritious *Coula edulis* nut. Those nuts resemble walnuts, and at the beginning of each new nut season, when they first ripen in the tree, they are protected by a thick green layer of outer skin. During this time chimpanzees often transport a tool up into the trees where they pick some nuts and use a branch as an anvil to crack them. This requires good coordination of positioning the tool, nut and their own body, which often leaves juvenile learners frustrated by fallen tools or nuts. When nuts start to ripen and fall to the ground chimpanzees collect them underneath a tree, using their hands, feet and mouth to carry multiple nuts at a time to a suitable anvil. The anvils in most cases are *Coula* roots that spread out underneath the nut tree. The chimpanzees place one nut at a time on the root and hit them with their hammer carefully, so as to not damage the inner kernel of the nut but still crack the outer hard shell.

Coula nut-cracking is a very social activity, where usually the entire group is foraging together in at least audio distance to one another. Family groups forage alongside each other with infants close by their mothers' side begging for bits and pieces of the nuts. The tasty nut gets a lot of attention already by very young individuals. Only much later, at the age of 3 or 4 years, will young chimpanzees start their own first nut-cracking attempts. It then takes many more years before they are skilled and proficient nut-crackers. The foraging circumstances of *Coula* nuts offer grounds for excellent social learning opportunities in young chimpanzee offspring.

Taï forest chimpanzees use wooden and stone hammers to crack the relatively soft *Coula* nut. Selected tools can vary in their size, shape and material. *Coula* nut-cracking is an excellent candidate to search for behavioural diversity in wild chimpanzees, as experiments in captivity have suggested that nut-cracking is potentially influenced by social learning and prone to variation. The tool selection of each individual is the only information we have available when identifying behaviour that is potentially influenced by social learning. We first investigate if tool selection is random or if we are able to pick up repeated pattern of preferred tool choice made by different individuals. From the individual we can move on to investigating the

similarity of specific subgroups in a community, for example, families or individuals with high association index (i.e. friends).

The fact that we can observe the behaviour and the tool choice of three neighbouring groups in the Taï forest provides the unique opportunity to take the comparison of tool selection pattern to a group level. After years of observations, comparisons of tool patterns show that neighbouring chimpanzee communities exhibit distinct tool selection which differ between groups (Luncz et al. 2012). The variety of tool patterns within the same community has been shown to be very low. When female chimpanzees reach sexual maturity, they leave their native community and immigrate into a different group. Our research has shown that at the onset of immigration, they quickly adopt the tool selection pattern of their new community which leads to long-lived, stable nut-cracking cultures in the Taï chimpanzee communities (Luncz and Boesch 2014, 2015; Luncz et al. 2018).

We therefore were able to observe cultural transmission in action. The underlying mechanisms that drive new females to conform to the nut-cracking norm of their new community remain to be identified. Natural observations do not allow for controlled tests, which leave multiple possibilities for the observed transmission. New females either adopt the tool selection or other prominent behavioural patterns to reinforce group belonging and minimize behavioural diversity between themselves and their new group. A more socially passive explanation could be that in order to stay with the group, they will have to adopt the foraging speed of their new group. Therefore they need to use the material the group is using at this given foraging location without regarding personal preference.

The transmission of cultural repertoire in chimpanzee groups can lead to very long-lasting and stable behavioural traits. The durability of stone tools has allowed an archaeological approach in recovering chimpanzee nut-cracking tools. The recovery of ancient chimpanzee nut-cracking sites revealed that this behaviour is at least about 4000 years old in the Taï National Park (Mercader et al. 2002, 2007).

Chimpanzees in a number of West African sites (although not all) are known to use pounding tools to crack open nuts. The next step in identifying different chimpanzee cultures therefore should include the comparisons of other nut-cracking communities. For example, extensive research has been done at the long-term field site of Bossou in Guinea (Carvalho et al. 2009), a site where chimpanzee nut-cracking culture does not involve the use of wooden clubs as hammers. The extended geographic distance between two nut-cracking populations that live further apart from each other can therefore be described as a greater cultural distance as well. This is one example of how we can investigate cultural behaviour starting from direct observation of individuals to populations across long distances.

3 Capuchins

Capuchin monkeys' behavioural studies in wild populations are more recent than those of chimpanzees. Several studies have been done regarding ecology and behaviour since the 1970s, most in rainforest populations, including the Amazon and Atlantic forests (Izawa 1978, 1979, 1980; Janson 1988). Although those studies comprised several hundred hours of observations, only a few cases of tool use were observed. This was unexpected, because capuchins are very manipulative towards objects (Fernandes 1991; Izawa and Mizuno 1977), and in captivity they have long been known to use objects as tools (Visalberghi and Trinca 1989; Westergaard and Fragaszy 1987).

Only when capuchin studies began in semiarid environments in Brazil (Cerrado and Caatinga) were regular stone tool-use behaviours reported in wild groups (Fragaszy et al. 2004; Mannu and Ottoni 2009; Moura and Lee 2004). To date, two long-term field sites in Piaui, Brazil, have been established for bearded capuchin monkey research, and although these cover similar environments and the same species (*Sapajus libidinosus*), the tool-use behaviour presented by those populations are different (Table 1). The Fazenda Boa Vista (FBV) site has been the home of the Etho*Cebus* project since 2003 (Visalberghi and Fragaszy 2013), and two groups have been closely studied in this site. The Serra da Capivara National Park (SCNP) capuchin population has been studied sporadically since 2000 (Moura and Lee 2004) and constantly since 2004 (Falótico and Ottoni 2013, 2014, 2016; Haslam and Falótico 2015; Haslam et al. 2016b; Mannu and Ottoni 2009; Proffitt et al. 2016). Four groups have been studied at SCNP to date, two of them long term.

Several other populations in Brazilian Cerrado and Caatinga environments have been surveyed in the last few years, and some of them present direct and indirect evidence of stone tool use by capuchin monkeys of two species, *S. libidinosus* and *S. xanthosternos* (Canale et al. 2009; De Moraes et al. 2014; Ferreira et al. 2010; Mendes et al. 2015). The reported pounding stone tools are primarily used to process

Table 1 Known tool-use behaviour in the two capuchin monkey long-term research sites, Fazenda Boa Vista and Serra da Capivara National Park, PI, Brazil

Behaviour	Fazenda Boa Vista	Serra da Capivara National Park
Pounding stone tools		
Palm nuts	Yes	No (ecology)
Cashew nuts (*Anacardium* sp.)	Yes (dry nuts)	Yes (fresh and dry nuts)
Grão-de-galo (*Cordia rufescens*)	No (ecology?)	Yes
Manihot seed	Yes	Yes
Stone-on-stone pulverization	No	Yes
Digging stone tools		
Underground storage organs	No	Yes
Trap-door spiders	No	Yes
Stone throwing (sexual display)	No	Yes (one group)
Probe stick tool	No	Yes (males)

palm nuts, when this resource is available, although in some areas the capuchins also process gastropods, other seeds and even cactuses. We can identify some similarities between those populations, such as the use of stones to process locally available, encased resources.

Some of the observed differences in tool use are clearly due to ecological variance, including the absence of palm nut processing in SCNP, at which the nut species opened by FBV capuchins are absent. An example of differences unrelated to ecology at the two sites involves cashew nut processing. FBV capuchins use two techniques to extract the cashew nut kernel: they rub the fresh nut on an abrasive surface to open a hole on the husk and use stone tools to crack the dry nuts (Sirianni and Visalberghi 2013; Visalberghi et al. 2016). On the other hand, capuchins at SCNP use stone tools to process all stages of cashew nut development and rarely use the rub technique (Falótico and Ottoni 2016; Falótico et al. 2016; Luncz et al. 2016a). These differences are not currently attributable to ecological variances but instead likely represent cultural differences. The same appears to be the explanation for ubiquitous digging with stones and probe tool use in SCNP (Falótico and Ottoni 2014; Falótico et al. 2017), behaviours never seen at FBV, as similar resources are present in both environments.

Tool-use variance can even be found within a well-studied population, such as stone throwing by females in one group in SCNP (Falótico and Ottoni 2013). This behaviour has not been registered in neighbouring groups in the area, which means that it could be a useful marker of cultural distinction. Females are the philopatric sex in capuchins, which may prevent the transmission of this variation to other groups at SCNP. Only long-term monitoring of these groups, spanning multiple generations, can determine whether or not the observed behaviours spread or disappear.

As we noted, studies on social learning in wild primates are challenging. The lack of control and the large number of variables make strong results difficult to obtain. Laboratory experiments and some field experiments can help in some instances to understand the learning involved, once field observations have found an ecologically relevant instance of behaviour. For example, from experiments we do know that socially biased learning is involved in the acquiring of stone tool-use behaviour by capuchins (Coelho et al. 2015; De Resende et al. 2008; Eshchar et al. 2016) and the same is likely true for other manipulative behaviours.

4 Conclusion

The results gained from years of patient field observations of wild chimpanzees and capuchins have demonstrated a high probability that cultural differences exist not just between widely separated groups of the one species but between neighbouring groups of the same species. This conclusion is one that cannot be reached merely by subjecting small groups of captive animals to a series of tests, no matter how rigorously controlled those tests may be. To some extent, this situation occurs because of factors inherent in keeping captive animals far from their natural environment, such as humans providing food and medical care (Haslam 2013). But more

importantly, it occurs because wild animals are encountering real problems, and devising novel solutions, as part of their everyday activities.

The costs of discovering and maintaining technological solutions may be much higher in the wild than would be the case in the sheltered world of captivity, with the result that cultural differences may be slow to develop or may appear independently in different groups faced with similar problems. However, it is these differences, when maintained through social learning, which allow us to identify how tool -using primates succeed or fail over evolutionary timescales. The continued development of primate archaeology as a means to record and interpret the behaviour of past primates (Luncz et al. 2015; Haslam et al. 2016a, b, 2017) will allow us to assess whether the small variations in technique or tool choice that we have observed over the past few decades reflect modern innovations or entrenched cultural differences, and it is the only way to study tool use and technology across many generations. That approach is complementary to current experimental approaches, but it allows us to go beyond the recent past in understanding how primate cultures emerge and change.

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