

Animal 'culture wars'

Rachel L. Kendal examines the evidence from the wild. What constitutes culture, do animals have it, and what does it mean for psychologists?

If we observe orang-utans blowing raspberries before bedtime, what does this mean? And why should psychologists, with their focus on human behaviour, be interested?

This article looks at what constitutes evidence for 'culture' in animals, and why the findings from long-term field studies are giving us valuable insight into the underlying cognitive processes, evolutionary bases and welfare implications for animals and humans alike.

questions

What makes human culture unique? Are animal 'culture' and human culture analogous, homologous, or neither?

resources

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The notion of animal culture has gathered momentum over the last 50 years, fuelled by the findings of long-term field studies of primates and cetaceans. Researchers have observed such diverse behaviours as chimpanzees fishing for ants, orang-utans blowing raspberries before bedtime, capuchin monkeys playing bizarre ritualised games, dolphins wearing sponges on their noses whilst foraging, and humpback whales singing distinctive songs (see Perry et al., 2003; Rendell & Whitehead, 2001; van Schaik et al., 2003; Whiten et al., 1999). In a pattern evocative of human cultural variation, animal populations vary in either the way they perform the behaviour or whether they perform it at all, purportedly due to differences in the spread of learned information between individuals (or social learning).

Interesting stuff you may be thinking, but why, as a psychologist, should I be interested? Well, such social learning allows naive individuals, whether human or non-human, access to adaptive behaviour invented by more knowledgeable individuals. Individual behaviour is governed then by the trade-offs made between knowledge obtained by oneself – in the process paying costs of time, energy and risk such as encountering toxic foods – and knowledge from others, which, although potentially less reliable, is often easier and safer to obtain (Kendal et al., 2005). Indeed, there is a vigorous debate amongst psychologists about whether social and asocial (or individual) learning are reliant on the same underlying cognitive processes and whether evidence

for some forms of social learning may be indicative of complex psychological capabilities, such as theory of mind.

As social learning can influence survival (e.g. through enhancing foraging) and reproduction (e.g. preferences for exaggerated traits in mates) it also has evolutionary implications. Indeed, it may well have been key in promoting the evolution of intelligence in animals, including humans (Whiten & van Schaik, 2007). Conversely, it is also responsible for the spread of maladaptive behaviours, such as smoking.

On a more applied note, social learning has implications for both human and animal welfare and conservation, for example in enhancing the dissemination of health advice in humans and the efficacy of life-skills training for animals to be reintroduced to the wild.

In this article I shall highlight the problem of identifying the all-important process of social learning in data from natural animal populations, questioning whether unequivocal evidence for social learning is sufficient to claim 'culture' in animals. The question of whether non-human animals exhibit culture, and the importance of this for understanding human behaviour, depends fundamentally on definitions of culture. Definitions range from those that deem a species cultural if it merely exhibits traditions transmitted via social learning, to those requiring that transmission involve teaching, imitation or the generation of group-specific norms and ethnic markers.

Identifying social learning

Although fieldwork is time-consuming and difficult, without it we cannot hope to understand the selection pressures that promote the evolution of 'culture'. However, evidence from the wild is often indirect and, by the standards used to judge laboratory experiments, lacking rigour.

The predominant ethnographic method pioneered by Andrew Whiten (Whiten et al., 1999) involves comparing

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variation in behavioural traits at multiple sites. Such variation is deemed cultural if there is no reason to believe it stems from inter-site genetic or ecological differences. A second approach, involving multifactorial analyses, provides a quantitative means of evaluating the influence of ecological, genetic and social associations (a proxy measure of social learning) upon behavioural similarity amongst individuals (Sargeant & Mann, in press; Whitehead, in press).

As such techniques do not directly assess whether social learning is required to produce the observed pattern of behavioural variation, they leave us open to both over- and underestimating its role (for a review, see Laland et al., in press). Hence, whether behavioural variation in the wild is deemed cultural is largely down to expert opinion, and heated debates have ensued which some have gone so far as to describe as 'war' (McGrew, 2002).

Consider one oft-debated example. Chimpanzee ant-dipping is frequently described as one of the strongest cases for culture in the wild (Whiten et al., 1999). At Gombe in Tanzania, a long wand is inserted into nests, withdrawn as the ants swarm up it, and then run through the hand forming the ants into a ball that is then placed in the mouth. In contrast, in the Tai forest of the Ivory Coast a short stick is used that is then pulled directly through the mouth. The question arises as to why the Tai chimps use this seemingly less efficient technique when sticks of varying lengths are available at both sites. Is the difference purely cultural?

Researchers studying at a third site, Bossou, discovered that the technique used was correlated with the species of ant being captured (Humble & Matsuzawa, 2002). They discovered, through using themselves as guinea pigs, that black ants swarm up sticks more aggressively and give more painful bites than red ants. Not surprisingly then, chimpanzees at Bossou use long sticks for black ants and short ones for red ants.

These findings suggest caution

is required when inferring a cultural explanation, but they do not indicate whether dipping techniques reflect differing ant prey at Tai and Gombe. Indeed a recent study, comparing ant-dipping at 13 African sites, suggests that variation in techniques cannot be explained by the ants present (Schoening

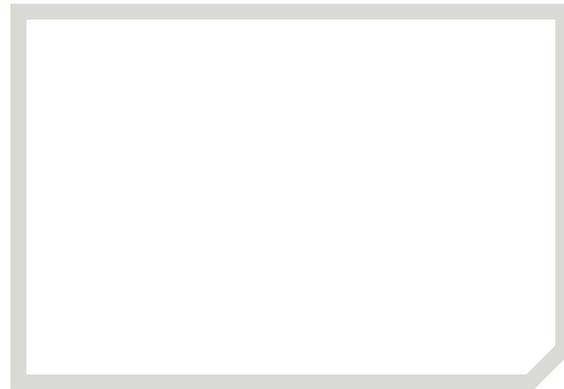
be implicated in natural behavioural variation.

Other researchers have gone some way to identifying social learning more directly in the wild using proxy measures, such as patterns of affiliation and observation. Both in capuchins and chimpanzees there is evidence that individuals selectively watch others from whom they can learn skills they have yet to master (Biro et al., 2003; Perry et al., 2003). Indeed the chimpanzee evidence stems from a particularly imaginative field experiment of the type I would like to encourage. Biro and colleagues took advantage of a natural forest clearing, through which chimpanzees travelled daily, in order to introduce them to novel nuts and observe the spread of any nut-cracking behaviour through the group.

Until we have tools that can provide widely acceptable evidence for social learning,

in any species, controversy over the extent of culture in animals will reign. The problem with field evidence to date is its inability to quantify the likelihood that the behavioural traits in question could be learnt without recourse to social learning. In an attempt to ameliorate this situation, my colleagues and I are currently working on methods which attempt to assess the likelihood that social learning is required to achieve the pattern of behaviour observed and also to identify potential signatures of social learning (Laland et al., in press).

One method we are developing is the 'option bias method.' It rests on the assumption that, within a group, social learning will generate a greater than expected homogeneity in the behavioural options used to solve a task (e.g. use of a short or long twig). We test whether a group's bias towards one option can be taken as evidence of social learning by



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A golden-headed lion tamarin obtains a raisin in a foraging task

et al., in press). But perhaps whether or not ant-dipping varies according to prey ferocity is beside the point. For Byrne (2006) the hallmark of culture is intricate complexity of behaviour, and as the skill of ant-dipping is intricate and unlikely to be learnt in its entirety by a solitary chimpanzee, there is an implied role for social learning.

The hard evidence that putative traditions are socially learnt is not yet there, largely because there are no methods for generating such evidence in the wild. Studies of captive chimpanzees (e.g. Whiten, in press) have shown they can sustain foraging traditions, across pseudo-generations, through high-fidelity social learning (ensuring the behaviour remains unaltered over time). Although these findings add credence to the supposition that social learning is behind inter-site variation in behaviour, it does not tell us whether social learning can

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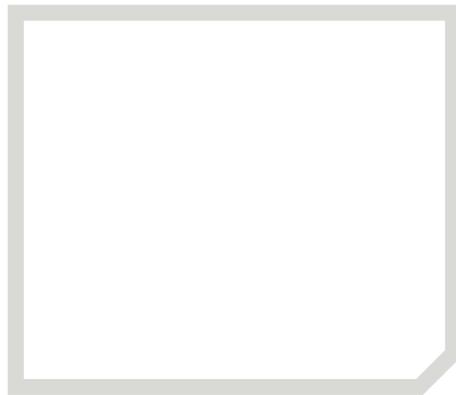
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comparing it to a probability distribution of the bias that would arise under individual learning. As collecting this data in the wild is usually impossible, we compute these probabilities through simulating what is essentially an individual learning, or control, condition. In this simulation we can account for factors, other than social learning, that may cause a bias (e.g. there could be a bias for use of short twigs because they are more readily available in the environment than long ones). If the observed bias exceeds 95 per cent of those expected were individuals to learn individually, then social learning can be inferred at the $p = .05$ significance level.



Golden headed lion tamarins manipulating an extractive foraging task

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cetaceans to the manipulations required to demonstrate social learning. For example, Warner (1988) showed that mating sites are socially learned in wrasse. He did this by exchanging fish, noting that immigrants adopted the traditional mating sites of residents.

Similarly, pine-seed eating by rats in Israel, enabling their survival in pine forests, is arguably the strongest example of social learning in the wild. Terkel (1996) showed that rats born to pine-cone stripping mothers but fostered by non pine-cone stripping dams did not learn to access pine-seeds, whereas those born to non pine-cone strippers and fostered by pine-cone strippers did. Further experiments showed that pups merely needed the 'tip-off' of exposure to partially stripped cones to learn the behaviour.

Even if the case for animal culture is accepted, it is obvious that the consequences of human culture are further reaching than that of non-humans. Human culture has enabled us to drastically alter environment and even walk on the moon; niche construction on an unprecedented scale (Odling-Smee et al., 2003). I now focus on what might set human culture apart from that of animals.

Does teaching and imitation equate to culture?

Many resist the idea of animal culture, preferring to speak of animal traditions (Galef, in press; Tomasello, in press). They insist on specific forms of social

transmission, such as imitation or teaching, due to their purported necessity for the emergence of cumulative culture (see box). This gradual accumulation of socially learnt variants, by allowing individuals to profit from the discoveries of previous generations, has enabled humans to achieve things not possible for one person to invent from scratch. Here, unless behavioural actions are taught or exactly imitated (rather than observers finding their own means to the same ends) there is insufficient fidelity of information transmission for the progressive modification of behaviour. In this view animal culture is merely analogous to human culture as teaching and imitation play, at best, a limited role in animals yet are defining features of human culture.

An additional criterion often stipulated is that of a repertoire of behavioural traditions. After all, human cultures are distinguished by the suite of traditions that make them unique; for example, people who eat roast beef on a Sunday are likely to speak English. It has been claimed, however, that chimpanzee, orang-utan and capuchin communities display unique sets of traditions relating to activities such as foraging, grooming and retiring for the night (Whiten & van Schaik, 2007). Similarly, sperm whale clans coexisting in the same habitat have unique vocal repertoires that covary with distinctive movement strategies (Rendell & Whitehead, 2001).

A case study may clarify the distinction between culture and tradition. Lonsdorf et al. (2004) discovered that chimpanzees spending more time observing their mothers fishing for termites acquired skills earlier. However, only females showed evidence that they had learnt how to fish for termites socially, as the depth to which their tools were inserted correspond to the depths used by their mothers. Here, we have evidence of the involvement of social learning in the development of a behaviour, yet some would claim termite fishing has little to do with 'culture'. We

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see that social learning in the form of local enhancement (attraction to termite mounds) or emulation (a desire to obtain termites) is functional for chimpanzees and that females learn something of the form of the behaviour (aka imitation) too. However, as males seemingly learn how to termite fish independently of their mothers it appears that 'imitation' is not necessary for the behaviour's transmission. Researchers of this camp would therefore oppose the claim that this was a cultural behaviour, preferring to call it a tradition. Quite a fine line to walk, especially with data from the wild.

In fact it is far from clear that humans are the only species capable of imitation, or that imitation is required for durability of transmission. Laboratory experiments have highlighted imitative abilities in birds, monkeys, apes and rodents (Zentall, 2006). The milk bottle-top opening tradition of British birds has been maintained since the 1930s and requires nothing more than exposure of birds to previously pierced tops (Sherry & Galef, 1990). Similarly, there is an ever-increasing number of reports of teaching in wild animals, including chimpanzees (Boesch, 1991) and meerkats (Thornton & McAuliffe 2006).

Do norms and ethnic markers equate to culture?

E.B. Tyler, the founder of cultural anthropology, proposed that culture includes the regulation of individual behaviour (law) and the development of symbolic reinforcement apparatus for that regulation (religion and morals). Here, seemingly arbitrary, non-functional, traits acquire moral significance such that a group is defined by the trait and between-group competition is based upon differences in this symbolic ethnic marker. Take, for example, the adoption of uniforms by football supporters and the abuse some suffer because of it.

So, in humans one 'culture' does not simply view another culture's behaviour as different to theirs but often, in some sense, wrong. There is currently little evidence that, for example, capuchins attempting to remove fruit from a husk by pounding it, are morally outraged at the sight of others scrubbing their fruit such that they punish these deviant 'scrubbers'! It is hard to see how we could acquire such evidence, and indeed evidence for processes such as cooperation and strong reciprocity, underlying such morality and

third-party punishment (that is punishment of norm-violators even when norm-adoption would not directly benefit you or your kin), is sparse even in captive primates (see Hill, in press).

An ability to learn the significance of arbitrary actions is often heralded as fundamental to human culture and appears to

be among the strongest arguments for distinguishing animal and human culture. Consider two candidate traits

in animals.

Researchers have documented the, apparently non-functional, hand-clasp of wild chimpanzees during grooming (Whiten et al., 1999). However, the spontaneous spread of this behaviour in a captive group indicated the behaviour symbolises a close relationship between the groomers rather than being a candidate for a symbol of group identity (Bonnie & de Waal, 2006). A similar story unfolded with wild capuchins, where researchers have documented many bizarre rituals including insertion of fingers into each other's nostrils and other ritualised games (Perry et al., 2003). Although initially Perry thought these rituals may signal group identity, evidence is not consistent with this. The games are inconspicuous and are not exhibited to a greater extent when encountering non-group members.

An end to the 'wars'?

One point of consensus is the necessity, if not sufficiency, of social learning in underpinning culture. New methods, such as those outlined at the beginning of this article, and their use in conjunction with existing methods, could in the future enhance peace in the culture 'wars'. Once we have resolved whether the traits in question are transmitted via social learning, then we can profitably enter into the debate as to whether animals have culture. We can but hope that the semantics of the issue do not obscure scientific progress and intercourse between disciplines. Despite

"We can but hope that the semantics of the issue do not obscure progress"

Cumulative culture?

There is currently little evidence, in animals, for the gradual accumulation of beneficial modifications to a behaviour. Boesch (2003) claims that nut-cracking in chimpanzees has increased in complexity and efficiency from banging nuts against trees, to using a stone hammer, to additionally using a stone anvil on which the nut is placed, and finally to use of a stone to stabilise the anvil. Similarly, New Caledonian crows have developed more complex ways of catching caterpillars using tools fashioned from leaves, moving from simple step-shaped tools to those with a thick handle and tapering tip (Hunt & Gray, 2003).

However, both examples merely note diversity of behaviour, consistent with cumulative evolution, rather

Chimpanzee female and infant watch male crack nuts with hammer

than actually monitoring the accumulation of modifications through social learning. As yet, we don't know what cognitive processes underlie a capacity for cumulative culture. If, for example, it involves theory of mind, then we must enter the debate as to which animals appear to possess a theory of mind akin to humans. Despite the apparent lack of evidence for cumulative culture in animals, it appears that use of imitation and teaching to distinguish animal 'tradition' and human 'culture' is open to question (see main text). The search continues...

the controversy, the field has important implications for our understanding of the continuity of the animal and human mind and how we characterise humans' place in nature.



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