

Do Animals Have Culture?

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Culture is probably not rare in animals, although hard experimental evidence is lacking. The strongest case for culture is found in the species most amenable to experimental manipulation, rather than in nonhuman primates. Human culture is much more likely to be cumulative than animal culture, but the reasons for this are not well established. At this point, there is no reason to assume that cumulative culture depends critically on teaching, imitation, language, or perspective-taking. Currently, animals are being judged according to stricter criteria than humans.

WHY IS CULTURE RARE IN ANIMALS? OR IS IT?

The concept of culture has become a quagmire for the social sciences. Intuitively, we all know what it is and feel it to be important, yet it has proven virtually impossible for social scientists to derive a consensual definition or to find a satisfactory means of operationalizing it.^{1,2} Indeed, after much painstaking self-analysis and soul searching, many social anthro-

pologists seem to have given up on the notion of culture altogether.^{3,4} Ironically, and perhaps benefiting from blissful ignorance of the problems, biologists and students of animal behavior are currently giving unprecedented attention to the "culture" of other animals.⁵⁻⁷ This community has witnessed an explosion of interest in animal social learning and purported animal culture^{6,8} exemplified by a proliferation of books, conferences, and papers dedicated to the topic.^{5,9-11} Whether or not the culture concept has utility for our own species, an increasing number of researchers are using it to explain both diversity and transgenerational continuity of behavior in animals.

In the absence of a satisfactory and universally accepted definition of culture, most answers to the question, "Do animals have culture?" take on a hackneyed appearance. Define culture one way and it is the exclusive province of human beings; another way, and a multitude of species are deemed worthy of the accolade. At one pole of the spectrum, many social anthropologists conceive of culture as so deeply shrouded in language, politics, morality and institutions, that it would be grossly devalued were it attributed to dolphins or apes. At the other extreme, biologists Charles Lumsden and Edward Wilson¹² concluded that in excess of 10,000 species, including some bacteria, manifest

some form of extra-genetic inheritance sufficient to be deemed cultural. Thus, central to the issue of whether animals exhibit culture is the problem of whether it is possible to come up with a nonarbitrary definition of culture; one that will prove useful to a substantive proportion of interested researchers. We begin by seeking such a definition, and in doing so are guided by the twin criteria of consensus and utility. In simple terms, we are looking for the kind of definition of culture that our professional colleagues will recognize as something with which they can work.

The first step is to ask whether such a definition would be more useful if it were broad and minimalist, reflecting the continuity between humans and other animals, or whether a narrow and exacting definition that stresses human uniqueness might have greater utility. We suspect that to most biologically minded researchers the answer to this question is immediately apparent. A narrow definition, say something like, "Cultures are systems of linguistically encoded conceptual phenomena that are learned through teaching and imitation, socially transmitted within populations, and characteristic of groups of people," is not likely to prove particularly useful, at least not to the issues addressed in this article. This is not only because the answer to the question of whether or not animals have culture is a *fait accompli*; by definition, they do not. But in addition, this denotation would act as a barrier to understanding of the evolutionary roots of culture. It would encourage the misguided view that humans are (uniquely) unique, which is only trivially true since all

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species are unique. No light would be shed on how culture came into existence, nor on human's place in nature. More fundamentally, it would act as a barrier to the integration of the biological and social sciences. Premature, over-exacting distinctions jeopardize the ability to see relationships between culture-like phenomena in diverse taxa.

Given the primitive state of knowledge of animal cultures and the current malaise in human culture studies, we suggest that a broader definition is likely to be more stimulating. It may prove valuable to debate the criteria by which cultural and acultural species are distinguished and perhaps, in time, even to make distinctions between different classes of culture. But such distinctions, if they are going to be informed, can be based only on empirical data. A broad definition encourages such data to be collected; a narrow definition does not. A broad definition has the additional advantages that it provides a comparative framework with which to investigate the evolutionary history of culture and that it encourages the cross-fertilization of information and methods between the biological and social sciences. Naturally, the definition could also be too all-encompassing, so that "culture" becomes unrecognizable and researchers become alienated. An overly broad definition, like an overly narrow one, would have neither utility nor consensus.

By what means can we settle on a broad and useful definition of culture? One approach is to synthesize the array of disparate definitions of human culture and isolate the criteria that are deemed essential by all, or at least most, parties.^{1,7} What then, when we strip it down to its barest bones, is the essence of culture? One central criterion is that culture is built upon socially learned and socially transmitted information. The term "culture" does not apply to inherited genetic information or the knowledge and skills that individuals acquire on their own. A second is that this socially transmitted information can underpin group-typical behavior patterns, which

may vary from one population to the next. Thus, culture helps to explain both continuity within groups and diversity between groups.

These considerations lead us to the following working definition of culture, toward which we hope a substantial proportion of researchers interested in cultural evolution would be sympathetic. Cultures are those group-typical behavior patterns shared by members of a community that rely on socially learned and transmitted information. (Later we will discuss additional characteristics that some researchers regard as essential to human culture.)

Which Animals Have Culture?

According to the preceding definition, which animals have culture? There are two kinds of answers to this question. The first kind is based exclusively on hard experimental evidence. That is, for which species do we have reliable scientific evidence of natural communities that share group-typical behavior patterns that are dependent on socially learned and transmitted information? The answer, which will surprise many, is humans plus a handful of species of birds, one or two whales, and two species of fish.

No doubt many readers will find this conclusion disturbing, while primatologists will probably be up in arms. How can we attribute culture status to fish and not chimpanzees? A full explanation will follow, but the short answer is that for chimpanzees, as for other nonhuman primates, the hard evidence that their "cultures" are socially learned is not yet there.¹³⁻¹⁵ Neither evidence of group-typical behavior patterns nor a demonstration that the species is capable of social learning is in itself strong evidence for culture.¹⁶

The second kind of answer to the question of which animals have culture is a best guess. If we were to say which animals we believe have culture, based on our knowledge of animal social learning, observations of natural behavior of animals, intuition, and the laws of probability, we would say that many hundreds of species of vertebrate have culture. After all, many vertebrates have been shown to be capable of social learning of a sort that theoretically could maintain cul-

ture.^{5,10} While our particular beliefs are of little intrinsic value, we suspect that many researchers that study animal social learning would agree with us on this point.

To return then to our question, culture is as rare or as common among animals as it is defined to be. On the assumption that broad definitions lead to greater utility and consensus than do narrow ones, we have defined culture according to its necessary conditions. This definition leads us to the view that culture is not at all rare, although hard experimental evidence of cultures among animals, including nonhuman primates, is currently lacking.

WHAT IS UNIQUE ABOUT PRIMATE CULTURE?

A "Brainist" Bias?

A slightly (but only slightly) facetious answer to the question of what is unique about primate culture is that primates uniquely benefit from the biased anthropocentric perspective of investigators who themselves, without exception, are primates. Nonhuman primates are probably studied more than most other species; the findings of these studies perhaps receive greater attention than those of other species; and arguably lower standards of evidence are required for primates than other species to be awarded some sophisticated psychological or social attribute, including culture. This bias, we suspect, stems in part from a need dating back to Darwin for researchers to demonstrate continuity of mental abilities between humans and other animals. The easiest and most convenient means by which such continuity can be demonstrated is to find the most sophisticated cognition in our closest relatives, the apes, slightly less impressive abilities in monkeys, and increasing levels of stupidity as the degree of relatedness with ourselves diminishes. Reinforced by the observation that brain size crudely fits this pattern (if we ignore some inconvenient outliers such as cetaceans), many of us begin our research expecting to find that nonhuman primates will be smarter than other animals. From an evolutionary perspective, this bias is unjustifiable, since convergent evolution could

manifestly have favored intelligence, sophisticated cognition, or culture in quite distinct lineages.

Indeed, the compelling assumption that species with larger volumes of the relevant brain structures will show greater cognitive sophistication is still disputed¹⁷ and remains largely untested. There is evidence among nonhuman primates for a link between brain size and behavioral flexibility, as measured by frequency of reports of innovation, social learning, and tool use.¹⁸ However, this finding demonstrates that big-brained species exhibit more social learning than small-brained species, and not that the former employ more sophisticated psychological processes than do the latter.

In sum, it is not clear that a big brain is necessary for culture as defined earlier. If some fish exhibit culture, as we will argue, then presumably a large brain is not a requisite feature. Given its expense to produce and maintain, all of the neural tissue that primates have in abundance must have some important function. Yet the fact remains that it may have little to do with culture. Most people, ourselves included, believe that nonhuman primates have culture in spite of the scientific evidence, rather than because of it.

Why There Is Better Evidence for Culture in Fish Than in Primates

What evidence is needed to demonstrate that a species exhibits culture, according to our definition? Researchers would need to establish that the animal concerned exhibits diverse group-typical behavior patterns in natural populations and, in addition, that these behavior patterns are underpinned by social learning. The latter criterion requires ruling out alternative explanations for the behavioral diversity, including that the populations exhibit genetic differences or that variant ecological conditions have resulted in different patterns of asocial learning.

In principle, ruling out these alternatives through experimentation is straightforward. Two experimental manipulations are necessary. In the

first experiment, a sample of individuals from population A are introduced into population B, and vice versa, ideally at a formative age. The observation that the introduced animals adopt the behavior exhibited by members of the host population is inconsistent with an explanation in terms of genetic differences between populations and consistent with an explanation reliant on some form of learning. In the second experiment, population A is collectively removed from its environment and replaced in the environment of population B, which in turn is removed and replaced in the

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environment of population A. If the introduced populations come to exhibit the same behavior as the former residents, this would suggest that the behavior results from shaping to divergent ecological conditions, and asocial learning could not be ruled out. However, the observation that the introduced population exhibits group-typical behavior that differs significantly from that exhibited by the former residents would be inconsistent with an explanation based on ecological differences between environments and consistent with culture.

Ideally, both experiments would be carried out on the same populations, which would potentially provide the most compelling evidence for culture. The first experiment, in combination with alternative evidence that the behavior in question cannot be learned asocially, or the second experiment, in combination with alternative evidence that there are no relevant genetic differences between populations, would also provide satisfactory evidence for culture.

To our knowledge these experiments have not been carried out in a systematic and rigorous manner in any nonhuman primates. What is more, in many cases, including for chimpanzees, it is difficult to envisage that they will. Not only would such experiments be extraordinarily expensive, and present enormous logistical challenges, but many people would regard such manipulations as unethical. Consequently, the claim that nonhuman primate populations exhibit culture rests exclusively on observations of natural populations *in situ*.

That there are population differences in the behavioral repertoires of many primates is now well documented. Best known are the distinct tool-using and other group-typical behavior patterns of chimpanzee populations.^{19–22} Similar behavioral diversity consistent with a cultural explanation is reported in several other primates, notably orangutans²³ and capuchins.^{11,24}

Differences in the behavioral repertoires of chimpanzee populations have become, for many, the jewel in the crown of nonhuman primate cultural traditions and the prime exemplar of animal culture. Yet, in the absence of the kind of experimental evidence described, the case for chimpanzee culture rests entirely on a plausibility argument. There is clear experimental evidence that chimpanzees are capable of social learning.²⁵ Indeed, the evidence for seemingly more complex forms of social learning, such as imitation, is as good in this species as in any other, humans aside.^{26,27} Many of the group-typical behavior patterns, such as termiting, appear quite complex, and researchers envisage that they would be difficult to learn alone. Some behaviors,

such as hand-clasp grooming,²⁸ appear arbitrary, even functionless, and consequently seem to many to be unlikely candidates for behavior shaped by ecological contingencies (see also the primate social conventions described by Perry and Mason²⁴). In their seminal paper on chimpanzee cultures, Whiten and coworkers²⁰ claim to have found “39 different behavior patterns, including tool usage, grooming and courtship behaviors, [that] are customary or habitual in some communities but are absent in others where ecological explanations have been discounted.” For most interested researchers, the probability is that at least some of the group-typical behavior patterns reported for chimpanzees are learned socially. Yet to our knowledge, in not one instance is there irrefutable evidence that a natural chimpanzee behavior is socially learned.

Indeed, there are serious grounds for being suspicious of this plausibility argument, and senior figures in the animal social-learning community remain unconvinced.^{13–15} The main problem is that it is difficult to rule out ecological explanations for the observed variation in behavior. Whiten and coworkers²⁰ consider the possibility of false-positive reports of cultural variation resulting from an “ecological explanation, for which absence is explicable because of a local ecological feature.” However, only three of sixty-five behavior patterns were actually removed because an ecological explanation could be given. Skeptics might be forgiven for questioning how seriously this alternative was considered. For instance, in the case of a population reported as not nut-hammering, a skeptic would want to know not only that there are suitable nuts and hammers present, but also that there are not alternative and more readily accessed alternative sources of foods with equivalent nutritive and energetic properties that render nuts a comparatively less profitable food source. Similarly, the skeptic would want to know whether populations reported to not fish for ants or termites are exposed to exactly the same species of ants and termites as those that do, and that the ants and termites behave the same way in each case.

This problem is highlighted by a recent analysis of chimpanzee ant dipping by Humle and Matsuzawa.²⁹ Whiten and coworkers²⁰ singled out ant dipping as a particularly compelling case of chimpanzee cultural variation where the differences between communities are not related solely to whether the behavior is present or absent, but where two different methods of ant dipping were employed. In the first or “pull through” method, reported as customary at Gombe, a long wand is held in one hand and a ball of ants is wiped off with the other. In the second “direct mouthing” method, customary at Tai, a short stick is held in one hand and used to collect a smaller number of ants, which are transferred directly to the mouth. Like Boesch and Boesch³⁰ and McGrew¹⁹ before them, Whiten and colleagues²⁰ were satisfied that ecological differences between the Gombe and Tai sites could not explain this variation. Furthermore, they concluded “it is difficult to see how such behavior patterns could be perpetuated by social learning processes simpler than imitation.” Humle and Matsuzawa²⁹ investigated ant dipping among chimpanzees of Bossou, in southeastern Guinea, a site at which both forms of ant dipping are observed. They found that both the length of the tools and the technique employed were strongly influenced by the nature of the prey. Several species of ants were preyed on, and these differed in their density, aggressiveness, behavior, and in whether they were migratory or at nest sites. In situations in which ants were abundant, aggressive, or had severe bites, the first method, with its long wand, was employed, and was probably associated with fewer bites than the second method, while in other circumstances the direct mouthing method was used. Skeptics would find it easy to envisage that chimpanzees could individually be shaped by biting insects to use the strategy that resulted in the fewest bites.

Humle and Matsuzawa’s²⁹ findings suggest that an ecological explanation for ant dipping cannot be ruled out. If confidence in this flagship example of cultural variation in chimpanzees must be suspended, then how many

other so-called chimpanzee cultural behaviors will eventually be questioned, when careful scrutiny reveals that variation coincides with ecological differences? Will all thirty-nine of Whiten and coworkers’²⁰ behaviors eventually be whittled away? Humle and Matsuzawa’s²⁹ analysis implies that, had the experimental manipulations described been employed by translocating Gombe and Tai chimps, we would have found Gombe-born chimps using the direct mouthing method in Tai and Tai-born chimps using the pull-through method at Gombe (that is, chimpanzees would have failed the culture test), although we will not know for sure unless this experiment is actually done. Let us be clear: Neither Humle and Matsuzawa’s²⁹ analysis nor the hypothetical translocation experiment would rule out a cultural explanation for ant dipping. However, while the alternative ecological explanation remains plausible there will always be a reason to doubt the claim of culture. The translocation experiment method is superior because, where such experiments have been carried out and behavior consistent with cultural variation has been observed, we are not left doubting whether unconsidered ecological factors might explain the variation.

While primatologists are forced to resort to circumstantial evidence for culture (illustrated by the plausibility arguments put forward by Boesch,²¹ Whiten,²² and Perry and Mason²⁴), other researchers are free to employ more direct experimental methods. Helfman and Shultz³¹ translocated French grunts (*Haemulon flavolineatum*) between populations and found that while those fish placed into established populations adopted the same schooling sites and migration routes as the residents, control fish introduced into regions from where the residents had been removed did not adopt the behavior of former residents. Helfman and Shultz’s study combines the procedures for experiment 1 and 2 described earlier in one of the most elegant demonstrations of animal culture to date. Their study is not quite the same as the symmetrical experiment suggested because only one population was introduced into the environment of the other. None-

theless, this is strong evidence for culture. Warner³² showed that translocated populations of Bluehead wrasse (*Thalassoma bifasciatum*), a Caribbean coral-reef fish, did not adopt the same mating sites as the populations they replaced, but rather maintained distinct sites long after the manipulations, consistent with a cultural explanation. This finding is a direct application of the experiment 2 method. Combined with the observation that high levels of mixing during the early life of this species mean that reef populations are not subject to significant genetic differentiation, this finding provides acceptable evidence of cultural variation.

In the light of a burgeoning literature on learning and cognition in fish, in which it is quite apparent that the abilities and complexity of social behavior of this group have been underestimated,³³ we should hardly be surprised that two species of fish should provide some of the best evidence for animal cultures. A recent review of fish cognition³³ reveals a rich experimentally derived databank reporting social intelligence (social strategies, Machiavellian intelligence, cooperative hunting) as well as sophisticated foraging skills, tool use, cognitive maps, and the construction of complex artifacts. Fish have comparatively small brains and are not renowned for their intelligence or learning abilities. Yet there is now unequivocal evidence from laboratory and field studies that a variety of different species of fish are capable of social learning, including learning how to find food, which foods to eat, how to recognize predators, how to avoid predators, and perhaps even with which fish to mate (see Brown and Laland³⁴ for a review). If fish can do all this with small brains, then maybe simple mechanisms could account for primate behavior.

When it comes to hard experimental evidence for culture, the only taxonomic group that comes close to fish is birds, for which the cultural credentials of song variants and mating preferences are reasonably well-established in several species.^{35–37} It has been observed that female quail (*Coturnix japonica*) at lekking sites prefer to mate with particular

males.³⁸ Furthermore, in the laboratory it has been demonstrated that preferences for particular male traits can be culturally transmitted between female birds.³⁷ However, to our knowledge it has never been demonstrated that differences in female preference at lekking sites in the wild are cultural. Freeberg^{39,40} has gone one step further toward demonstrating culture in cowbirds (*Molothrus ater*). Male cowbirds in two distinct populations exhibit different types of courting behavior and the females in each population prefer to mate with males who court in the local fashion. Freeberg found that juvenile birds of a common genetic background, when housed with adult birds from one or other of the populations, adopted the courting behavior and mating preferences of the population they were housed with (see also Freeberg and coworkers⁴¹). This case introduces the possibility of an unusual transmission mechanism in which juvenile males' courting behavior is shaped by adult females and juvenile females' preferences are shaped by the behavior of adult males. However, we cannot entirely rule out an ecological explanation, since during the experiment each population was housed at a different location. However, this would seem to be unlikely to account for the observed differences in behavior. Indeed, there is a large body of evidence that the vocal signals of many avian species may be cultures (reviewed by Freeberg³⁶). However, as far as we are aware, there is no case where an ecological explanation for population differences in vocal repertoire can be ruled out entirely.

There is also some suggestive evidence for culture in several species of cetaceans. Killer whales (*Orcinus orca*) show a number of pod-specific behavior patterns, including foraging specializations, migration patterns, and vocal dialects. Rendell and Whitehead⁴² argue that ecological explanations can be ruled out, since sympatric pods develop different pod-specific behaviors. They also consider a genetic explanation unlikely since pods are matrilineal, so that inheritance of behavior would have to be principally from the mother. However, sex-linked genetic traits or genomic imprinting

(the inactivation of an allele dependent on the parent it was inherited from) could account for this pattern. Likewise, an ecological explanation could be viable if sympatric pods use the same habitat in different ways. Of course, such behavior itself could be cultural but, alternatively, different pods could have genetic predispositions to use a habitat in a particular way. Rendell and Whitehead⁴² provide what we feel is stronger evidence for culture in Humpback whales (*Megaptera novaeangliae*). During the breeding season all males in a population sing, at any one time, "nearly the same song," but this song evolves over time, changing even within a breeding season. The rapidity of change would seem to rule out a genetic explanation, although demographic changes or common external influences might account for song evolution; however, neither would seem likely to account for the observed synchronized change in song between many individuals. This evidence that can be mustered for birds and cetaceans is at least as strong, and in some cases stronger, than that for nonhuman primates.

The primate-centric brainist bias is well illustrated by a reconsideration of one of the most well-known cases of animal social learning, that of sweet-potato washing by Japanese macaques.⁴³ For a novel cultural behavior pattern to spread through an animal population two processes are necessary: There must be the initial inception of the behavior, which we refer to as innovation, and its spread to others by social learning, which is diffusion. Imo, the famous originator of potato- and wheat-washing, has become celebrated as a great innovator, and therefore as an initiator of macaque "culture." For instance, E.O. Wilson⁴⁴ in *Sociobiology* and John Bonner⁴⁵ in *The Evolution of Culture in Animals* both refer to Imo as "a genius," while Kummer and Goodall⁴⁶ describe her as "gifted." In the 1960s, food washing seemed an unlikely natural behavior for monkeys. Hence, these behavior patterns were regarded as novel and intelligent. When the food-washing behavior spread it was described as "preculture" or "protoculture," the clear implication being

that it could be regarded as an analog, or perhaps even a homolog, of human culture.

With the benefit of hindsight, and in the light of accumulated scientific knowledge, Imo's achievements and those of her troop members appear more modest. It seems that food washing is a stable feature of macaque behavior, and Imo's innovation involved the application of an established behavior pattern to novel foods.⁴⁷ Experimental studies have revealed that food washing is learned relatively easily by monkeys and can become common in a troop through processes other than the imitation of a rare "creative genius."⁴⁷ There is no evidence that food washing spread through Imo's troop by imitation, teaching, or any unusually sophisticated form of social learning. Indeed, there are grounds for concern that it may even have been an artifact of human provisioning.¹⁴ The lauding of Imo as a genius and the use of the terms "protoculture" or "pre-cultural" to describe this case of social transmission were widely accepted only because the behavior was reported for a primate. Would the scientific community have accepted the same terminology to describe social learning in rats or budgerigars?

The members of our laboratory have carried out a detailed analysis of the factors that underpin innovation in fish, birds, and monkeys, and found that state-dependent factors (sex, size, social rank, hunger level) account for much of the variation. These and a host of other findings⁴⁸⁻⁵² lead us to the view that the adage, "Necessity is the mother of invention" probably applies to most animal innovation. Certainly when it comes to foraging innovation, more often than not the innovators are those individuals with the greatest motivation to find food. To our knowledge, no consideration has been given to the possibility that Imo was the first individual to apply food washing to sweet potatoes merely because she was among the hungriest individuals in the troop, yet this would seem a real possibility. Our experiments have found evidence for personality differences in the problem-solving ability of guppies, a small freshwater fish. Laland and Reader⁴⁸

found that some fish consistently solved foraging problems, not because they were hungrier, faster swimmers, more active, or healthier, but because of some stable personality characteristic. To our knowledge there is no equivalent experimental evidence for personality differences in problem-solving ability in any species of non-human primate. Many primate studies report differences in performance between individuals, but none have ruled out alternative explanations for individual differences (for example, motivational factors). Hence, the variation cannot reliably be interpreted as reflecting differences in personality. The one study of which we are aware that sought such evidence, Fragasz

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and Visalberghi's⁵³ investigation of innovation in capuchin monkeys, failed to find it.

Let us give the single fish that consistently solved our maze problems faster than others the name of Bertha. We do not yet know whether it is appropriate to describe the personality trait that Bertha exhibits as intelligence or creativity as opposed to, say, boldness, perseverance, or nonconformity but at least we know that there is some feature of Bertha's make-up that makes her an effective problem solver. Gifted highbrow intellectual qualities, as opposed to less salubrious personality traits, have been attributed to Imo in an essentially arbitrary man-

ner and, indeed, in the absence of any evidence that it was her personality to which her success can be attributed. Under such circumstances, Bertha seems to have greater claims to the "genius" plaudit than does Imo.

To return to the question that heads this section, it remains conceivable (indeed, we view it as quite likely) that nonhuman primates exhibit a greater richness of cultural variation compared with other taxa. What is striking about the repertoires of chimpanzees is the multifaceted nature of their purported culture, in comparison with which the cultural repertoires of fish and birds appear impoverished (see Boesch²¹ and Whiten²²). Yet we see no reason to value weak evidence for primate cultures over strong evidence for culture in birds and fish. The best evidence for culture is found in the species that are most amenable to experimental manipulation.

We would not wish primatologists to forsake the study of population variation in behavior just because they cannot prove that the differences are cultural. How can primatologists get around their inability to carry out translocation experiments? We have two suggestions. First, appropriate data collection would allow the feasibility of genetic and asocial learning explanations to be assessed and rejected if the probability that they can account for the data is unrealistically small. Laland and Kendal⁵⁴ describe simple statistical methods that would allow alternatives to the social-learning explanation to be dismissed if researchers have access to good pedigree and diffusion data (see also Fragasz¹⁶). For instance, experimental data from laboratory or captive studies estimating the probability of asocial learning could also be used to assess the probability that a particular pattern of diffusion or level of incidence is explicable in terms of asocial processes.

Second, researchers could carry out a careful analysis of the small number of cases in which individuals have dispersed, transferred between populations, or reintroduced into established populations, or in which populations have been introduced into new areas (see Boesch²¹ for examples). A careful analysis of these natural translocation

experiments may eventually shed light on primate cultures. This, after all, is one reason that we can be confident that humans have culture.

WHAT (IF ANYTHING) IS UNIQUE ABOUT HUMAN CULTURE?

If we are to identify unique factors of human culture, then we must compare its quantifiable characteristics with purported animal culture on a level playing field. On what grounds can human and animal cultures be distinguished?

Intuitively, the sheer complexity of human behavior seems to divide us from the rest. Driving cars, building houses, and writing articles on culture would be orders of magnitude more complex than the most intricate chimpanzee tool-using behavior. Yet to suggest that what renders human culture unique is its complexity merely begs the question of why human culture should be more complex. Complexity is a consequence of the features of humanity that render our culture unique, and not itself such a feature.

Galef^{14,15} has suggested that the similarities between animal and human culture may be more superficial than real because animal and human culture rest on different processes. Galef places emphasis on teaching and imitation, which he regards as underpinning human culture but unimportant to animal social learning. Conversely, Galef regards purported animal cultures as heavily dependent on local and stimulus enhancement, and other comparatively simple processes that mediate social learning. Boyd and Richerson⁵⁵ make a similar argument. While these researchers have not specified precisely how teaching and imitation are deemed to render human culture more stable, complex, or cumulative than purported animal cultures, to many the hypothesis is both intuitive and compelling.

Tomasello¹³ identified three important characteristics of human culture: universality, the observation that some behavior patterns are exhibited by virtually everyone in the society; uniformity, or widespread conformity to con-

ventions; and history, manifest in a stable, transgenerational, cumulative culture. He suggested that while chimpanzee behavioral traditions exhibit strong evidence for universality, there was only weak evidence for uniformity or history. Tomasello hypothesized that, compared with chimpanzee “cultures,” the greater universality, uniformity, and history of human culture are a manifestation of higher fidelity of information transmission among humans, reflecting differences in the psychological mechanisms employed. In accord with Galef,¹⁴ Tomasello¹³ argues that human culture alone is reliant on teaching and imitation, together with language and perspective taking.

In reconsidering these hypotheses, we begin with a focus on teaching. We

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know of no single widely accepted case in any nonhuman animal that satisfies contemporary definitions of teaching,⁵⁶ while human children are taught vast amounts of cultural knowledge. At first sight, it is difficult to conceive of a clearer dichotomy in the intellectual abilities of animals and humans. Yet this dichotomy is vulnerable to criticism from both sides. Purported instances of animal teaching are evaluated according to strict criteria. For example, Caro and Hauser⁵⁶ defined teaching as follows:

An individual actor A can be said to teach if it modifies its behavior only in the presence of a naïve ob-

server, B, at some cost or at least without obtaining an immediate benefit for itself. A’s behavior thereby encourages or punishes B’s behavior, or provides B with experience, or sets an example for B. As a result, B acquires knowledge or learns a skill earlier in life or more efficiently than it might otherwise do, or that it would not learn at all.

The use of this rigorous definition has led to the view that information transmission in animals is inadvertent and not actively facilitated by the demonstrator. Yet there are other means by which animals actively adjust their behavior in a manner that facilitates learning in another animal, which do not satisfy definitions of teaching. The opportunity teaching of felids provides one example;⁵⁷ the food calls of adult callitrichid monkeys,^{58,59} the food and alarm calls of mother hens,⁶⁰ and the stranding of whale calves⁴² may be others (see also the “stimulating” and “facilitating” of infants by chimpanzee mothers described by Boesch²¹). Irrespective of their goal or knowledge of the learner’s abilities, the demonstrators appear to function as teachers in these examples. Indeed, leading researchers have called for teaching to be redefined in functional terms.⁶¹ There seems to be a gradation of teaching-like phenomena, yet this has received little attention from students of animal social learning. As a result, there is no satisfactory classification scheme or terminology to describe animal teaching. Just as the reputations of animals have suffered from the treatment of teaching as an all-or-nothing phenomenon, so our own species has benefited. Human teaching is not required to satisfy the strict criteria applied to animals, and “teaching” in common parlance when applied to humans is a much broader concept altogether. It would be interesting to know what proportion of human teaching actually satisfies Caro and Hauser’s⁵⁶ definition. Teachers recognize the value for children of opportunity teaching, and many believe that allowing children to discover and learn for themselves is frequently more productive than more classical forms of pedagogical instruction.

(Boesch²¹ and Whiten²² make similar arguments.)

The same point can be made with regard to imitation, where once again animals are being judged according to a stricter definition than is applied to humans. The fact that humans are capable of imitation is no reason to regard it as the sole or even principle process of information transmission underlying human culture. Perhaps children learn how to get around their neighborhood, where the grocery store is, and which locations are dangerous by following parents around, like reef fish. Perhaps humans acquire many skills through emulation, like other primates.⁶² Even when they “imitate,” do humans really copy each other’s exact motor patterns? We suspect that “program-level imitation,”⁶³ where the underlying organization of behavior is copied, rather than the surface details, is more common. While we are open to the idea that teaching and imitation may be more important to human culture than to animal social learning, we would like to reserve judgment until humans and other animals are evaluated according to the same standards. It is conceivable to us that a careful analysis of teaching and imitation in humans would leave our species looking considerably less distinct.

For Tomasello,⁶² teaching and imitation are significant because they are deemed to generate a higher degree of fidelity of transmission among humans than is found for animals. We see two problems with this argument. First, we know of no evidence that there is greater fidelity associated with human than animal culture. Cavalli-Sforza and coworkers⁶⁴ survey of patterns of cultural transmission reported average parent-offspring correlations for habits, entertainments, and sports to be as low as 0.07, 0.16 and 0.13, respectively. Boyd and Richerson⁵⁵ reported parent-offspring correlations ranging from 0.34 for attitudes towards feminism to 0.8–0.94 for political party affiliation, with values of around 0.5–0.6 being common. Can we really be sure that humans have higher cultural fidelity than animals? Second, to our knowledge, there is no experimental evidence that imitation results in higher fidelity transmission

than do other forms of social learning. Heyes⁶⁵ argues compellingly that the fidelity of cultural transmission is independent of the learning processes that individuals employ to acquire a behavior; rather, it depends on the patterns of reinforcement that individuals subsequently experience. As we argued earlier, much of what in common parlance is described as human imitation is more appropriately termed program-level imitation, yet this will not necessarily have high fidelity.

Moreover, universality and uniformity do not seem to be features on which human culture and animal social learning can be distinguished. Field evidence for purported animal culture is provided either by different behavior in two or more populations of the same species (group-typical behavior) or by an increase in the frequency of a novel behavior in a single population (diffusion). In the former case, unless the differences between the populations’ behavioral repertoires are substantive they are likely either to be unnoticed or to be attributed to random fluctuations, observer error, or ecological differences. It is when behavioral variants are customary in one population and not in others that a claim of cultural variation is most likely to be put forward. Similarly, diffusions typically are identified only when a significant proportion of the population has acquired the novel variant. Not all diffusions reach universality in animal populations, but not all human traditions are universal either. The claim for animal culture usually rests on the recording of behavioral variants that are universal, near universal, or at least common within a population.

Mathematical analyses have found that in most circumstances where natural selection favors reliance on social learning, conformity is also favored.^{55,66} These theoretical considerations lead us to expect most animal social learning to be conformist, with individuals commonly adopting the behavior of the majority. This prediction has empirical support across a broad array of species, and social learning in which the probability of adopting a pattern of behavior increases with the proportion of demon-

strators is reported in animals as diverse as guppies, pigeons, and rats.⁶⁷ Conformity may be a characteristic feature of animal social learning, as it is for humans. If, as Tomasello¹³ notes, chimpanzee populations are characterized by individuality rather than uniformity, then it is chimpanzees that are “unique.”

A stronger case can be made for history: Much human culture is characterized by the “ratchet effect,”¹³ with an increase in the complexity or efficiency of technology over time (see also Alvard⁴). There is little direct evidence within animal populations of additive, incremental improvement in behavior or technological advance. Evidence for cumulative evolution in tool manufacture has recently been reported in New Caledonian crows (Hunt and Gray, personal communication). There are one or two primate behavior patterns, such as leaf clipping and nut cracking by chimpanzees, and sweet-potato washing by Japanese macaques, for which a case can be made for ratcheting,^{21,68,69} but they remain speculative and contentious.

However, before we congratulate ourselves for isolating a distinctive and unique feature of human culture, it is worth reflecting on two points. First, one can look at millions of years of our ancestors’ lithic technologies and many ethnographic studies of traditional peoples without seeing evidence for ratcheting. Oldowan and Acheulean hand-axe technologies lasted without significant changes for over one million years each.⁷⁰ Cultural evolution in other primates could be cumulative at rates equivalent to those in early *Homo* or even preindustrial societies, and we might not notice. Second, the assertion that animals do not exhibit ratcheting is tantamount to the argument that all nonhuman group-typical behavior patterns could have been invented in their final form by a single innovative individual. Many researchers, particularly those familiar with the complex behavior of apes, find this difficult to believe. Yet it matters little whether nonhuman animals exhibit no ratcheting, slow ratcheting, or very little ratcheting: There clearly is a fundamental quantitative difference in the

degree to which contemporary human and animal cultures are cumulative.

If purported animal cultures do not exhibit cumulative evolution, then why not? Tomasello's and Galef's emphasis on human's capacity for teaching and imitation provides one sort of explanation, but from the preceding discussion it is apparent that this has only limited support. What is more, explanations that posit the historical emergence of a special character (teaching, imitation, language) as critical to the evolution of human culture do little to stimulate empirical research. These explanations betray an underlying assumption that only a unique human characteristic can explain unique human culture. We do not accept this logic. Not that we think capabilities such as teaching, imitation, and language are unimportant to the evolution of human culture, but rather that an emphasis on them puts the cart before the horse. When it comes to the issue of what is unique about human culture, we see two key questions: Why do so few animal innovations spread and why is so much human culture stable and transgenerational? While we are not yet able to provide clear answers to these questions, we see no barriers to their empirical investigation, and believe such research would contribute significantly to understanding of what makes human cultures unique.

Reader (personal communication) found that of 606 cases of learned behavioral innovation in nonhuman primates only 16% spread to a second individual, and an even smaller proportion spread throughout the group. Parallel observations, with many innovations but comparatively few diffusions, have been made in bird populations.⁷¹ This seems to contrast with human innovation, where many, although still by no means all, advantageous innovations spread.⁷² What are the barriers to the spread of innovation in animals?

First, we suspect that one reason cumulative culture appears rare in animals is that there are comparatively few natural circumstances where it would pay an individual to adopt a more advanced means of doing something when a simpler solution works well. A prime question seems to be,

are humans less content to sacrifice (that is, make do with a functional but sub-optimal solution to a problem) than other animals? If so, why?

Second, in hierarchical animal societies a disproportionate amount of innovation appears to be carried out by low-status individuals.^{50,51} Low-rankers often occupy the periphery of the social group, are attended to less than high-ranking individuals, have less influence on group behavior, tend to move away or are behaviorally inhibited when approached by higher-ranking group members, and are more vulnerable to scrounging than are high-ranking individuals. All these characteristics would mitigate against the diffusion of innovations generated by low-rankers. Conversely, in more egalitarian societies social learning appears commonly to exhibit conformity, and experimental studies have found that conformity makes it less likely that animals will adopt novel behavior.⁶⁷ Human societies obviously are not more egalitarian or less conformist than animal societies. (Indeed, Henrich and McElreath⁶⁶ describe conformity and prestige learning biases as characteristic of humanity.) So how are these inhibiting effects circumvented? Does language allow innovators to advertise their inventions? Does trade give them an incentive to do so? Do social contracts reduce the likelihood of their exploitation? Again, there are clear opportunities for empirical investigation.

Why is so much human culture stable and transgenerational? Purported animal cultures are largely reliant on short-lived horizontal transmission,^{73,74} while humans appear to acquire large amounts of information from the parental generation.^{64,75,76} These findings suggest that the lineage leading to *Homo sapiens* has been selected for increasing reliance on vertical and oblique cultural transmission. Theoretical analyses imply that a shift toward increased transgenerational culture reflects greater constancy in the environment over time,⁵⁵ yet there is no evidence that ecological environments have become more constant over the last few million years. Culture may be adaptive for a larger range of conditions in humans than

other animals because humans exhibit a greater capacity to construct and regulate those conditions, that is, for "niche construction."^{16,77,78} Regulatory behavior such as tracking game, storing food, and building shelters damps out temporal variation in conditions and resources to ensure that cultural behaviors maintain their utility from one generation to the next.^{77,78} While the capacity for niche construction is universal to living creatures, human niche construction is extraordinarily powerful, in part as a consequence of our culture. Perhaps what is unique about human culture is that, through niche construction, cultural transmission has become self-reinforcing, with transgenerational culture modifying the environment in a manner that favors ever more culture.

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REFERENCES

- 1 Durham WH. 1991. *Coevolution: genes, culture and human diversity*. Stanford University Press.
- 2 Kroeber AL, Kluckman C. 1952. *Culture: A critical review of concepts and definitions*. Cambridge, MA.
- 3 Kuper A. 2000. If memes are the answer, what is the question? In: Aunger R, editor. *Darwinising culture: the status of memetics as a science*. Oxford: Oxford University Press.
- 4 Alvard M. 2003. The adaptive nature of culture. *Evolutionary Anthropology* 12:3:136–149.
- 5 Heyes CM, Galef BG. 1996. *Social learning in animals: the roots of culture*. London: Academic Press.
- 6 Shettleworth SJ. 2001. Animal cognition and animal behavior. *Anim Behav* 61:277–286.
- 7 de Waal F. 2001. *The ape and the sushi master*. London: Penguin.
- 8 Galef BG Jr, Giraldeau L-A. 2001. Social influences on foraging in vertebrates: causal mechanisms and adaptive functions. *Anim Behav* 61: 3–15.
- 9 Zentall TR, Galef BG Jr. 1988. *Social learning: psychological and biological perspectives*. Hillsdale, NJ: Erlbaum.
- 10 Box HO, Gibson KR, editors. 1999. *Mammalian social learning: comparative and ecological perspectives*. Cambridge: Cambridge University Press.
- 11 Fragaszy D, Perry S, editors. n.d. *Traditions in nonhuman primates: models and evidence*. Chicago: University of Chicago Press. In press.
- 12 Lumsden CJ, Wilson EO. 1981. *Genes, mind and culture*. Cambridge: Harvard University Press.

- 13 Tomasello M. 1994. The question of chimpanzee culture. In: Wrangham R, McGrew W, de Waal F, Heltné P, editors. *Chimpanzee cultures*. Cambridge: Harvard University Press. p 301–317.
- 14 Galef BG Jr. 1992. The question of animal culture. *Hum Nat* 3:157–178.
- 15 Galef BG Jr. n.d. Social learning: promoter or inhibitor of innovation? In: Reader SM, Laland KN, editors. *Animal innovation*. Oxford: Oxford University Press. In press.
- 16 Fragaszy D. 2003. Making space for traditions. *Evol Anthropol* 12:61–70.
- 17 Macphail EM. 1982. *Brain and intelligence in vertebrates*. Oxford: Clarendon Press.
- 18 Reader SM, Laland KN. 2002. Social intelligence, innovation and enhanced brain size in primates. *Proc Natl Acad Sci USA* 99:4436–4441.
- 19 McGrew WC. 1992. *Chimpanzee material culture: implications for human evolution*. Cambridge: Cambridge University Press.
- 20 Whiten A, Goodall J, McGrew WC, Nishida T, Reynolds V, Sugiyama Y, Tutin CEG, Wrangham RW, Boesch C. 1999. *Cultures in chimpanzees*. *Nature* 399:682–685.
- 21 Boesch C. 2003. Is culture a golden barrier between human and chimpanzee? *Evol Anthropol* 12:82–91.
- 22 Whiten A, Horner V, Marshall-Pescini S. 2003. *Cultural panthropology*. *Evol Anthropol* 12:106–108.
- 23 van Shaik C. n.d. In: Fragaszy D, Perry S, editors. *Traditions in nonhuman primates: models and evidence*. Chicago: Chicago University Press. In press.
- 24 Perry S, Manson J. 2003. Traditions in monkeys. *Evol Anthropol* 12:71–81.
- 25 Whiten A, Custance DM. 1996. Studies of imitation in chimpanzees and children. In: Galef BG Jr, Heyes CM, editors. *Social learning in animals: the roots of culture*. New York: Academic Press. p 291–318.
- 26 Whiten A, Custance DM, Gomez J, Teixidor P, Bard K. 1996. Imitative learning of artificial fruit processing in children (*Homo sapiens*) and chimpanzees (*Pan troglodytes*) *J Comp Psychol* 110:3–14.
- 27 Whiten A. 1998. Imitation of the sequential structure of actions by chimpanzees (*Pan troglodytes*) *J Comp Psychol* 112:270–281.
- 28 McGrew WC, Tutin CEG. 1978. Evidence for a social custom in wild chimpanzees. *Man* 13:234–251.
- 29 Humle T, Matsuzawa T. n.d. Ant dipping among the chimpanzees of Bossou, Guinea and some comparisons with other sites. *Am J Primatol*. In press.
- 30 Boesch C, Boesch H. 1990. Tool use and tool making in wild chimpanzees. *Folia Primatol* 54:86–99.
- 31 Helfman GS, Schultz ET. 1984. Social tradition of behavioral traditions in a coral reef fish. *Anim Behav* 32:379–384.
- 32 Warner RR. 1988. Traditionality of mating-site preferences in a coral reef fish. *Nature* 335:719–721.
- 33 Bshary R, Wickler W, Fricke H. 2002. Fish cognition: a primate eye's view. *Anim Cogn* 5:1–13.
- 34 Brown C, Laland KN. 2001. Suboski and Templeton revisited: social learning and life skills training for hatchery reared fish. *J Fish Biol* 59:471–493.
- 35 Catchpole CK, Slater PJB. 1995. *Bird song: biological themes and variations*. Cambridge: Cambridge University Press.
- 36 Freeberg TM. 2000. Culture and courtship in vertebrates: a review of social learning and transmission of courtship systems and mating patterns. *Behav Processes* 51:177–192.
- 37 White DJ, Galef BG. 2000. "Culture" in quail: social influences on mate choices of female *Coturnix japonica*. *Anim Behav* 59:975–979.
- 38 Kirkpatrick M. 1987. Sexual selection by female choice in polygynous animals. *Ann Rev Ecol Syst* 18:43–70.
- 39 Freeberg TM. 1996. Assortative mating in captive cowbirds is predicted by social experience. *Anim Behav* 52:1129–1142.
- 40 Freeberg TM. 1998. The cultural transmission of courtship patterns in cowbirds, *Molothrus ater*. *Anim Behav* 56:1063–1073.
- 41 Freeberg TM, Duncan SD, Kast TL, Enstrom DA. 1999. Cultural influences on female mate choice: an experimental test in cowbirds (*Molothrus ater*). *Anim Behav* 57:421–426.
- 42 Rendell L, Whitehead H. 2001. Culture in whales and dolphins. *Brain Behav Sci* 24:309–382.
- 43 Kawai M. 1965. Newly-acquired pre-cultural behavior of the natural troop of Japanese monkeys on Koshima islet. *Primates* 6:1–30.
- 44 Wilson EO. 1975. *Sociobiology*. Cambridge: Harvard University Press.
- 45 Bonner JT. 1980. *The evolution of culture in animals*. Princeton: Princeton University Press.
- 46 Kummer H, Goodall J. 1985. Conditions of innovative behavior in primates. *Philos Trans R Soc London, Series B* 308:203–214.
- 47 Visalberghi E, Fragaszy D. 1990. Do monkeys ape? In: Parker ST, Gibson KR, editors. *Language and intelligence in monkeys and apes*. Cambridge: Cambridge University Press. p 247–273.
- 48 Laland KN, Reader S. 1999. Foraging innovation in the guppy. *Anim Behav* 52:331–340.
- 49 Laland KN, Reader SM. 1999. Foraging innovation is inversely related to competitive ability in male but not in female guppies. *Behav Ecol* 10:270–274.
- 50 Reader SM, Laland KN. 2001. Primate innovation: sex, age and social rank differences. *Int J Primatol* 22:787–805.
- 51 Reader SM, Laland KN. n.d. Animal innovation: an introduction. In: Reader SM, Laland KN, editors. *Animal innovation*. Oxford: Oxford University Press. In press.
- 52 Day RL, Coe RL, Kendal JR, Laland KN. n.d. Neophilia, innovation and social learning: a study of intergeneric differences in callitrichid monkeys. *Anim Behav*. In press.
- 53 Fragaszy DM, Visalberghi E. 1990. Social processes affecting the appearance of innovative behaviors in capuchin monkeys. *Folia Primatol* 54:155–165.
- 54 Laland KN, Kendal JR. n.d. What the models say about animal social learning. In: Fragaszy D, Perry S, editors. *Traditions in nonhuman primates: models and evidence*. Chicago: Chicago University Press. In press.
- 55 Boyd R, Richerson PJ. 1985. *Culture and the evolutionary process*. Chicago: The University of Chicago Press.
- 56 Caro TM, Hauser MD. 1992. Is there teaching in nonhuman animals? *Q Rev Biol* 67:151–174.
- 57 Caro TM. 1980. Predatory behavior in domestic cat mothers. *Behavior* 74:128–148.
- 58 Roush RS, Snowdon CT. 2000. Quality, quantity, distribution and audience effects on food calling in cotton-top tamarins. *Ethology* 106:673–690.
- 59 Roush RS, Snowdon CT. 2001. Food transfer and development of feeding behavior and food-associated vocalizations in cotton-top tamarins. *Ethology* 107:415–429.
- 60 Nicol CJ, Pope SJ. 1996. The maternal feeding display of domestic hens is sensitive to perceived chick error. *Anim Behav* 52:767–774.
- 61 Shettleworth SJ. 1998. *Cognition, evolution and behavior*. New York: Oxford University Press.
- 62 Tomasello M. 1990. Cultural transmission in the tool use and communicatory signalling of chimpanzees? In: Parker S, Gibson K, editors. *Chimpanzee cultures*. Cambridge: Harvard University Press.
- 63 Byrne RW. 1998. Learning by imitation: a hierarchical approach. *Behav Brain Sci* 21:667–721.
- 64 Cavalli-Sforza LL, Feldman MW, Chen KH, Dornbusch SM. 1982. Theory and observation in cultural transmission. *Science* 218:19–27.
- 65 Heyes CM. 1993. Imitation, culture and cognition. *Anim Behav* 46:999–1010.
- 66 Henrich and McElreath. 2003. *Evolutionary Anthropology* 12.
- 67 Day RL, Macdonald T, Brown C, Laland KN, Reader SM. 2001. Interactions between shoal size and conformity in guppy social foraging. *Anim Behav* 62:917–925.
- 68 Boesch C. 1993. Toward a new image of culture in wild chimpanzees? *Behav Brain Sci* 16:514.
- 69 McGrew WC. n.d. Twenty lessons learned from labors in cultural primatology. In: Joulain F, editor. *How the chimpanzees stole culture. Culture and meaning in apes, ancient humans and modern humans*. Kluwer/Plenum Press.
- 70 Foley R, Lahr MM. 2003. On stony ground: lithic technology, human evolution and the emergence of culture. *Evolutionary Anthropology* 12.
- 71 Lefebvre L. 2000. Feeding innovations and their cultural transmission in bird populations. In: Heyes C, Huber L, editors. *The evolution of cognition*. Cambridge: MIT Press. p 311–328.
- 72 Rogers EM. 1995. *Diffusion of innovations*, 4th ed. New York: Free Press.
- 73 Galef BG Jr. 1988. Imitation in animals: history, definition, and interpretation of data from the psychological laboratory. In: Zentall TR, Galef BG Jr, editors. *Social learning: psychological and biological perspectives*. Erlbaum. p 3–28.
- 74 Laland KN, Richerson PJ, Boyd R. 1993. Animal social learning: towards a new theoretical approach. *Perspect Ethol* 10:249–277.
- 75 Hewlett BS, Cavalli-Sforza LL. 1986. Cultural transmission among Aka pygmies. *Am Anthropol* 88:922–934.
- 76 Aunger R. 2000. The life history of culture learning in a face-to-face society. *Ethos* 28:1–38.
- 77 Laland KN, Odling-Smee J, Feldman MW. 2000. Niche construction, biological evolution, and cultural change. *Behav Brain Sci* 23:131–175.
- 78 Odling-Smee J, Laland KN, Feldman MW. 2003. *Niche construction. The neglected process in evolution*. Princeton, NJ: Princeton University Press.