the uestion *of* Animal Culture

EDITED BY KEVIN N. LALAND AND BENNETT G. GALEF

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INTRODUCTION

KEVIN N. LALAND AND BENNETT G. GALEF

Chimpanzees from the Gombe Stream Reserve in Tanzania use sticks to fish for termites, while those that live in the Taï Forest in the Ivory Coast do not; conversely, the use of a stone hammer to crack open nuts is observed at Taï but not at Gombe. Some orangutans in Borneo make leaf-bundle "dolls," others use tools as sexual stimulants, and still others blow raspberries at bedtime. Groups of white-faced capuchin monkeys in Costa Rica exhibit peculiar social conventions that are not seen in other capuchin populations, such as sniffing each other's hands and placing fingers in each other's mouths. Humpback whales from different regions sing different songs, and some female dolphins and their daughters use sponges as tools while foraging.

At first sight, such reports of behavioral differences among species members that live in different locations are evocative of human cultural variation. Just as people from different regions of the world eat different foods, have varying customs, and speak different languages, some animals also appear to have local traditions. Much circumstantial and some experimental evidence suggests that as in human societies, these traditions are learned from others and are handed down from one generation to the next. But are the similarities between animal "cultures" and those of humans meaningful or superficial?

No one who reads about animal behavior can be unaware of the recent spate of articles in prominent scientific journals, newspapers, and news magazines that argue that differences in the behavioral repertoires of animals living in different locales provide evidence that they, like humans, are cultural beings. Those with a slightly deeper interest in the possibility of culture in animals are probably also aware that many experts in behavioral development are unconvinced by the data that field biologists claim support the view that animal and human culture are fundamentally similar.

The question whether the traditions of animals and the culture of humans are truly similar is contentious, and psychologists, primatologists, behavioral ecologists, and anthropologists often hold somewhat different positions. Until now, these conflicting perspectives were to be found only in a widely scattered and often esoteric literature. Consequently, anyone who sought a comprehensive overview of the various opinions had to undertake a demanding search of the primary literature to find relevant materials. *The Question of Animal Culture* is designed to make that task far easier. The book's contributors, each an established authority on either social learning or a related field, address the question whether, in their opinions, animals have culture. The authors were asked to provide a précis of the data that they find most relevant to the issue, and to emphasize their interpretation of those data with respect to the question of the ways in which animal and human cultures are similar or different. By carefully choosing contributors who represent the full range of perspectives on this issue, we hope to have provided an up-to-date, comprehensive overview of the controversy.

A Brief History of the Animal Culture Debate

The idea that animals might acquire important components of their behavioral repertoires by copying others has a long history that dates back to Aristotle, who provided the first evidence of social learning of song in birds. Charles Darwin was aware of animal traditions, noting in *The Descent of Man* (1871, p. 161) that "apes are much given to imitation . . . and the simple fact previously referred to, that after a time no animal can be caught in the same place by the same sort of trap, shews [*sic*] that animals learn by experience, and imitate each other's caution." Early evolutionists, including Alfred Wallace, George Romanes, Conwy Lloyd Morgan, and James Baldwin, placed great emphasis on learned traditions as a source of adaptive behavior. In spite of his belief that the human brain required a special explanation, Wallace (1870) did not regard the handing on of skills and habits from one generation to the next as restricted to humans, and he saw a great deal of similarity between the processes that underlay the construction of nests by birds, deemed to be learned, in part, through imitation, and the building of shelters by humans. Romanes (1884) regarded imitation as the critical means by which animals, particularly mammals, refine their instincts. Morgan stressed birdsong dialects and traditional food preferences in animals as suggesting continuity of

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mental abilities between humans and other animals (C. L. Morgan 1896a). Further, C. L. Morgan (1896b), Baldwin (1896), Spalding (1873), and Osborne (1896) independently suggested that organisms could survive ecological challenges by virtue of their acquired knowledge and skills, frequently learned from others, and that this would then channel natural selection to favor unlearned versions of the same adaptive behavior.

Over the last century field researchers have reported many cases of the spread of novel foraging behaviors in natural animal populations. Lefebvre and Palameta (1988) document many "possible socially transmitted foraging behaviors" in a variety of vertebrates, going back to 1887, when Carpenter reported the putatively socially transmitted habit of cracking oysters with stones in crab-eating macaques. More familiar examples include the drinking of cream from milk bottles by some European birds (Fisher and Hinde 1949) and the spread of food-washing techniques in Japanese macaques (Kawai 1965). Such behavioral innovations appear to have spread too quickly to be explained plausibly by population genetic, ecological, or demographic factors and have been assumed to spread through social learning. However, in general, researchers have rarely been able to substantiate the claim that such diffusions are actually the product of social (as opposed to asocial) learning, and this has left the assumption that the behaviors are spread socially open to criticism.

The modern debate over animal culture began in earnest in Japan a little more than half a century ago. Inspired by Imanishi's claim that culture is widespread in animals, Japanese researchers began to document traditions in free-living, but often provisioned, primate populations (Kawai, 1965; de Waal 2001). The most famous among these is the washing of sweet potatoes by Japanese macaques.

In September 1953 Satsue Mito first saw Imo, an 18-month-old, female Japanese macaque, wash a dirt-covered sweet potato in a small freshwater stream on Koshima Island in the Sea of Japan. A dozen years later, when the first publication appeared in the West that described the pattern of diffusion through Imo's troop of the habit of washing dirt from sweet potatoes before eating them, its author referred to this behavior and other unique patterns of behavior seen on Koshima as "precultural" (Kawai 1965), much as Kawamura, the author of an earlier article on socially learned behaviors of macaques in Japan, had referred to the behavioral variants he described as "sub-cultures" (Kawamura 1959). The implication was, as Kawai made explicit in a more recent

publication (Hirata et al. 2001, p. 489), that "we must not overestimate the situation and say that 'monkeys have culture' and then confuse it with human culture." At the same time, the use of the word "culture," even prefixed as it was, implied some unusual degree of correspondence between monkey and human behavior, be it homologous or analogous.

For several years after Kawai's publication, most researchers who studied behaviors that observation suggested had been socially transmitted through a population referred to the behavioral phenomena that they were interested in as "precultural" (e.g., Menzel 1973a), "protocultural" (Menzel et al. 1972), or "traditional" (e.g., Beck 1974; Strum 1975). Possibly because all the socially transmitted behaviors studied during this period, like many human cultural traditions, functioned primarily to increase the efficiency with which bearers of a tradition could extract resources from the environment, primatologists seemed reluctant to think of such animal traditions as equivalent to human traditions, which often have important social and symbolic as well as practical functions.

In 1978 McGrew and Tutin reported the first evidence of a tradition involving an apparently arbitrary pattern of behavior, the grooming handclasp, prevalent in a troop of chimpanzees at Kasoge in western Tanzania but never observed at Gombe, a mere 50 kilometers distant. McGrew and Tutin (1978) argued forcefully that handclasp grooming satisfied many of the criteria used to identify cultural patterns in humans and that use of the term "culture" to refer not only to handclasp grooming but also to other population-specific behaviors of chimpanzees was justified. McGrew and Tutin's article was the first in the modern era to directly address the question of the relationship between the traditions of animals and the culture of humans. McGrew and Tutin appeared to initiate a trend. Increasingly the prefixes were dropped as talk of "preculture" and "protoculture" changed to discussion of "culture," particularly when speaking of chimpanzees (Goodall 1986; Nishida 1987; McGrew 1992; Boesch 1993a; Wrangham, McGrew et al. 1994).

McGrew went on to document substantial differences in the behavioral repertoires of populations of chimpanzees scattered across Africa. He set out to study this behavioral variation systematically and to make detailed comparisons between sites. He found a number of different behavior patterns, ranging from foraging to sexual, aggressive, and even medicinal behavior, that varied systematically among chimpanzee populations, and he argued that these were passed across generations as learned traditions.

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The variation in chimpanzee behavioral repertoires and McGrew's interpretation of this variation as cultural received considerable attention through his influential book *Chimpanzee Material Culture* (1992) and Wrangham, McGrew, and colleagues' (1994) edited volume *Chimpanzee Cultures*. McGrew's argument was seconded in widely read popular books, notably Frans de Waal's *The Ape and the Sushi Master,* that presented further evidence of humanlike cognition, emotions, ethics, and culture in other primates, especially chimpanzees (de Waal 2001).

Not everyone was convinced by these arguments. Critics, notably psychologists Bennett Galef (1992, 2003b) and Michael Tomasello (1994, 1999a), took issue with claims of animal culture, primarily on two levels. First, they criticized the data; any claim of culture demanded clear demonstration that putative traditions are a consequence of social learning. Critics pointed out that the observed behavioral differences between populations of chimpanzees could be the result of variation in ecological resources between sites (see Galef this book). Second, they suggested that parallels between animal and human culture rested on superficial analogies rather than on homologies in cognitive processing (see Galef this book; Tomasello this book). In particular, Galef and Tomasello insisted that human culture was supported by imitation and teaching, different psychological mechanisms than those that supported animal traditions. Tomasello (1994) further suggested that imitation and teaching were critical for traditions to exhibit the "ratchet effect" (Tomasello 1994, this book) that produced an increase in the complexity or efficiency of technology over time that was never observed in animal traditions. With publication of the articles by Galef and Tomasello, the debate over animal cultures began in earnest.

Meanwhile, biologists had begun to use the term "culture" in a broad manner. John Tyler Bonner (1980, p.9), in his widely read book *The Evolution of Culture in Animals,* defined culture as "the transfer of information by behavioral means" and was willing to describe invertebrates as exhibiting rudimentary culture. He traced the increasing complexity of acquired information transmission from simple imprinting mechanisms through crude forms of social learning in birds and mammals to "imitation" in chimpanzees and then to full-blown human culture. Similarly, in their book *Genes, Mind, and Culture* Charles Lumsden and Edward Wilson (1981) attributed culture to some 10,000 species, including even some bacteria. Lumsden and Wilson deemed any extragenetic form of acquired information transmission "cultural." Mundinger (1980) took a slightly

more restricted line, describing as culture vocal learning in passerine birds, a label that stuck (Catchpole and Slater 1995). For Mundinger, culture simply implied social learning.

In the late 1990s experimental evidence of imitation by chimpanzees began to appear (Whiten et al. 1996; Whiten 1998), which some regarded as undermining the animal culture skeptics' position (Whiten et al. 1999; Whiten this book; van Schaik this book). The case for chimpanzee culture was given a major boost by a remarkable international collaborative effort among nine leading primatologists, each of whom had spent many years studying chimpanzee behavior (Whiten et al. 1999). These researchers collated behavioral information from seven long-term field studies of chimpanzees at different sites across Africa. This mammoth undertaking revealed patterns of variation far more extensive than had previously been documented for any animal species other than humans. Sixty-five categories of behavior were described, 42 of which exhibited significant variability across sites.

Although some of this variation was attributed to differences in the availability of resources (absence of algae fishing can be explained by the rarity of algae at some sites), some behavior patterns, including tool use, grooming, and courtship behaviors, were common in some communities but absent in others, and this distribution had no apparent ecological explanation. Moreover, the repertoire of such traditional behavior patterns in each chimpanzee community was highly distinctive, a phenomenon characteristic of human cultures but previously undiscovered in any nonhuman species.

Whiten and colleagues' (1999) systematic analysis of multiple sites, documentation of the absence, as well as the presence, of behaviors, and recording of frequencies of behavioral variants were important improvements in the scale and rigor of analyses of animal traditions. On the basis of their data, Whiten and colleagues (1999) felt comfortable titling their article "Cultures in chimpanzees." Whiten (2005, this book) later stressed that it was no coincidence that our nearest relatives exhibit the traditions most like those of human culture of all animals, and he argued that chimpanzee and human cultures result from homologous processes.

Whiten and colleagues' (1999) analysis precipitated a series of articles that applied similar methods to other species (van Schaik, Ancrenaz et al. 2003; Perry, Panger et al. 2003; Krützen et al. 2005). Collectively these papers implied that differences in the behavioral repertoires of many large-brained mammals living in different locales provided evidence that

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they were cultural beings. That articles proposing animal culture were often published in highly prestigious journals (*Nature, Science, Proceedings of the National Academy of Sciences USA*) illustrates the attention that the topic of animal culture could now garner. A conference on the topic of animal traditions, followed by an edited volume (Fragaszy and Perry 2003a), drew further attention to the field.

In an article titled "Orangutan cultures and the evolution of material culture," van Schaik, Ancrenaz, and colleagues (2003) identified 24 putative cultural variants (including feeding techniques and social signals) in six populations of orangutans, with each population again characterized by a distinctive repertoire of traditional behaviors. Primatologists who studied free-living populations of orangutans provided additional support for their interpretation of this variation as reflecting socially transmitted traditions by demonstrating correlations between geographic proximity and cultural similarity of populations and between opportunities for social learning and size of cultural repertoire. There is no doubt that van Schaik, Ancrenaz, and colleagues' (2003) use of the term "cultural" implied homology with human culture: "The presence in orangutans of humanlike skill (material) culture pushes back its origin in the hominoid lineage to about 14 million years ago, when the orangutan and African ape clades last shared a common ancestor" (p. 105).

At about the same time, researchers who were studying capuchin monkeys published results of a major, long-term collaborative study of white-faced capuchin monkeys (*Cebus capucinus*) that revealed behavioral variation in the social conventions of 13 social groups throughout Costa Rica (Perry, Panger et al. 2003). Several striking and often bizarre social conventions were candidates for traditional status, including hand sniffing, sucking of body parts, and placing fingers in the mouths of other monkeys. What is particularly compelling about these data is that it is all but impossible to attribute variation in such conventions to ecological differences among sites. However, Perry, Panger and colleagues (2003) carefully avoid describing these traditions as culture (see Perry this book).

In parallel to the debate over interpretation of primate foraging traditions, material culture, and social conventions, similar controversies were starting to develop over vocal traditions in birds, dolphins, and whales. The existence of socially transmitted vocal dialects in birds had been known since Marler (1952), and geographic variation in the songs of many passerines has been documented, notably white-crowned sparrows

and chaffinches (Marler and Tamura 1964; Catchpole and Slater 1995). From the 1970s evidence began to appear for vocal traditions in mammals, particularly cetaceans (Caldwell and Caldwell 1972; Janik and Slater 1997). Much of the research on vocal traditions in cetaceans has focused on bottlenose dolphins (*Tursiops* spp.) and humpback whales *(Megaptera novaeangliae)* (Janik and Slater 1997). For example, all males in a humpback whale population share a song that changes gradually during the singing season, a change much too rapid to be explained by changes in genotype (Payne and Payne 1985). Most striking, off the east coast of Australia, a song was observed to change in 2 years to one previously heard only off the west coast of Australia, possibly as a result of movement of a few individuals from west to east (Noad et al. 2000).

Claims of cetacean social learning have also been made in domains other than vocalization, particularly foraging and migratory traditions, and have moved the topic of culture to the center of cetacean research. A review titled "Culture in whales and dolphins" (Rendell and Whitehead 2001) lists a broad range of traits that can be interpreted as cultural, including killer whales *(Orcinus orca)* beaching themselves during foraging and bottlenose dolphins using sponges to grub for prey.

As this brief historical account reveals, over the last two decades there has been a profound change in the frequency with which scientists who write about population-specific behaviors in animals refer to the phenomena they discuss as "culture." The growing number of long-term behavioral studies of primate and cetacean populations, detailed comparisons of the behavioral repertoires of different populations, and documentation of diversity in animals' use of tools, foraging patterns, vocalizations, and modes of social interaction have brought to the fore behavioral variation in animals that many researchers view as similar to human culture. However, the species that are most commonly put forward as culture bearing (primates and cetaceans) are often among the most difficult animals to study. Several have endangered or threatened status, and for a variety of ethical and practical reasons, at least in the field (but see Matsuzawa et al. 2001), investigation of purportedly traditional behaviors of most is largely restricted to observational studies. As a consequence, the evidence that advocates of animal cultures are able to muster is largely circumstantial in nature. Although, in theory, one major component of the controversy over animal culture could be resolved by experimental manipulations, for instance, the translocation of individuals between populations or of populations between sites, as has been

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successfully used to demonstrate traditional behavior in fishes (Warner 1988, 1990), in reality, it is not possible to apply this methodology to chimpanzees or humpback whales. One ramification of these methodological constraints is that the case for animal culture rests largely on judgments of plausibility (Laland and Hoppitt 2003), about which opinions vary considerably, as this book demonstrates.

Part of the disagreement over animal culture reflects definitional issues. Biologists (see, for instance, Whitehead or Laland, Kendal, and Kendal's chapters in this book) seemingly tend to employ less exacting definitions than do anthropologists (as exemplified by Perry or Hill's contributions), and psychologists often take an intermediate position between the two. Some researchers deem a species cultural if it exhibits socially transmitted traditions, while others raise the bar to demand, for instance, teaching, group-specific norms, or ethnic markers. The range of definitions adopted reflects, in part, variability in the questions that researchers from different disciplines address.

As Perry (this book) points out, in the main, sociocultural anthropologists have not yet engaged in the animal culture debate: "Cultural anthropologists are so dismissive of the notion of animal 'culture' that it is difficult to find one who thinks it worth his time to articulate his objections in print." Given that human culture is widely regarded as the "type specimen" for animal culture, the lack of input from the very researchers who dedicate their lives to its investigation is surely a major omission. In this respect, the contributions of Hill and Perry in this book are particularly valuable.

However, there is more to the debate over animal culture than squabbles over definitions. A large part of the controversy concerns the kinds of evidence sufficient to establish that differences in the behavior of geographically separate populations of a species result from social learning rather than from genetic differences between populations or differences in the way diverse ecologies shape behavioral development of individuals. Here researchers differ in the degree to which they are willing to rely on circumstantial evidence and plausibility arguments, and laboratory experimentalists and field researchers often take different sides.

In addition, researchers disagree over whether human culture and animal cultures are fundamentally different or fundamentally similar (or perhaps more accurately, in what ways human and animal cultures are similar to or different from one another). Naturally, animal culture advocates stress the similarities of animal traditions to human culture, focusing on

common characteristics, such as behavioral variation underpinned by social learning, group-specific repertoires, or the diffusion of innovations, while skeptics stress the many differences, such as social learning mechanisms, evidence of cumulative culture, and norms.

As noted earlier, the range of perspectives on the question of animal culture has produced a widely dispersed and, at times, esoteric literature. Nonetheless, the field has important implications for both our understanding of the continuity of animal and human minds and the way in which we characterize *Homo sapiens*. The goal of this book is to capture the current breadth of opinion and to get to the heart of the issues. We are fortunate in having recruited essentially all of today's major players in the debate about the nature of culture and thus can provide the reader with a comprehensive, concise, and accessible overview of the current state of the field.

The Structure of This Book

Because of the nature of this book, the participants rather than the issues shaped it. However, the editors asked each author to address, at least in passing, one or more of a small number of questions: What is the most useful way to conceptualize culture? If you feel that a definition of culture is helpful, what is yours? Which animals, if any, exhibit culture? What data and which methods provide the best evidence for culture in animals? Which commonly employed methods or commonly cited data fail to provide such evidence? In what ways are animal and human cultures similar and different? What is the source of the controversy over animal culture, and what would be required to resolve that controversy?

The authors' contributions have been organized sequentially from the strongest advocates of animal culture to the strongest skeptics. In structuring the book in this manner, we acknowledge that the reduction of a multifaceted debate to a single dimension results in a somewhat arbitrary placement of individuals in the debate. Nonetheless, we persisted with the ordering because no matter how crude it is, it does serve to place the various contributions in context and makes it very easy to see the breadth of opinion.

In chapter 2 Frans de Waal, author of numerous books on chimpanzee social behavior, and his student, Kristin Bonnie, present their view that "there is good evidence for culture in many mammals, fish, and birds."

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The chapter opens with a spirited opposition to the idea that the products of only a limited set of mechanisms of transmission qualify as cultural. The authors instead advocate a functional, biological perspective in which mechanisms are secondary to social relationships.

The chapter presents observations and experimental findings on brown capuchin monkeys and chimpanzees that, together with data on other aspects of primate behavior, support the Bonding- and Identification-Based Observational Learning (BIOL) model first proposed in de Waal's (2001) book *The Ape and the Sushi Master*. Instead of being dependent on external rewards, "BIOL is a form of learning born out of the desire to belong and fit in." Young individuals ("the apprentices") identify with a certain model ("the master"), whom they copy, often without receiving extrinsic rewards for doing so. Observations such as the inheritance of rank positions, culturally learned communication, handclasp grooming, and other arbitrary conventions in various primates are regarded by de Waal and Bonnie as providing evidence for affiliation and relationship-dependent forms of learning, consistent with BIOL. For these authors, social learning is more than just individual learning in a social context; it is subject to powerful social modifiers and motivators.

Chapter 3 is by William McGrew, a chimpanzee primatologist and, as indicated earlier, the first researcher to make the case that a nonhuman animal, the common chimpanzee, possesses culture. McGrew remains among the strongest proponents of the view that chimpanzees are cultural animals. Drawing on his three books (*Chimpanzee Material Culture* [1992], *Great Ape Societies* [1996], and *The Cultured Chimpanzee* [2004]) and numerous other publications on the topic, McGrew describes variation in chimpanzee behavior across different populations in Africa and argues that this variation cannot be explained by individual learning or genetic or environmental influences. Rather, this rich diversity in social and material culture reflects socially learned traditions, in many respects more similar to cultural variation in humans than is the behavior of other animals.

The title of his chapter, "Ten Dispatches from the Chimpanzee Culture Wars, plus Revisiting the Battlefronts"[1] betrays the hostile reception that the notion of animal culture evoked among anthropologists. McGrew outlines the criteria by which he believes a species can legitimately be categorized as cultural, which extend beyond behavioral diversity, social learning, and tradition. He challenges the assertions (Tomasello 1994) that cumulative culture is uniquely human and a definite feature of

human culture and that language and culture are both isomorphic and inseparable to conclude that "mounting evidence gives a rationale for cultural primatology."

Chapter 4 by Carel van Schaik focuses on orangutan culture. Van Schaik is a long-term student of traditions in orangutans and has catalogued orangutan behaviors that vary systematically across sites (van Schaik, Ancrenaz et al. 2003). In a robust defense of the "method of elimination," van Schaik describes why he feels that there are no realistic alternatives to accounts of orangutan behavioral variation in terms of culture. He also describes simple statistical analyses that support interpretation of this variation as socially transmitted traditions, for instance, correlations between geographic proximity and cultural similarity and between opportunities for social learning and size of cultural repertoire. For van Schaik, the attribution of culture requires multiple traditions, interpopulation variation, and group-typical behavioral repertoires.

Andrew Whiten studies social learning and imitation, particularly in chimpanzees and human children. He is also the first author of the primary article on culture in chimpanzees (Whiten et al. 1999), regarded by many as a methodological breakthrough in its pioneering use of detailed comparisons of the behavior of chimpanzees between sites across Africa. In chapter 5 Whiten presents the findings of his "method of exclusion" (ethnographic) approach to chimpanzee behavioral variation, which has become the standard method within the field, subsequently echoed in studies of orangutans, dolphins, and monkeys. On the basis of extensive experimental and comparative evidence, Whiten concludes that the "cultural" credentials of chimpanzees exceed those of other species capable of traditional behavior, with chimpanzees (and perhaps one or two other species) possessing multiple diverse traditions. Whiten describes experimental data (including studies of imitation and of transmission chains), in addition to comparative analyses of chimpanzee behavior across populations in Africa, that he argues collectively make a compelling, if circumstantial, case for chimpanzee culture.

Chapter 6 is by Hal Whitehead, a biologist who has investigated whale behavior for many years, with a focus on their social systems, migration, and "culture." Whitehead is also the author of *Sperm Whales: Social Evolution in the Ocean* (2003a), in which he argues that whales have culture, and co-author, with Luke Rendell, of a highly cited target article in *Behavioral and Brain Sciences* that put the topic of cetacean culture on the scientific map (Rendell and Whitehead 2001). In chapter 6

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Whitehead argues, on the basis of behavioral variation in wild populations, that there is good evidence for culture, that is, socially learned traditions, in several species of whales and dolphins.

Humpback and sperm whales, in particular, Whitehead suggests, exhibit complex vocal traditions, characterized by specific dialects in local populations (clans). Whitehead argues that these patterns cannot be explained by ecological differences together with individual learning, because clans use the same areas, or by genetic factors, because genetically unrelated animals perform clan-specific behaviors. However, Whitehead recognizes the need for new tools to address these issues, and much of his chapter is devoted to the development of novel statistical methods that use similarity matrices to isolate cultural variation in animals. For Whitehead, the key question relating to animal culture is not whether a particular behavior is socially learned, but rather how much of the variation in a behavioral pattern is determined by social leaning.

Chapter 7, by Brooke Sargeant and Janet Mann, focuses on within-population variation in dolphin foraging behavior. Janet Mann is a director of the Shark Bay Dolphin Research Project and heads a longitudinal study, the Dolphin Mother-Infant Behavioral Ecology Project, initiated in 1988, that investigates calf development, female reproduction, genetics, ecology, and behavior. Together with her student Brooke Sargeant, Mann has identified a number of distinctive foraging behaviors in a dolphin population and has catalogued the behavioral repertoires of numerous individuals, including many mother-daughter pairs. Sargeant and Mann argue that a small number of dolphin foraging behaviors may meet stringent definitions of cultural traditions. They hold that if the main criterion for animal culture is reliance on social learning, many species are likely to be deemed "cultural." Like Whiten, they present a variety of sources of evidence, ranging from experimental studies suggesting imitation to parent-offspring correlations in behavior in the field, that collectively make an impressive plausibility argument for dolphin culture.

Chapter 8 is by Kevin Laland, Jeremy Kendal, and Rachel Kendal. Laland has carried out extensive laboratory-based research into animal social learning in fish, birds, rodents, and primates, as well as mathematical analyses of cultural evolution and gene-culture coevolution. Laland and colleagues favor a broad and minimalist definition of culture, reflecting the continuity between humans and other animals, and are sympathetic to the idea that a range of vertebrates may possess culture. At the same time, they are critical of much evidence put forward in favor of primate

and cetacean culture. Laland has claimed that currently the experimental evidence of culture in fish is stronger than that in chimpanzees, since the best evidence for culture is found in species most amenable to experimental manipulation. However, Laland and colleagues are also critical of the arguments of those who are resistant to the notion of animal culture, and they suggest that the case against animal culture is often mediated by an anthropocentric bias. They maintain that the disparity of views over animal culture reflects the paucity of methodological tools available to researchers in this field, and they draw attention to some new mathematical and statistical methods that potentially could resolve the debate by allowing social learning to be identified inferentially.

In chapter 9[2] Michael Tomasello, a lifelong student of primate cognition and leading skeptic concerning claims of animal culture, stresses that the psychological mechanisms that underlie human culture and animal traditions are quite different. He criticizes claims of imitation in chimpanzees (although in his postscript Tomasello acknowledges recent work showing imitation in chimpanzees). For Tomasello, animal social learning is primarily reliant on simple mechanisms, such as local enhancement and emulation, that cannot support cumulative culture, while human culture is based largely on imitation and teaching.

According to Tomasello, the differences in the psychological processes that underpin social learning in humans and other animals are sufficient to explain why animal traditions do not have the "ratcheting" (cumulative) property that characterizes human culture. Tomasello identifies three key characteristics of human cultural traditions: *universality* (some traditions are practiced by virtually everyone), *uniformity* (people exhibit a high degree of similarity), and *history* (cultural traditions are passed faithfully between generations and accumulate knowledge). He concludes that although chimpanzee behavioral traditions exhibit strong evidence for universality, there is only weak evidence for uniformity or history. Tomasello hypothesizes 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.

Psychologist Bennett Galef has spent a long career engaged in laboratory experiments on social learning in rats and quail. Galef (1992) was one of the first to argue in print that the evidence of culture in primates is seriously flawed and not sufficient to support the claims of those who would call traditions in animals cultural.

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In chapter 10 Galef illustrates, through a series of examples, some of the difficulties associated with drawing the conclusion that an animal exhibits culture. He focuses primarily on the problem of how to exclude ecological explanations for behavioral variation. Galef also argues that human culture and animal behavioral traditions are analogous, not homologous, characters and suggests that there are fundamental differences in the mechanisms that underlie the two. Like Tomasello, Galef places particular emphasis on imitation, teaching, and language, which he regards as vital to human culture but largely or completely absent in animals. Galef discusses a small number of possible examples of teaching in animals, but he concludes that they provide "essentially no insight into evolutionary precursors of teaching in humans" since they rely on unrelated behavioral mechanisms. He suggests that using different terms to refer to socially transmitted behaviors in animals and humans serves to focus attention on the differences, as well as the similarities, between traditions of animals and culture in *Homo sapiens*. Galef maintains that it remains to be determined whether traditions of animals provide any insight into the evolution of human culture.

Chapter 11 is authored by Susan Perry, an anthropologist who is the lead researcher in a major, long-term collaborative study of social conventions in white-faced capuchin monkeys and primary author of several publications on capuchin behavioral traditions. Perry, Panger, and colleagues (2003) have described behavioral variation in the social conventions of capuchin monkeys across 13 social groups in Costa Rica. Several striking social behavior patterns meet Perry's criteria for traditions, including hand sniffing, sucking of body parts, and placing fingers in the mouths of other monkeys. Perry (this book) argues that monkeys use group-specific social conventions to test the quality of their social relationships. However, in spite of her impressive data, Perry is unwilling to describe capuchin traditions as culture.

For Perry, human culture is characterized more by issues of group identity, expression of this identity by means of culture-specific symbols, and manipulation of cultural meanings to achieve social change than by socially transmitted behaviors. Perry stresses how human socially learned traits are clustered into bundles that are associated with group identity. Particular traits serve as ethnic markers (indicators of shared membership in particular ethnic groups), which relate to shared understandings about proper ways to behave. Perry concludes that to establish an animal as cultural, it is necessary to produce evidence of between-group variation in

social norms and group identity, as well as correlations between socially learned traits and group identity. Perry maintains that no nonhuman animals currently satisfy these criteria, although she does not rule out that possibility.

Kim Hill is a biological anthropologist and human behavioral ecologist. He is the author of both a book and numerous articles on the Ache, a group of hunter-gatherers in Paraguay. Hill's research focuses on human behavior, and he was chosen to participate in the volume as one who is well versed in debates over human culture but is an outsider to the field of animal behavior. In chapter 12 Hill provides an external perspective on the debate, pointing out how biological and cultural anthropologists regard human culture, and how animal traditions fall short of these conceptions in two important respects. First, like Tomasello (1994, this book) and Galef (1992, this book), Hill argues that because of animals' "deep cognitive differences" from humans, animal "culture" does not accumulate significantly. Second, Hill specifies critical components of the human culture complex that are absent in animals. These include the regulation of individual behavior enforced by rewards and punishments and symbolic reinforcement of, and signaling adherence to, a specific rule system.

In Hill's view, human culture consists of communication in the form of rituals and ethnic markers. Cultural signaling sessions are public and emotionally charged, often with norms linked to supernatural rewards and punishments, and are designed to produce an emotional investment in continuation of the rules (ethics and morality). Hill argues that animals do not exhibit "socially learned law, ethics, rituals, religion, or morality, which are critical and universal components of human culture." Rather, animals are like "psychopaths," showing no remorse, empathy, anxiety, guilt, or moral indignation. Indeed, Hill argues that culture, as he defines it, may not even have been present in hominid species other than *Homo sapiens* and is probably a very recently evolved character.

The final chapter is by Kim Sterelny, a philosopher of biology with an interest in the evolution of mind. Sterelny analyzes the preceding 11 chapters and extracts the major themes and issues that lie at the heart of the debate. He accepts that socially stabilized local traditions are an established, and probably important, feature of the lives of a fair range of animals but voices doubts about what this tells us about human evolution. Sterelny notes that earlier skeptics of animal culture were preoccupied

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with the problem of transmission fidelity (e.g., Tomasello 1994), but he places more emphasis on a line of skepticism that has come to prominence more recently, that human (but not animal) behavior is regulated by norms. Sterelny argues that the roots of norm-guided action will be much more elusive than the roots of fidelity. "Fidelity is empirically tractable . . . Normativity is much less scrutable because it has no overt ethnographic behavioral signature." For Sterelny, animal societies are not cooperative enough to exemplify the earlier stages of the coevolution of norms, cooperation, and the division of labor. He regards human culture as an emergent property of other evolved human traits rather than a specific adaptation.

Sterelny argues that the idea of social learning, juxtaposed with asocial learning, is problematic since it neglects the important role of niche construction, by which he means information transmitters shaping the learning experience of the observer, which breaks down the social-asocial dichotomy. Teaching is just one of several ways that parents can shape the learning environment of their young. From the niche-construction perspective, the evolutionary transition from agents that learn mostly by individual exploration of their environment to agents that live in social worlds with stabilized traditions need not involve the transformation of the individual cognitive equipment of the agents. Social learning is not an individual trait but an interaction.

Sterelny criticizes social learning researchers for failing to distinguish between the content of socially transmitted information (by which he means what the information is about) and the channel through which the learning agent has access to that information (which may be social or asocial). This has implications for interpreting the animal culture literature. For instance, other contributors to this book suggest that interspecific variation in social behavior (from songs to handclasp grooming) provides the most compelling examples of culture since it is unlikely to reflect variation in ecological resources. To the contrary, Sterelny regards such examples as comparatively weak since they provide evidence only that the animals can learn social facts rather than that such facts are learned socially. When we are considering ecological skills, Sterelny accepts the method of exclusion as a decent, though overly conservative, indicator of social learning. However, when the information source is the agent's social environment, Sterelny complains that the method of exclusion cannot show that agents learn in a distinctive socially mediated or socially enhanced manner.

It will be apparent from this brief overview that there is indeed a broad range of opinions over how to interpret "animal culture," and a rich set of issues is at stake. We encourage you to study the remaining chapters in detail and to make up your own mind.

Notes

1. Reprinted, with permission, from F. B. M. de Waal and P. L. Tyack, *Animal Social Complexity* (Cambridge, MA: Harvard University Press, 2003).

2. Reprinted, with permission, from R.W. Wrangham, W.C. McGrew, F.B.M. de Waal, and P.G. Heltne, *Chimpanzee Cultures* (Cambridge, MA: Harvard University Press, 1994). Unfortunately, because of previous commitments, McGrew and Tomasello were unable to write new chapters for this volume but both kindly consented to the reprinting of their earlier chapters and provided updates of them.

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