

CA☆ FORUM ON THEORY IN ANTHROPOLOGY

Social Cultures among Nonhuman Primates

by Robert M. Sapolsky

The study of nonhuman species often challenges our notions of what makes humans unique. These challenges include the growing recognition that other species possess rudiments of “culture”—regional variation in behavior that is not rooted in genetics or ecology and is transmitted beyond its originators. Such studies have hinted at the existence in nonhuman species of “social culture,” in which a particular style of sociality permeates an array of behaviors, collectively constituting a culture. A recent case in which a distinctive social tradition of low aggression and high affiliation was established in a troop of wild baboons appears to represent an instance of social culture in that the social style has been transmitted across generations for nearly two decades. The behavioral features of this troop culture and its likely mechanisms of transmission are reviewed and some of its evolutionary implications discussed.

One of the most striking consequences of the study of animal behavior is the rethinking that it often forces of what it is to be human. A number of realms traditionally thought to define our humanity have now been shown to be shared, at least partially, with nonhuman species, among them tool use, symbolic elements in communication, theory of mind, self-awareness, and a wide affective palette that may even include nonhuman homologues of laughter (Panksepp 2005; Gallup 1970; Cheney and Seyfarth 1990; Tomasello and Call 1997; Matthews 2000). In recent decades, the idea that nonhuman species also have elements of culture (Bonner 1980; McGrew 1992; de Waal 2001) although resisted by some animal behaviorists (Galef 1990) as well as, more predictably, by social anthropologists and sociologists, has gained increasing acceptance. Elements of culture have now been observed in a wide range of species and in a number of social contexts. The main purpose of this piece is to review recent research suggesting that the notion of culture could be applicable to broader, more structural elements of the social behavior of a nonhuman group, one encompassing the notion of a “social culture.”

“Culture” as Animal Behaviorists See It

The features that constitute culture can seem intuitively ob-

vious (captured well by McGrew’s definition of culture as “the way we do things” [2004] and by de Waal’s as the “transmission of habits and information by social means” [2001]). Nevertheless, numerous scientists have attempted to identify the facets of culture more precisely and in ways that are relevant to considering nonhuman culture (see de Waal 2001 and McGrew 2004). Kroeber (1928), for example, emphasized the features of innovation, dissemination across generations and groups, and standardization among practitioners. Laland and Hoppit (2003) and McGrew (2004) focus on the need for the behavior to be standardized and to be performed by a large proportion of the group in question and on the idea of shared behaviors’ giving rise to a group identity or solidarity (with McGrew noting that there is, at best, minimal evidence for this among nonhuman species). De Waal (2001) has emphasized that a set of shared behaviors cannot be considered cultural if it arises from ecological or genetic factors. Bonner (1980) discusses the likely adaptiveness of “cultural” behaviors in nonhumans, while de Waal (2001) focuses on the potential arbitrariness of cultural behaviors. Amid this dissection of culture into its component parts, a number of investigators have noted the sterility of reducing these ideas to a checklist of requirements for the label of culture (King 2004; McGrew 2004). An important clarification is that these features of culture only partially overlap with tradition—behaviors that have become habitual (with or without a social context) and, most important, are manifested over long periods of time. One example of this would be the style of hunting in a group of olive baboons (Strum 1975). In contrast, culture is em-

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Table 1. Some Instances of Culture in Nonhuman Species

Species and Behavior	Material	Food-Related	Communicative	Social Interaction
Chimpanzee (<i>Pan troglodytes</i>)				
Termite and ant sticks	a	a	—	—
Nut-breaking with rock hammers	b	b	—	—
Leaf molding for sponging water	a	a	—	—
Means of drawing attention (knuckle knocking versus branch slapping)	—	—	c	—
Hand-clasp grooming	—	—	—	d
Rain dances	—	—	—	a
Orangutan (<i>Pongo pygmaeus</i>)				
Insect sticks	e	e	—	—
Lowland gorilla (<i>Gorilla gorilla</i>)				
Patterns of insect consumption	—	f	—	—
Use of sticks to test water depth	g	—	—	—
Japanese macaque (<i>Macaca fuscata</i>)				
Potato washing	—	h	—	—
Separating particles of foods from sand	—	h	—	—
Orca whale (<i>Orcinus orca</i>)				
Regional differences in song	—	—	i	—
Prey preferences	—	i	—	—
Hunting techniques	—	j	—	—
Humpback whale (<i>Megaptera novaeangliae</i>)				
Regional differences in song	—	k	—	—
Various songbird species				
Regional dialects of song	—	—	l	—
New Caledonian crow (<i>Corvus moneduloides</i>)				
Stick construction for food acquisition	—	m	m	—
African elephant (<i>Loxodonta africana</i>)				
Acquisition of Indian elephant vocalization	—	—	n	—
Arboreal ants				
Tool construction for trapping of prey insects	—	o	o	—

Sources: a, Goodall (1986); b, Boesch and Boesch (1983); c, Whiten et al. (1999); d, McGrew et al. (2001); e, Van Schaik et al. (2003); f, Tutin and Fernandez (1992); g, Breuer, Ndoundou-Hockemba, and Fishlock (2005); h, Kawai (1965), Kawai, Watanabe, and Mori (1992), Watanabe (1994); i, Rendell and Whitehead (2001); j, Guinet and Bouver (1995); k, Noad et al. (2000); l, Marter and Slabbekoorn (2002); m, Emery and Clayton (2004); n, Poole et al. (2005); o, DeJean et al. (2005).

bedded in sociality but need not be long-term (van Schaik et al. 2003; Perry and Mason 2003; McGrew 2004).

While the notion of nonhuman culture has been controversial, nearly as contentious has been thinking about the mechanisms of such transmission. Most provocative and intriguing would be instances of overt instruction (for example, a chimpanzee mother's explicitly shaping the hands of her offspring attempting to master some aspect of tool construction); there is little or no evidence for this (Boesch 1991). Far more evidence has accumulated for observational or facilitation models of transmission. In the latter case, mere proximity to tools or the materials for constructing the tools increases the chances of a novice's experimenting with and independently inventing the tool use. Discerning the mechanism of transmission will be particularly difficult in the case about to be considered, social culture; it will be far easier to observe the circumstances under which an individual adopts a type of tool use than to identify the performance of a pre-existing behavior but to a unique extent.

Some Elements of Culture among Nonhumans

Most of the instances of culture among nonhumans can be roughly grouped into four partially overlapping categories: (a) material culture (i.e., the construction of tools or shelter or the use of preexisting objects as either); (b) food acquisition, processing, and consumption; (c) communication (the use of a signal such as a vocalization in only a subset of populations or a unique local variant of a species-typical signal); and (d) social interactions (i.e., elements of cultural transmission that happen to be social). Table 1 presents a sampling of the cases of nonhuman culture, grouped into these categories. The richest set of examples is found among chimpanzees; this is not surprising, given their social and cognitive complexity, their widespread distribution across Africa, and the relative multitude of long-term field studies of their behavior. In one celebrated study pooling the data from six long-term chimpanzee studies from across Africa, 39 dif-

ferent features of culture were documented (Whiten et al. 1999). In some cases, gradients of variation in a particular behavior occurred among the chimpanzee population of a region, implying invention and diffusion (Whiten, Horner, and de Waal 2005); in others, behaviors appeared to have been invented independently in widely separated populations. Each population displayed a unique assemblage of the 39 cultural features, implying a level of cultural richness transcending variability in a single behavior. Finally, most investigators suggest that the mechanism of transmission in their study group involves observation and/or facilitation. A particularly striking recent demonstration of chimpanzee culture involved two groups of captive animals. The two matriarchs were removed from their groups and allowed to develop techniques for removing food from complex puzzle boxes. When they were returned to their groups, along with the puzzle boxes, the techniques they had developed proceeded to spread within their groups (Whiten, Horner, and de Waal 2005).

While instances of culture have most commonly been reported in nonhuman primate species, reports have come from nonprimate species as well. One notable example concerns humpback whales, in which a small population of males living west of Australia migrated into an eastern population and resident males soon adopted the song of these immigrants (Noad et al. 2000). Another recent example concerns an African elephant living for years in a zoo in an enclosure with two Asiatic elephants (*Elephas maximus*). Over that time, the elephant acquired and began to use a vocalization otherwise exclusive to Indian elephants—a first case of vocal imitation by a nonprimate terrestrial mammal (Poole et al. 2005).

Building Blocks of Social Culture among Nonhumans

The instances of culture just presented prepare us to consider the evidence for broader cases of “social culture”—instances in which a particular style of sociality permeates an array of behaviors, creating an assemblage of traits that fulfills the criteria for culture. Examples of social culture in humans might include Yanomamo retributive violence (Chagnon 1988), Bedouin food sharing (Lancaster 1981), and the American pattern of having infants sleep alone at an early age (Small 2001), which are not isolated cultural attributes but representative of and woven into a larger fabric of group values. By this definition, even though individual chimpanzee populations have unique assemblages of cultural attributes, these do not constitute social cultures. Two striking studies demonstrate some of the building blocks of social culture in nonhumans.

The first, a small pilot study carried out by Hans Kummer in Ethiopia, took advantage of the close proximity of two different species of baboons. Anubis baboons live in large, multimale, multifemale troops, with high degrees of polygamy and aggression. In contrast, hamadryas baboons have a multilevel social system; during some times of the day hundreds

of animals share a limited resource (e.g., cliffs used for sleeping), while at other times males herd young females into their groups, forcibly retaining them in stable “harems.” When Kummer moved a female anubis into a hamadryas group and a female hamadryas into an anubis troop, within hours the anubis female had assimilated the hamadryas social style, following a male who had herded her into his harem. This could readily be attributed to the physical coercion involved in being herded by a larger male. However, this could not explain the fact that within hours the hamadryas female had ceased attempting to align herself with (and be herded by) an adult male and adopted the more open anubis system (Kummer 1971).

The second example comes from the work of Frans de Waal and Denise Johanowicz (1993), in this case exploiting the differences in social style between two macaque species. Rhesus macaques form social groups with rigid, “despotic” hierarchies, in which dominant individuals have disproportionate access to desirable resources and maintain their dominance through force or threats of force. Moreover, rhesus societies have high rates of aggression and low rates of reconciliation following fights. In contrast, stump-tailed macaques have more fluid hierarchies (with more tolerance of reversals of dominance), low rates of escalated aggression, and high rates of postfight reconciliation.

In this study, rhesus and stump-tailed juveniles were combined into single mixed-sex groups (with sex ratios balanced between the species). Remarkably, over the course of months, rhesus assimilated the stump-tailed social style—eventually achieving, for example, equal rates of reconciliation—despite their being in the majority. Moreover, the acquired “stump-tailed style” persisted when the rhesus were returned to larger, all-rhesus groups. Rhesus rarely directly experienced the more “relaxed” style of stump-tails, as most social interactions were within rather than between species. Moreover, stump-tails and rhesus each had species-specific gestures and vocalization for postfight reconciliation, and it was their own reconciliative behavior that the rhesus now used more commonly. Thus, it was the meaning rather than the specifics of the stump-tailed reconciliative style that was adopted. In discussing the mechanisms underlying the cultural transfer, the researchers suggested something akin to a facilitation model: that the novel rhesus social style emerged as a by-product of living in a less tense and aggressive social milieu. This is a particularly striking possibility given that the stump-tails were in the minority but in this interpretation were able to establish a dominating and permissive social setting.

Social Cultural Transmission among Nonhuman Primates

The studies of Kummer and de Waal and Johanowicz hint at elements of social culture among baboons and rhesus, but their applicability to the broader issue of social culture is limited by their artificiality (i.e., the formation of multispecies

groups in captivity and the translocation of feral individuals between species) and the relatively short-term nature of the behavioral changes observed. Most important, neither study was sufficiently prolonged to demonstrate the transmission of the behaviors beyond their originators, a key prerequisite for instances of culture (which quite possibly occurs in the wild, as hamadryas/olive-baboon hybrids do occur naturally [see Bergman and Beehner 2004]).

A recent instance of what appears to be the transmission of social culture in a nonhuman primate involves a population of anubis baboons living in the Masai Mara Reserve of Kenya, part of the Serengeti ecosystem (Sapolsky and Share 2004). Subjects in the Forest Troop had been studied continuously since the mid-1970s and constituted a "typical" anubis troop with regard to social structure and atmosphere. Females resided in their natal troop for their entire lives, and their dominance ranks were inherited and static. In contrast, males left their natal troops at puberty for new troops; male hierarchies were despotic in nature, with high rates of aggression and ranks fluctuating intermittently, mostly as the outcome of fights. Finally, affiliative behaviors among adults were most common between females (who were often but not always relatives), far less frequent between the sexes, and virtually nonexistent between males, with the exception of the occasional and transient fighting coalition.

In the early 1980s, a neighboring troop began to exploit a garbage dump at a tourist lodge and soon shifted all of its feeding to this site. Within a short period, approximately half of the adult males in the Forest Troop began to forage for refuse at this dump as well. For two reasons, these males tended to be the most aggressive and least socially affiliated in the troop. First, this garbage foraging required fighting with the larger number of males from the troop whose territory encompassed the dump, and second, it took place in the early morning, when a disproportionate percentage of socially affiliative behaviors (such as grooming) would normally occur in Forest Troop.

In 1983, an outbreak of bovine tuberculosis, traceable to contaminated meat in the garbage dump, occurred in the neighboring troop. This resulted in the deaths of most members of that troop and all of the males from Forest Troop that foraged in the dump (Tarara et al. 1985; Sapolsky and Else 1987); in contrast to the pattern of tuberculosis transmission seen among densely housed captive primates, there was no secondary transmission of the tuberculosis from garbage foragers to others in Forest Troop. As a result, the female-to-male ratio among adults in Forest Troop shifted from 1:1 to an approximate 2:1, and the remaining adult males were atypically affiliative and unaggressive. This produced some dramatic changes in the social culture of the troop.

Among the most marked of these changes concerned male-male dominance interactions. Dominance rankings are typically determined by "approach-avoid" interactions, in which the individual judged as subordinate by the human observer

is the one who relinquishes a contested resource (such as a desirable food item or resting spot) and/or gives a stereotypical subordination gesture (e.g., crouching on the ground). Dominance interactions are often summarized in "dominance matrices" (see fig. 1). Prior to the tuberculosis outbreak, male-male dominance interactions in Forest Troop were typical of the species and resembled the hypothetical dominance matrix shown in fig. 1, *A*. *A* wins 5 interactions with *B*, 2 with *C*, and so on. The animal in a dyad winning more interactions is judged dominant. This matrix indicates a disproportionate percentage of interactions between nonadjacent animals; very low-ranking animals are often subject to subordination by high-ranking animals (e.g., the treatment of *E* by *A*.) This is highly unlikely to reflect a threat to the high-ranking male (e.g., *E* could plausibly be displacing *A* from the alpha position and thus being preferentially subject to subordination by *A*). Such nonadjacent interactions often reflect displacement by high-ranking animals onto extreme subordinates after some frustrating situation for the former (e.g., a failed hunt) (Sapolsky 1983). This overall pattern has been termed "suppressive" dominance (de Waal 2000).

Following the tuberculosis-related deaths, one way in which the dominance structure shifted is shown schematically in figure 1, *B*. In it, rankings are as in *A* and, again, 0% of the interactions are reversals of the direction of dominance, but 65% of the interactions occur between animals of adjacent ranks and 94% between animals within two ranks of each other. Thus, an extremely low-ranking animal (e.g., *E*) is rarely subject to being subordinated by an extremely high-ranking animal (e.g., *A*).

The new Forest Troop pattern of dominance interactions was also atypical with respect to reversals. Figure 1, *C*, shows the pattern of dominance reversals seen in typical troops. While in the prior two examples, *A* wins 100% of interactions with *B*, in this example *A* wins only 56% (i.e., 5/9). Reversals between animals of adjacent ranks indicate instability in that dyadic relationship and the possible impending switching of the ranks of two. In contrast, in the schematic of figure 1, *D*, in Forest Troop the sole reversals occur between the lowest-ranking and highest-ranking animals (e.g., *E* dominating *A* twice) and amount to 5% of interactions (2/39). Such nonadjacent reversals are unlikely to be a threat by *E* against *A* and instead may indicate a relaxed, affiliative relationship between the two (e.g., where *A* is willing to relinquish a spot in the shade to *E*).

The posttuberculosis social milieu had other distinctive features. The approach-avoidance interactions just discussed are defined as not involving overt aggression. In a typical baboon troop, a large percentage of overt, escalated aggression involves a male's displacing frustration aggression onto females or subordinate males. Such displacement aggression was less prevalent in Forest Troop. In addition, there was significantly more intersexual grooming and closer physical proximity among animals.

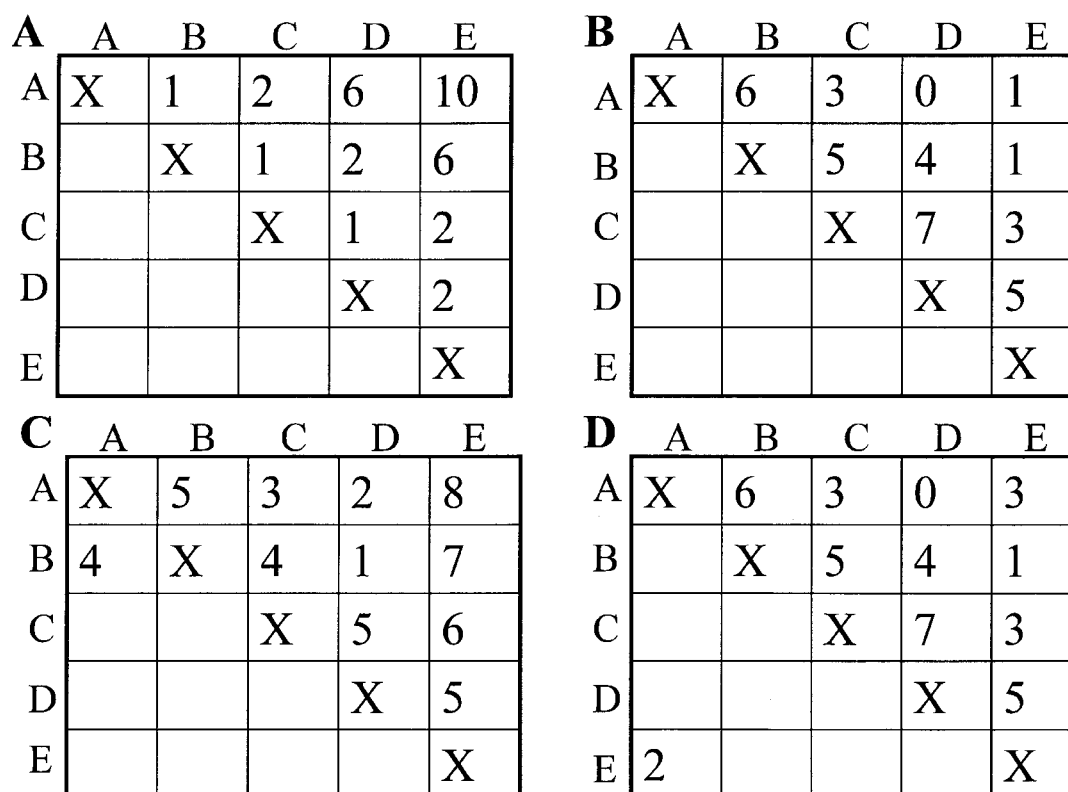


Figure 1. Schematic representation of dominance matrices. The number in each box indicates the number of times that the animal in the row dominated the animal in the column. Open boxes indicate no dominance interactions in that dyad with that outcome. A, before tuberculosis; B, after tuberculosis; C, pattern of dominance reversal in typical troop; D, pattern of dominance reversal in Forest Group.

The distinctive features of Forest Troop extended into the physiological realm. While not a universal feature of social subordination in nonhuman primates, in many species socially subordinate individuals are more at risk for stress-related diseases (with, for example, lower levels of hormones involved to wound healing, impaired testicular physiology, immune suppression, less “good” cholesterol, and increased incidences of atherosclerosis) (Sapolsky 2005). This is seen among subordinate males living in more typical savanna baboon troops. Specifically, such males have elevated resting levels of cortisol (a key hormone secreted in response to stress, an excess of which has numerous deleterious effects) and enhanced tone of a neurochemical system meant to quell anxiety (involving chemical messengers called benzodiazepines, a class of compounds including the drugs Valium and Librium) (Sapolsky and Share 2004). In contrast, these indices of chronic stress were not observed among the subordinate males of the posttuberculosis Forest Troop (fig. 2).

The social milieu of Forest Troop has persisted since its

establishment approximately two decades ago. All of the adult males who survived the tuberculosis pandemic in the mid-1980s had died by the early 1990s, and therefore the behavioral style of this group had been transmitted to adolescent males as they transferred into the troop, with an average of six months of residence until it was adopted. Thus this constitutes a case of multigenerational culture transmission.

Some insights are available as to the mechanisms of this transmission. Potentially, the transfer could reflect observational learning; this, however, would be difficult either to demonstrate or to rule out. As is arguably the case with all examples of nonhuman culture, there is no evidence of active teaching on the part of resident animals. Potentially, the transmission could arise from contingent shaping of the behaviors of new transfer males by resident animals. Thus, for example, a transfer male who has acted in an affiliative manner might be rewarded by being groomed. Such shaping of behavior would have to be understood in the context of triangular relationships. If A grooms B, it is likely that the grooming

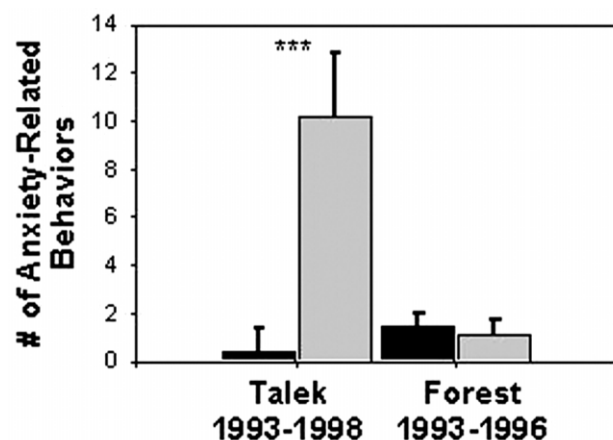


Figure 2. Number of anxiety-related behaviors observed 10–20 minutes after darting animals with a benzodiazepine receptor antagonist (versus the number of such behaviors after darting animals with saline) in Talek, (a typical baboon troop) and Forest Troop. *Black*, males ranking in the highest 50th percentile (by approach-avoidance criteria); *gray*, males ranking in the lowest 50th percentile. “Anxiety-related” behaviors include self-scratching, rhythmic head shaking, assuming a vigilant stance with no other animal in the immediate vicinity, repeated wiping of nose, and jaw grinding in a solitary male (Sapolsky and Share 2004).

will be reciprocated. Contingent shaping would, instead, take the form of a transfer male’s being groomed by A in response to an affiliative behavior on that male’s part directed toward B. However, no evidence of such contingent shaping has been observed in Forest Troop.

A distinctive social style in a baboon troop might reflect genetic factors related to aggression and risk-taking behavior. However, this seems unlikely to apply to the Forest Troop because the males propagating the culture multigenerationally were born into other troops.

Another possibility might be self-selection. Adolescent transfer males may briefly join a number of troops before settling into one, and it is conceivable that adolescents who already tended toward the social style of Forest Troop would elect to remain there. However, transfer males during their first few months in Forest Troop are behaviorally indistinguishable from transfers into a more “traditional” neighboring troop.

At present, the best evidence suggests some kind of an emergent default model for the cultural transmission. Transfer males into Forest Troop and into other troops are treated similarly by resident males (despite the unaggressive behavioral style of Forest Troop resident males among themselves). In contrast, resident females are more affiliative with transfer males in Forest Troop than in other troops; they first groom or give a species-typical greeting gesture to new males far sooner than in other troops, groom them more often, and sit closer to them (fig. 3). This situation is similar to a transgender mechanism for song dialect acquisition among male

cowbirds (Smith, King, and West 2000) with the important difference that the treatment of transfer males by female baboons is not contingent upon the males’ behavior whereas cowbird females reward the singing of the correct dialect with copulation solicitation.

These findings suggest that the transmission of the Forest Troop culture occurs, in effect, by default. In a typical baboon troop, females experience considerable physical and psychological stress, being subject to particularly high rates of displacement aggression and domination by males (Albert, Altmann, and Sapolsky 1992; Sapolsky 2004). Such stress is much

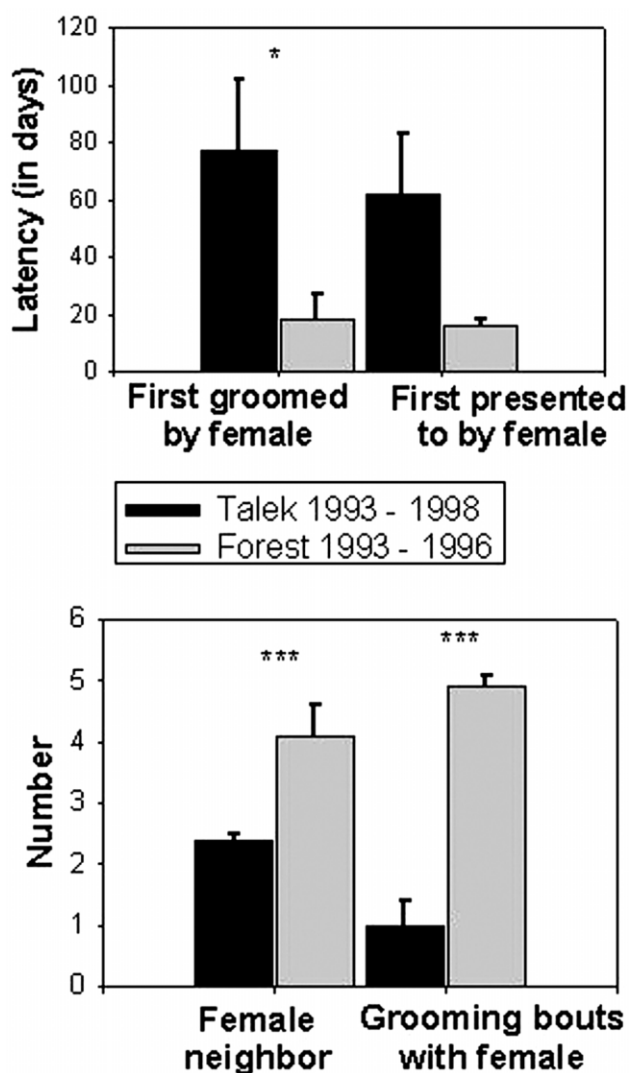


Figure 3. Quality of interactions between resident females and transfer males in Talek and Forest Troop. *Top*, number of days until the newly transferred male is first groomed by a female (*left*) or presented to by a female (*right*). *Bottom*, average number of adult female neighbors (i.e., within 3 m) per scan (*left*) and average number of grooming bouts with females per 100 hours of observation for transfer males (*right*) (Sapolsky and Share 2004).

reduced in Forest Troop. In principle, this could merely be the result of group size and the 2:1 female-to-male ratio (which, for unknown reasons, persists to the present). However, similar group sizes and sex ratios have been observed in a few reports of other troops of savanna baboons (i.e., olive, yellow, or chacma baboons), which did not demonstrate this culture (Seyfarth 1976, 1978; Noe 1994; Strum 1982; Bercovitch 1985). Instead, it most likely reflects the affiliative, unaggressive behavioral style of the adult males, perhaps coupled with the skewed sex ratio. Whatever its cause, in an atmosphere of less harassment females seem more likely to risk initiating an affiliative interaction with an unknown transfer male. And, plausibly, in the presence of these spontaneous affiliative behaviors, transfer males default into a state in which they, in turn, are more likely to risk spontaneously affiliative behaviors and to suppress aggressive ones.

Discussion

The behavior of Forest Troop baboons appears to constitute an example of a social culture in a nonhuman species. A number of features distinguish this culture from examples of culture in other nonhumans and from human culture as well.

Many of the nonhuman examples concern material culture (i.e., tool construction) or a behavior occurring in only some populations of a species (e.g., the rain dance of some chimpanzee groups). The social culture of Forest Troop does not involve either. Instead, all of the elements of its social style involve typical behaviors (e.g., grooming or the supplanting of one animal by another at a food source). Moreover, the intensity of these behaviors is not unique to Forest Troop (there have been other troops with similar high rates of, for example, female/male grooming). What is distinctive and constitutes a social culture is that the troop displays an *array* of typical behaviors occurring to atypical degrees (and therefore newcomers do not need to acquire entirely new behaviors but must simply adjust the rate at which they perform preexisting ones) and the collectivity of these extremes of behavior forms a coherent social whole (one of low aggression and high affiliation).

This example of social culture differs, however, in numerous ways from that of humans. Human culture differs markedly, of course, in the complexity of its social culture—the number of individual cultural elements, the potential ornateness of each (e.g., the decades to centuries spent building many cathedrals), and the interrelations among them. Second, human cultural innovations show the phenomenon of “accumulation” (Whiten, Horner, and Marshall-Pescini 2003); new innovations can build upon previous ones. The social style of a community may be extended, for example, from pacifism to vegetarianism to vegan diets to the refusal to kill insects, with each step being viewed as logically built upon the prior ones. Some cases of cultural accumulation have been documented in nonhuman cultures—for example, among the Japanese macaques, the techniques for washing potatoes and

for separating wheat from sand in sea water have both become more ornate over time (Kawai, Watanabe, and Mori 1992; Watanabe 1994), and killer whales’ techniques for briefly beaching themselves in order to prey on sea-lion pups have become more ornate across generations (Guinet and Bouvier 1995)—but these cases are rare.

Finally, while Forest Troop’s array of typical behaviors taken to atypical extremes forms a coherent whole of affiliation and unaggressiveness, this whole has no resemblance to the core idea that shapes social culture in humans (e.g., extreme nationalism, multiculturalism) (Tomasello 2000; Whiten, Horner, and Marshall-Pescini 2003).

The case of Forest Troop raises other issues as well. Current thinking about the evolution of behavior focuses heavily on the notion of individual selection, as pioneered by W. D. Hamilton (1964) in response to the then-dominant models of group selection (Wynne-Edwards 1962). In recent years there has been increasing interest in multilevel selection, including group selection (in a form bearing virtually no resemblance to earlier ones, now discredited). The contemporary view of group selection is that individual altruists may be less fit than individual nonaltruists within a group but groups of altruists are more fit than groups of nonaltruists (Wilson 1997). Forest Troop readily fits this model in that it approximates a group of altruists amid more typical baboon troops approximating groups of nonaltruists, and the advantage of its altruism may be good health, both because of fewer aggression-related injuries and because of lower basal levels of the potentially pathogenic stress hormone cortisol (Sapolsky and Share 2004) and less vulnerability to food shortages in that it expends less energy on aggression and its consequences (Sapolsky 1986). In addition, males in Forest Troop show an unprecedented behavior, namely, defense of each other during a predator threat.

Another issue raised by these findings is what happens to natal male members of Forest Troop when they transfer to neighboring troops. As will be recalled, in the study in which groups of adolescent rhesus and stump-tail macaques were housed together, it was the rhesus who assimilated the more affiliative style of the stump-tails, despite their being in the majority. This suggests the optimistic possibility that social styles of affiliation are more readily assimilated than are styles of nonaffiliation (although the unexpected direction of behavioral assimilation in the rhesus/stump-tail study may reflect the fact that the rhesus were somewhat younger). Game-theoretical studies demonstrate a marked disadvantage for a sole noncontingent cooperator such as a Forest Troop male amid a sea of defectors (Nowak and Sigmund 2004).

A very different scenario could occur if two adolescent males from Forest Troop transferred into the same neighboring troop. In the more typical situation among baboon populations, if two adolescents transferred into the same troop they would be unlikely to form a cooperative coalition for a number of reasons. First, they would be unlikely to have the same mother, a circumstance that biases toward coop-

eration (since this scenario would require them to transfer around the same time despite being a minimum of nearly two years apart in age). Second, although in theory two adolescent males may be the offspring of the same father and there is some indication that males will show paternal behavior toward youngsters likely to be their offspring (Buchan et al. 2003), it seems unlikely that paternal certainty about two sons of the same father of the same age would prompt greater cooperation between them. Finally, the nature of male baboon maturation in a typical troop precludes the formation of such an affiliative dyad. In contrast, if two Forest Troop males transferred into the same troop they might maintain a stable relationship of cooperation, and game-theoretical models suggest that such a dyad would out-compete the surrounding defectors. This would be akin to the game-theoretic situation in which an inbred founder population that had established reciprocity through kin selection was reintroduced to the larger population and was therefore at a competitive advantage (Nowak and Sigmund 2004). In this case, the driving force would be not kin selection but the pseudo-kinship of the Forest Troop culture.

In human populations, the spread of cultural innovation between populations can arise from the conquest of one group by another, the economics of intergroup trade, or emigration (Cavalli-Sforza 2000). While it is extremely rare for two males from the same troop to transfer into the same neighboring troop at roughly the same time (Pusey and Packer 1986), that scenario is one in which the social culture of Forest Troop could be exported to other baboon troops. Studies are currently planned in which that scenario will be artificially created.

Finally, one must ask what circumstances might destroy the Forest Troop culture. One might imagine that the culture could be endangered through the mass-action effect of a large number of (typical) male baboons' transferring into the troop at roughly the same time. Assimilating transfer males into the Forest Troop culture can be "costly" for the resident females, who seem to play a key role in that assimilation. Because newly transferred males displace aggression upon females as readily as do transfer males in others troops, Forest Troop females probably endure an atypical amount of stress (and, perhaps, physical injury) because of their voluntary proximity to and noncontingent affiliative behavior toward such males. Perhaps, then, the costs of assimilating two males simultaneously might be high enough to cause females abandon their unique treatment of recent transfer males.

Game-theoretical models similarly suggest that assimilating a pair of transfer males might endanger the Forest Troop culture. Such models demonstrate the vulnerability of a population of noncontingent cooperators to the invasion of a defection strategy (Nowak and Sigmund 2004). In principle, this should happen as readily with the immigration of a single (defector) transfer male into Forest Troop, and the fact that this has not occurred argues against this scenario. However, if two transfer males were to join at the same time and focus

their energies upon exploitively competing with resident males rather than on defecting in conflict with each other, they might establish an atmosphere of aggression and non-affiliation that would push resident males toward similar behaviors. To date, no such dual transfer into Forest Troop has occurred.

In conclusion, a growing literature now viewed as mainstream in animal-behaviorist circles demonstrates features of culture in nonhuman species. The present case of a nonhuman social culture must challenge notions often held about primate social systems (perhaps including our own). Whereas savanna baboons such as these have long been considered textbook examples of a certain type of society—aggressive, highly stratified, and male-dominated—within a relatively short period of time a very different system was established and propagated among them. This must call into question assumptions about the immutability of any primate society.

Acknowledgments

Funding for the studies described was provided by the Harry Frank Guggenheim Foundation and the Templeton Foundation. Some similar material concerning the animal culture literature is reviewed in a paper currently in press in a sociology journal but with an emphasis for a sociological audience.

Comments

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Missing from this article is an explanation of how to differentiate "social culture" from functional behavior. Behavior can vary functionally with social context just as it can with ecological context, but Sapolsky does not address this possibility. If resource-poor environments were associated with low levels of energetically expensive behaviors, we would not initially attribute this to culture. Rather, we would hypothesize some degree of behavioral flexibility in response to different cost-benefit scenarios imposed by the ecological conditions. Thus, individuals facing the same conditions have similar behavior because they independently arrived at the same behavioral state, not because they share a culture. Problems with the concept of social culture arise because, in some sense, the social milieu acts like an ecological factor. That is, it determines the costs and benefits of different behaviors. Consider a male baboon with an estrous female in his group. He could mate with her, but the costs of doing so depend on the immediate social context. Are there higher-ranking males in the area? Is the female already in consort with another male? If

so, which male? Independent responses to cost-benefit scenarios (i.e., functional flexibility) can generate behavioral similarity in specific social contexts—an explanation that may account for much of the behavior Sapolsky discusses.

For example, the translocated olive and hamadryas females might behaviorally resemble members of their new groups simply because they are responding to differing costs of straying from males. The anubis female placed in a hamadryas group gets bitten every time she strays from the leader male. Straying is now costly, and therefore she ceases to stray. In the reverse case, the hamadryas female placed in an anubis group no longer experiences the costs of straying. Straying is cheap, and therefore she strays. Sapolsky considers the former a case of “coercion” and the latter an elementary example of social culture, but he never makes it clear how we might make the distinction. If, rather than a bite when she strayed, the hamadryas male offered the anubis female a reward when she remained close, would this example now be eligible to be considered culture? The cost-benefit perspective avoids these difficulties, explaining both groups of females’ translocations equally well while identifying the underlying causal similarities in the behavioral transformation.

The behavioral changes in the Forest Troop might also be explained by new cost-benefit scenarios related to the group’s shifted demographics. The tuberculosis event reduced the number of males in the group and created a more female-biased sex ratio. In the new context, immigrants might have been approached more readily by females simply because there were many more females per male. Perhaps when females greatly outnumber males they have few opportunities to express mate choice and benefit from seeking out new males. Furthermore, with more mating opportunities and fewer competitors, the males might no longer have benefited from enforcing a strict hierarchy and engaging in high levels of aggression. Rather than adopting a new culture, immigrant males might simply have been responding to the reduced benefits of aggressive behavior in the Forest Troop. Thus, for both the initiation and the maintenance of less aggressive/more affiliative behaviors, a simple, noncultural explanation exists—a facultative response to new costs and benefits created by changed demographics. Sapolsky dismisses this possibility by pointing to other baboon studies with a high female-to-male sex ratio (mainly yellow and chacma baboons) that do not resemble Forest Troop behaviorally. However, these comparisons fail to take into consideration the pronounced behavioral differences across baboon populations—differences that become even more so across baboon taxa (Henzi and Barrett 2003). While the type of comparative data needed (e.g., rates of inter- and intrasexual aggression within the same population across different sex ratios) may not be readily available, this does not justify the dismissal of a simpler explanation in favor of a more complicated one.

This failure to account for costs and benefits in different social contexts leads to an oversight in the discussion. Sapolsky refers to the Forest Troop males as altruists but does

not mention any costs to nonaggressive behavior that might qualify them as such. Rather, he indicates that individuals derive considerable health benefits and energetic savings from nonaggressive behavior. Sapolsky might consider their behavior altruistic because, generally, the benefits of aggression (access to food and females) outweigh the costs (energetically expensive, risky), but this does not appear to be the case in Forest Troop, where the benefits can be had without aggression. Of course, social context can change. In the future, a male (or males) might monopolize resources in Forest Troop through aggressive behavior, possibly reinstating the benefits of aggression. Nevertheless, pacific behavior currently does not appear to be costly.

The requirement that social culture form a “coherent whole” exacerbates the problem because function is a likely source of coherence. Perhaps Sapolsky does not see the need to differentiate cultural and functional explanations (his “default model” actually seems to approach a functional explanation). However, if socially functional behavior is considered culture, then it becomes difficult to exclude ecologically functional behavior from this expanded definition. Identifying social culture requires the ability to differentiate social and ecological contexts—a nontrivial task. Rather than broaden the definition of culture beyond utility or require the ability to make impractical distinctions (e.g., influence versus coercion, social versus ecological context), priority should be given to functional explanations regardless of what is determining the underlying costs and benefits. Only after such hypotheses are tested and eliminated might it be necessary to invoke a cultural explanation.

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Sapolsky’s exciting contribution provides fascinating evidence for the emergence and cultural transmission of a style of sociality in a troop of baboons. His case draws attention to the importance of long-term field studies and offers valuable insight into the behavioral plasticity of primate social systems and into nonhuman primate culture.

Sapolsky notes that some evidence for the transmission of social culture has been found in primates but prior studies have not been long enough to determine whether this behavior was transmitted past the originators. His case underscores the value of observing multiple groups and populations of the same species over a long period of time. The evidence he provides suggests that baboon social behavior considered “typical” may need to be reevaluated as more groups and populations are studied. One of the values of long-term research such as this is the ability to reveal the strength of demographic influences on the emergence and transmission of culture in general in nonhuman primates. For example,

long-term studies by Perry et al. (2003) describe games that were invented by a single juvenile male and were transmitted through the group and continued to be played for ten years. In Sapolsky's case, the disappearance of several male members of the group created a significant demographic change in the group's sex ratio and behavioral frequency that continued for over two decades. His long-term observation of the baboon troop provides insight into the behavioral stability of such a change, leading to speculation concerning the type of behavior that is most likely to be culturally transmitted over time.

An interesting facet of this case is the idea that a small change in individual behavioral frequencies of aggression and affiliation could lead to a new social culture. Incoming males were able to easily adopt the new social style, needing only to change the frequency of their behavior. Consequently, minor individual changes in behavior frequency led to a dynamic transformation in sociality that could have significant evolutionary consequences. It is interesting to examine this case in relation to Cairns, Gariepy, and Hood's (1990) work on the frequency of aggressive behavior in mice. Cairns and colleagues bred different lines of mice for high and low aggression and found, among other results, that the frequency of aggressive behavior in the two aggression lines had a great deal of plasticity and even converged through experience. These researchers argue that changes in behavioral frequency present opportunities for rapid developmental and micro-evolutionary change. With this in mind, Sapolsky's baboon troop may be useful for an understanding of the plasticity of primate social behavior and how this plasticity provides avenues for rapid change in primate social systems.

Another remarkable feature of this case is that the behavioral style of the baboon troop was culturally transmitted through multiple generations. Sapolsky discusses several mechanisms of possible transmission including observational learning, contingent shaping, genetic factors, self-selection, and, the most likely, emergent default. It is interesting to look at this case in relation to Whiten, Horner, and de Waal's (2005) study, in which captive chimpanzees showed conformity bias during an investigation of cultural transmission. The chimpanzees in this study continued using a food-procuring method that the rest of the group used even when they discovered different ways of obtaining food from an experimental food apparatus. According to the researchers, there is an intrinsic motivation to copy others, and it is influenced by social bonds rather than material rewards. This tendency to conform has important consequences for the evolution and transmission of culture. In Sapolsky's case, incoming males adopted the behavioral style of the group even though this style was uncommon in other troops. The implementation of this behavioral style by new males provides the opportunity to consider the possible influence of conformity bias in this wild troop of baboons.

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Baboons are one of the most thoroughly studied primate taxa, with some studies spanning several decades of continuous observation. Yet, as with many large-bodied and long-lived species, we have so far studied only relatively few subjects living in even fewer groups; our sample sizes are still small, and we know little about the variation not only between but also within different baboon taxa. Up to now, many of the groups studied served as a kind of prototypical baboon group. How misleading this might be becomes clear after the observation of the emergence of a new "social culture" in a troop of wild savanna anubis baboons. Following a singular event during which all aggressive young males were removed from the troop, the remaining group members adopted a more relaxed and egalitarian style, and even immigrant males adopted it.

What does this tell us? For one thing, it reminds us that, despite considerable research effort, a lot more needs to be done, preferably in a comparative framework. Moreover, it tells us something about the observers' attitude. With the advent of sociobiology, the search was on for an understanding of the general patterns and principles that explain animal behaviour. With regard to infanticide, for instance, the typical view is that infanticide occurs in species in which males compete intensely for females and that recent immigrants should kill infants in order to increase their chances of fathering own offspring. Yet, behavioural observations indicate that not all males commit infanticide. How much of this can be attributed to the short-term availability of females, how much to the behaviour of resident males, and how much—possibly—to the "personalities" of the immigrants? And how do these factors interact? Just how flexible is the behaviour of individuals, and how does it affect the dynamics within a social group? In sum, what appears interesting now is to chart the extent of variability and diversity of primate behaviour.

However, collecting reports about the behaviour of individual subjects or individual groups is not enough—such reports do not amount to data. Having gained insight into the possible adaptability of baboon behaviour, we should be careful not to extrapolate too much from singular observations. Instead, it is time to initiate a more thorough investigation of the factors that give rise to variation and diversity of behaviour. When assessing the evolutionary significance of such variation, the long-term goal should be to formulate predictions of which kind of behaviour or which combinations of behaviour patterns might constitute evolutionary stable strategies and which might not.

Whether it is really helpful to invoke the concept of "cultural variation" to understand behavioural diversity is a matter

of debate. Sapolsky points out that the idea of nonhuman culture is gaining increasing acceptance. Claiming the mainstream position, however, does not address the substantiated criticisms formulated not just by the “usual suspects” identified by Sapolsky (animal behaviourists and social anthropologists). To understand the emergence of varying traditions among different groups, one needs to examine the mechanisms that give rise to them. As far as the social styles discussed in this paper are concerned, it seems quite likely that these are maintained via a process known as “ontogenetic ritualization,” in which two animals mutually affect their communication through repeated instances of social interaction (Tomasello 2004). Having said that, I think that the tendency to dismiss the insights gained from animal learning theory that seems so common among people interested in the evolution of culture needs to be overcome; it should be clear that the different camps have a lot to learn from each other. In this light, I am unable to follow Sapolsky’s argument that the lack of physical coercion does not explain why hamadryas females translocated into an anubis group would cease to follow the males. Why shouldn’t the female be able to learn that her veering away from males is no longer negatively reinforced?

Therefore, while I find Sapolsky’s descriptions exciting and interesting, I am not convinced that they tell us much about the evolution of human culture. Behavioural flexibility is a precondition for evolving culture, but it is not equivalent to it. The drive to find evidence that “blurs the line” between humans and nonhuman primates may not always be helpful for reconstructing evolutionary history, since it is difficult to identify similarities and differences when the lines are blurred.

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Sapolsky’s final sentence spotlights a central significance of his findings about the shift in Forest Troop’s patterns away from the expected profile of baboon male aggression: “This must call into question assumptions about the immutability of any primate society.” His data demonstrate elegantly the effect of individual primates’ temperaments on a group’s behavioral profile.

The idea of immutability has been hard to eliminate from primate studies. Frans de Waal recalls the time when he first “lost the ability to generalize about ‘the chimpanzee’ in the same way that no one ever speaks about ‘the human.’ . . . No two chimpanzees are the same” (2005, 53). Much of his research and writing supports this assertion, but it is difficult for him to hang onto: In the same book he contrasts the “power-hungry and brutal chimp . . . with the peace-loving and erotic bonobo” (p. 5) and asserts that “the simple truth” is that “brutal violence is part of the chimp’s natural makeup”

(p. 24). Why is this idea so tempting? How does it get locked into a dance with a notion of nonhuman species character? It is worth exploring to what degree tossed-off characterizations of behavior at the species level are tied to deliberately crafted generalizations at the study-population level.

A literature review suggests that qualitative research such as mine (King 2004) is not common among primatologists, who tend to seek the group (or subgroup) average for some behavior(s) and may equate qualitative research with anecdote-vending. (Of course, the irony here is that I am generalizing myself.) I do not mean to say that qualitative methods are invariably better than quantitative ones: Sapolsky’s paper shows the value of integrating the two. Far less radical, my point is akin to Fogel’s (n.d.) about dynamic-systems research on interindividual communication: Stable patterns of behavior are maintained by a dynamic process of change. As a result, although quantification “is not inherently concretizing and reifying,” it may—depending on the research question—“lose the evolving process for the sake of trying to capture it.”

The study of primate culture is poorly served by counting the ways in which populations differ behaviorally and then composing lists of “culture” based on them. Sapolsky’s focus on cases “in which a particular style of sociality permeates an array of behaviors” makes far better sense. I cannot agree, however, that “culture is embedded in sociality.” One thing embedded in another means that two separate somethings exist, but what could “culture” possibly mean apart from “sociality”? Embeddedness aside, a genuine embrace of social culture could support the first swells of a sea change in North American/European primatology, a willingness to see the dangers as well as the benefits of elevating statistical analysis to *inevitable* alpha status in the hierarchy of methodologies. I have space enough for only two examples.

While “revisiting primate conflict resolution,” Fuentes suggests moving beyond a focus on reconciliation: “What if we shift to a holistic focus on multiple facets of long-term relationships? Conflicts might then be seen as perturbations in an overall system” (2004, 222). One study he discusses involves a group of five captive chimpanzees in which different dyads exhibited very different postconflict behavioral patterns. He notes that it is “possible that each individual is behaving somewhat differently after conflicts across years as relationships and circumstances change and as chance events surrounding conflicts come and go” (p. 226). A situation like this one is ripe for testing hypotheses with qualitative data.

The chimpanzee researchers Nakamura and Nishida, observing that “subtle social behavioral patterns” were far less likely to be incorporated into studies of primate culture than patterns of tool use and feeding, embarked upon “culture hunting,” filming and comparing details of subtle behaviors across populations. This approach, they believe, may contain “a key to understanding complex and rich relationships within

societies, cultures, and individuals in the variations of seemingly simple and subtle behaviors" (2006, 41).

Some may respond to these examples with a shrug, but let's ask the hard questions: Is qualitative research more acceptable in Eastern rather than Western schools of thought, or is this suggestion a product of misguided essentialism? When is detailed qualitative tracking of change within and across groups reduced to the same status as presenting a series of anecdotes? Do primatologists worry about whether it is acceptable to build rigorous qualitative methodologies into our grant proposals and to submit the results to our peer-reviewed journals instead of only reporting them in our public lectures and popular books? Do we feel free to urge our students to describe changes in behavioral patterns over time with a mix of qualitative and quantitative methods? As much as Sapolsky's baboon data set informs us about long-term patterns of cultural change in nonhumans, its greatest value may be in the questions it raises for the future of theory and method in primatology.

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Dialogue between primatology and anthropology might become very interesting; we have to share more—we are sometimes limited by our own disciplinary paradigms and prerequisites. Sapolsky's paper reduces the distance between humans and nonhuman primates, although an animal culture is not exactly a human culture, properly speaking. Many papers propose male dominance, selfish genes, or egoistic strategies as social adaptations to natural constraints. The immutability of primate societies is weakened by Sapolsky's fieldwork. Nevertheless, three questions remain.

First, about the utility of the new concept of "social culture": According to Sapolsky, culture is embedded in sociality and tradition is not, but every culture has a tradition. Similar observations have led primatologists to use different terms (tradition, culture) because one means "collective habits" and the other is the opposite of "nature." The term "animal cultures" has recently been proposed. Tradition and culture differ not in their strict definitions but because of their different cultural acceptability. This has to do with methodology. Nonhumans have to show more than humans (independence from environment and genes; who would insist on independence from the monsoon, the desert, or the Nile in human cultures?); to establish cultural variants in primates, cultural phenomena have to differ regionally. This methodology leads to some confusion between society (typical hierarchy, interactions, mating) and species, both separated from culture (as a set of variants). Society and culture used to be distinguished by ethologists though not by social anthropologists; transmission between individuals must be social, each culture pro-

duces a kind of sociality (signs, symbols, behaviours), and all knowledge is socially transmitted.

Second, about the demographic change since the appearance of tuberculosis; that the sex ratio has been modified and males are less aggressive shows an emergent type of sociality that could be endangered by another demographic change (which is a kind of constraint). The first generation showed behavioural plasticity, and from then on behaviours could be reproduced implicitly, without facilitation or demonstration (hexis and habitus, as in humans, according to Bourdieu). As Sapolsky says, many primatologists have probably underestimated the real interest of variations in degree in behaviours because they have had to cope with things such as material culture and interactions. But the observation of body techniques (Mauss) among primates ought to be developed in the way suggested in this paper.

Third, the baboons of the Forest Troop are healthier and less aggressive, vulnerable, and stressed; females and infants may be more secure. But should we legitimate these facts with a theory of selective advantage, either direct or indirect? French anthropology abandoned functionalist theories many decades ago because of a confusion between cause and consequence in the notion of evolutionary advantage. This theory remains as an epistemological gap separating primatology and social anthropology even though humans and nonhuman primates share an important common, even cultural, core. Social change among these baboons was caused by an accident of their own history; it might promote a new ethological paradigm profoundly different from the eternal methodological individualism.

Reply

As a nonanthropologist venturing into this subject, I'm pleased to see that my ideas have evoked a range of responses. These commentaries encompass a number of themes.

One concerns how much behavioral flexibility exists in primates. I discussed Kummer's translocation of a female hamadryas baboon to an anubis troop and of a female anubis to a hamadryas troop; female transfers, in both cases, adopted the social structure of the new species within hours. Fischer and Bergman both point out that when the newly translocated anubis female, bitten each time she strays from the harem male, begins to stay closer to him, one need not invoke the notion of her assimilating a local culture. Instead, it is far simpler to view her behavior as having been shaped in a functional manner. Moreover, they suggest that when the hamadryas female, translocated into a troop in which straying from a male is not punished, begins to stray, she is also displaying nothing more interesting than functional behavior. I fully agree that this counts as simple "functional" behavior,

but I think the main point is how unexpected it would be for such individuals to manifest such functional behavior quickly. A major contribution of ethology has been to vanquish the most simplistic notions of reinforcement learning theory, namely, the uniform applicability of its rules of learning to species far and wide. Instead, ethology ushered in the notion of “prepared learning,” in which species-specific hard-wired biases make the learning of some associations more likely than that of others (for example, the *sauce béarnaise* syndrome in humans, which shows that we are predisposed to associate nausea with a neutral gustatory signal rather than with an aural one). What was most striking about the Kummer study was the sheer speed with which behavior changed in the two females—in other words, how rapidly the potential for behavioral plasticity overcame whatever hard-wired prepared learning there might have been to impede certain functional responses.

This leads to the larger issue of whether the emergence of a “social culture” is anything more than an artificial construct describing an array of individual functional changes in behavior, an idea explored at length by Bergman and (with a very different conclusion) by Louchart. I readily agree with Bergman that the atomistic building blocks of the new baboon social culture that I discussed likely reflect very local functional adaptations on the parts of individuals. What makes the whole larger and more interesting than the mere sum of those individual functionalist parts is the way those local adaptations form a self-reinforcing circle of interactions. Specifically, at present, the most likely description of the way this novel social culture is propagated involves (a) the initial state, following the selective deaths, in which males were atypically unlikely to displace aggression onto females, (b) resulting in a lower level of female stress and thus a greater willingness on the part of females to risk spontaneous affiliative gestures to unknown, new transfer males, (c) who, in the face of this atypically affiliative environment, default into a less aggressive, less displacing style of behavior, (d) thereby perpetuating the more relaxed social style of the females. It is this interconnecting circle of steps which makes this case more interesting than a mere collection of individual functional responses.

As noted by Bergman, my use of the word “default” to describe this process does (intentionally) intermix cultural and functional explanations. Bergman is correct that ecologically functional behavior could, theoretically, work the same way. Appropriately, the typical definitions of culture rule out variability as a mere function of ecological variables. However, should an ecological variable jump-start a series of functional behavioral adaptations that form a self-reinforcing circle that is eventually free from the initial ecological starting point, this would, I think, qualify as a social culture as well.

Further, I think that Bergman would say that, amid this potential intermixing of cultural and functional levels of interpretation, the latter is preferable in that it is “cleaner,” more reductive and parsimonious. But the self-reinforcing, self-perpetuating features of the reductive parts, by definition, make

the whole bigger than the sum of those parts. This is implicit in Fischer’s pointing out that while behavioral flexibility is a prerequisite for culture it is not equivalent to culture; the latter is a far more emergent phenomenon. This idea is also very strongly emphasized by Louchart, who notes that studies such as these “might promote a new ethological paradigm profoundly different from the eternal methodological individualism.”

The idea of wholes’ being bigger than the sums of their parts also runs through the commentary by King. Primatology has long had two traditions, one big-picture qualitative, the other reductive-quantitative. Each has its own weakness; the quantitative approach, one might suggest, has produced unassailable state-of-the-art data concerning issues of deadening minutia, while the qualitative approach tackles the most profound and important issues in the field but in a way that produces nothing of scientific use (i.e., where the plural of “anecdote” does not equal “data”). Currently, the field is heavily tilted in the quantitative direction, and these studies of social culture prompt two very valid criticisms. The first is that in considering the possibility of “social culture” it is impossible to rely solely on quantitative approaches. And, taking this idea a step higher in an analytical hierarchy, in considering different cultures it makes even less sense to compare these qualitatively rich cases in solely quantitative ways. I wholeheartedly agree with this.

Chancellor brings up two ideas that I find to be valid and important. A culture could emerge from individuals’ carrying out completely novel behaviors (e.g., the invention of a new type of tool use). Chancellor notes that in the cases of possible social culture that I have discussed what is interesting is that they did not require anything as dramatic as new behaviors. Instead there was the need “only to change the frequency of [preexisting] behavior.” This is important. For example, generating a more peaceful human world does not require the invention of new types of human behaviors. It merely requires people to make use of behaviors typical of interactions with close family members and increase the frequency with which they are used in interactions with nonrelatives. What strikes me as particularly interesting and subtle about the Forest Troop case is that the culture emerges from context-specific changes in frequencies of types of behavior. Specifically, Forest Troop males were not less aggressive in all circumstances. Instead, males of adjacent ranks expressed aggressive behaviors at typical rates; the decreased frequency occurred only with respect to high-ranking males aggressively displacing onto very subordinate animals. Chancellor points to the extraordinary recent work of Whiten, Horner, and de Waal (2005) and the general importance of thinking about conformity in the realm of culture. This emphasis is important for a number of reasons, including helping to make sense of instances in which individuals, in the name of conformity, take on behaviors that cannot remotely be considered functional.

A final point runs through all of the commentaries, a truism

that we all cite when trying to get more funding—the need for more and broader primatology research. More research would help answer very specific questions. For example, the Forest Troop case involves a shift both in the temperament of males in a troop and in the female-to-male ratio. The fact that a similar social culture has not been observed in other baboon troops with a similar ratio argues against the culture's being “merely” a function of the skewed ratio. However, as Bergman points out, most of those other studies were of related baboon species rather than of anubis baboons themselves; therefore more anubis examples would be helpful.

More research is also desirable in that it will identify social clines across populations and species that help predict patterns of sociality. For example, there are now sufficient data acquired across an array of primate species in different social settings to help predict whether it will be dominant or subordinate individuals who suffer the worst health in a particular primate group (Abbott et al. 2003; Sapolsky 2005).

Finally, more primatology research will no doubt provide additional examples of extensive behavioral plasticity in primates. But, as emphasized by Chancellor and King, it will ultimately question the very notion of a “typical” behavioral profile from which an individual or a group can diverge. In many ways, the most fundamental accomplishment of primatology has been to erase an array of supposed differences between humans and other primates. An outcome of this trend may ultimately be to find the idea of a there being a typical chimp, baboon, or marmoset as untenable as the idea of there being a typical human.

—Robert Sapolsky

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