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The Cognitive Animal

Empirical and Theoretical Perspectives on Animal Cognition

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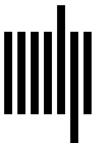
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37 Gestural Communication in Olive Baboons and Domestic Dogs

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Most research investigating how communication may shed light on primate social cognition has focused on vocal rather than visual (gestural) signals (Tomasello and Call 1997). Since visual signals predominate when individuals relate “up close and personal,” their study is especially useful for understanding how animals establish, maintain, and negotiate affiliative and cooperative relationships. Here I describe research on gestural communication in wild baboons and domestic dogs. “Gestures” include all nonvocal actions with potential communicative significance, including facial expressions; body postures; tail carriage; variations in gait and body carriage; and motions of limbs, muzzles, and other body parts that may or may not involve touching another animal. Most of this work relies on detailed analysis of videotaped interactions and only preliminary results are available.

Greetings among Male Olive Baboons

During a long-term study of male–female relationships in a large group of olive baboons (*Papio anubis*) near Gilgil, Kenya (Smuts 1999), I became intrigued by ritualized greetings between adult males in which one male would present his posterior to another and then allow him to handle or even mouth his genitals. Literally placing the source of one’s future reproductive success in the hands of another male seemed like an act of extreme trust inconsistent with the highly aggressive nature of male baboons.

To address this paradoxical behavior, I teamed up with John Watanabe, a cultural anthropologist interested in ritual (Smuts and Watanabe 1990; Watanabe and Smuts 1999). Olive baboons live in female-bonded societies (Wrangham 1980), so males spend much of their adult lives with unrelated and initially unfamiliar others. Most male–male interactions involve mutual antagonism, including occasional severe wound-

ing. Adult males virtually never groom or play with one another and participate in only two kinds of nonagonistic interactions with other males: greetings and alliances.

When one male baboon approaches another, the other usually threatens or avoids him. However, a subset of approaches is accompanied by an exaggerated gait and the “come hither” face (a striking expression with eyes narrowed and ears flattened back against the skull). Sometimes the approaching male also lip smacks, another friendly sign. These very distinctive signals invite the other male to greet, and, compared with routine approaches, the approached male is much less likely to move away. Typically, he will indicate acceptance of the greeting by reciprocating eye contact (in other contexts, eye contact constitutes a threat) and often by lip smacking and making the come hither face in return.

Upon completion of the approach, the males usually begin an exchange of gestures that typically involves one presenting his hindquarters while the other either grasps his hips, mounts him, touches his scrotum, or pulls his penis. Less often, one greeter nuzzles the other, or, very rarely, they embrace and play briefly (this is the only context in which I have seen adult males playing with one another). The gestures used during a single greeting most often entail asymmetrical roles, with one male taking the more active, dominant role (e.g., mounting). Occasionally, a mutual exchange occurs in which each one mounts the other in turn, or each touches the other’s genitals simultaneously or in rapid succession. Immediately after the exchange, one (or occasionally both) of the males moves rapidly away using the same exaggerated gait characteristic of the approach. The entire sequence usually takes no more than a few seconds.

Initiation of a greeting never guaranteed its completion. Either male may break off at any time simply by moving away, and in our sample

of 637 adult male greetings, nearly half of the time one male pulled away before completing the exchange. Occasionally (7 percent of our sample) attempts to greet ended in threats, chases, or fights. Remarkably, however, of the roughly 1000 greetings documented in this study and subsequent research by Smuts (see later discussion), not one resulted in a discernible injury. Thus these greetings stand in striking contrast to the agonism of virtually all other male baboon interactions.

The 12 fully adult males in our troop were either old males (non-natal males past their physical prime who had lived in the troop for at least 2 years, many for much longer) or young males (recently matured natal males or recently transferred males in physical prime). Based on the outcomes of dyadic agonistic encounters, all young males individually outranked all old males. Among baboons in general, higher-ranking males mate more often with estrous females than do lower-ranking males, but during our study—and typical of this larger population of olive baboons (Bulger 1993)—consort frequency and male rank were uncorrelated. Lower-ranking old males achieved unexpectedly high mating success, in part by forming coalitions with each other in which they jointly harassed a male in consort with a fertile female until a consort turnover occurred. All of these challenges targeted young males; we never saw old males challenge each other's consorships. After the turnover, the female almost always ended up with one of the old males involved in the coalition (Smuts 1999).

Although some of these coalitions probably represented mutualistic opportunism (Noe 1992), many of them entailed repeated alliances between the same partners, roughly equal access to the female, and inhibition of competition against alliance partners in other contexts; they thus appeared to involve reciprocal altruism (Packer 1977). To form such valuable coalitions, an older male must somehow cooperate with potential allies who are usually the very rivals whom he has long tried to harass, intimidate, bluff, and occasionally wound. How do these males convey to each other their readiness to establish coop-

erative relationships that rely on a degree of trust?

This is where male greetings, we hypothesized, play a decisive role. The patterns of greeting tended to reflect coalitional behavior (or its absence). Greetings between young males almost always displayed considerable tension, if they occurred at all. Young males had the lowest percentage of completed greetings (one-third) because each one attempted to adopt the dominant, active role while avoiding being in the subordinate, passive role. This resulted in mutual circling and failure to greet. Young males never formed coalitions with one another, and except for their attempted greetings, they mostly avoided each other and even avoided associating with the same females (Smuts 1999). In contrast, the old males who formed coalitions with each other tended to have relatively relaxed greetings, and they completed most (two-thirds) of them.

Several examples illustrate these patterns. The two highest-ranking males, at the time engaged in a tense standoff for dominance, repeatedly attempted to greet, but we never saw them succeed because neither would adopt the passive role. In contrast, between pairs of young males that had achieved a relatively stable dominance relationship, one was usually willing to accept the subordinate role during greetings. Repeated greetings between such pairs acknowledge (and perhaps reinforce) established dominance relationships with minimal risk of aggression. To the extent that both animals benefit from such acknowledgment, these greetings constitute a rudimentary form of cooperation.

One pair of old males, Alex and Boz, greeted more often than any other males. Unrelated but familiar to one another after 7 years of cohabitation in the same troop, they had the longest-standing, most consistent alliance of any pair of males and routinely helped each other take fertile females away from younger rivals. Unlike all other male pairs, neither tried to dominate the other, and they remained the only pair of males observed defending each other in fights with other males.

These two males' greetings showed a unique combination of features. First, they completed nearly all of their greetings. Second, almost half of their greetings included genital touching (the seemingly most risky and intimate form of greeting) compared with only 18 percent of greetings overall. Third, neither Alex nor Boz ever resisted having his genitals handled by the other, although in other dyads males often pulled away from attempts at genital touching. Finally, in contrast to the asymmetry of greeting roles characteristic of most male–male dyads, their greetings reflected near-perfect symmetry (out of a total of 43 gestural exchanges, Alex adopted the passive role in 22, the active role in 21). Indeed, whenever we saw them greet twice in rapid succession, the male who took the active role in the first greeting initiated the subsequent greeting by inviting his partner to adopt the active role. Their greetings thus paralleled their “turn-taking” in coalitions.

How exactly might greeting rituals foster cooperation? The distinctive approach that initiates a greeting seems to function as a kind of meta-communication (see Bekoff and Allen, chapter 53 in this volume) signifying that what follows is no ordinary approach. Thus, greetings appear to constitute a neutral ground that allows exploration of social roles through asymmetric, symmetric, or reciprocal actions. This exploration occurs in a context in which, because no resources are at stake, the chances of escalated aggression are minimized. The possibility of breaking off a greeting at any time without fear of retribution provides an incremental mechanism for testing another male's willingness to cooperate while minimizing one's own investment in the relationship. Because allowing another male to handle one's genitals presumably poses risks, it may function as an honest signal of willingness to cooperate. Males interested in establishing reliable alliances could thus be using the greetings as a way of expressing their good intentions in a world of otherwise suspicious, highly competitive individuals (Smuts and Watanabe 1990).

This hypothesis is indirectly supported by two other facts. First, the gestures used in greeting derive from two kinds of cooperative relationships: the mother–infant bond (lip smacking, embracing, and nuzzling) and sexual invitations and mating (presenting hindquarters, grasping hips, mounting, and genital contact). Second, when adult males solicit each other as allies in the heat of a contest for an estrous female, they employ telegraphic versions of the same gestures used during greetings to request and offer aid. In short, we hypothesize that male baboon greetings involve intentional communication designed to probe and evaluate another male's willingness (or lack of willingness) to cooperate, and that such communication allows potential allies to: (1) more wisely choose whom to solicit for aid and (2) more effectively coordinate actions during actual coalition formation.

Two kinds of evidence are needed to evaluate this hypothesis further. First, the relationships we identified between greeting behavior and alliance formation were correlational and do not demonstrate causation. Causation would be supported if we could show that changes in greeting behavior (such as a shift to more reciprocal roles) predict changes in alliance formation (such as an increase in reciprocal coalition formation). Unfortunately, the tendency for competing males to disappear into thick vegetation makes it difficult to obtain a large sample of alliances.

The second kind of evidence entails more fine-grained analysis of exactly what transpires during greetings and especially during successive greetings between pairs of males over periods of time. To this end, I videotaped over 400 greetings between adult male olive baboons at Gombe National Park, Tanzania. Preliminary analyses indicate that although most greetings conform to the basic formula described earlier, the precise form a particular gesture (e.g., presenting) takes, the choice and timing of gestures relative to what the partner is doing, and the way gestures are combined, vary between dyads and within individuals, depending on whom they are greeting. This microvariation supports our claim that

baboons use greeting gestures flexibly and creatively in a way that suggests intentional communication (Tomasello and Call 1997, p. 10). Future analyses will focus on patterns of gestural variation within and across dyads in order to determine whether some variations predict, or at least correlate with, specific aspects of relationships.

In addition to male–male greetings, the videotaped sample also includes several hundred greetings involving all other possible combinations of age–sex classes. These greetings are currently being analyzed to address questions about how greetings relate to alliance formation and friendship among females and between the sexes. We also aim to investigate the development of greeting behavior. Although the basic gestures used in greetings appear within the first few months (or even weeks) of life, young animals probably learn through experience how to use and combine these gestures in ways that help them achieve social goals.

Bekoff and Allen (chapter 53 in this volume) hypothesize that play fighting may also help animals to establish cooperative relationships. Male baboon greetings and play fighting have at least two unusual features in common. First, each involves “metacommunication” (e.g., the play-bow in canid play and the exaggerated gait and come-hither face in baboon greetings) signaling that what is about to transpire follows special rules. Second, each allows the opportunity for suspension of the behavioral asymmetries characteristic of routine interactions between animals of different ranks. Combined, these two features, which may be unique to play and greetings, create opportunities for rich communication about cooperative possibilities between the actors.

Play Fighting in Dogs

Intrigued by these similarities between greetings and play, my graduate student Erika Bauer and I have begun a quantitative study of self-handicapping and role reversal (see Bekoff and Allen, chapter 53 in this volume, for definitions)

during play fighting between pairs of domestic dogs. Like the baboon studies just described, this research analyzes videotaped sequences to allow detailed investigation of roles. Our sample includes about 20 domestic dogs (adults or adolescents) in various partner combinations.

Dog play is a particularly interesting and suitable arena in which to investigate variation in role asymmetry–symmetry during play because: (1) dogs play a lot; (2) outside of play, it is possible to discern clear asymmetries in dominance status for most dyads (personal observation); and (3) they descend from wolves, a species characterized both by adult play and by a complex interplay of cooperation and competition.

Several patterns emerge from preliminary analyses. First, the degree of role reversal varies dramatically. For example, out of a sample of 12 different dyads, in one pair the dominant animal never adopted a subordinate role, whereas in another pair the dominant animal adopted the subordinate role 80 percent of the time (most dyads fell somewhere in between). Second, particular individuals reversed roles more often with some partners than with others. Third, even within dyads, the degree of role reversal can vary considerably from one play bout to another. Fourth, in at least some dyads, dogs seem much more willing to reverse roles than the primates for whom quantitative data exist (such as rhesus macaques and squirrel monkeys; Biben 1998). Rhesus and squirrel monkeys have quite rigid dominance hierarchies compared with some other primates, such as chimpanzees (de Waal 1989). Dog and wolf dominance hierarchies (personal observation and Zimen 1982, respectively) appear more like those of chimps, in that subordinates are sometimes quite relaxed around dominants.

These comparisons raise the possibility that styles of play fighting may reflect species differences in styles of dominance relationships. To evaluate this hypothesis, we plan to extend our study of role reversals during play to include chimpanzees, captive wolves, and other mammalian species that exhibit different dominance styles. We also intend to analyze the videotapes

for contingencies within and between play bouts that may influence the degree of role reversal. For example, if animal *A* shows little role reversal and her partner, *B*, loses interest in playing, does *A* then exhibit more role reversal as a strategy for inducing *B* to play more? Or, if one animal begins to challenge another's dominance rank, does he begin by decreasing his willingness to adopt the subordinate role during play (Pellis, chapter 52 in this volume)?

These sorts of questions establish common ground between our study of mammalian play and our research on baboon greetings. In each instance, we examine subtle behaviors detectable only through analysis of videotapes to find out what cues the animals emit and respond to, and how these cues may be used to negotiate concerns that extend beyond the immediate transaction to include alternative future paths for how the relationship may unfold. In our own species, such negotiations rely so much on verbal communication that we tend to assume that without words, animals cannot "talk" about the future. These studies represent one small step toward determining if this is true.

The Value of Videotaping Interactions

While videotaping greetings among baboons, whenever possible we also taped other interesting social phenomena, such as aggression, play, and formation of coalitions. Although this footage has not yet been analyzed systematically, casual perusal suggests that it will provide indisputable documentation of behaviors that may provide insights into social cognition. For example, one videotaped sequence shows two male baboons, *A* and *B*, allying against a third male, *C*, who is sitting minding his own business. *A* is a young alpha male, and *C* and *B* are young, recent immigrants of roughly equal rank. (Although coalitions among young males were rare at Gilgil, among the Gombe baboons, males used them to probe the fighting ability of other young males.) *A* and *B* jointly threaten *C* as they approach

him. *C*, who generally avoids all fights, at first ignores them. As *A* and *B* come closer, *C* gets up and begins to move away. Just as *C* leaves, *B*, who is on the far side of *A* from *C*, reaches out and apparently deliberately shoves *A* into *C*'s path. Because *C* is not looking at them, he does not see the shove, and from his perspective it must seem as if *A* suddenly lunged at him. *C* turns and attacks *A*, *A* flees, and *C* chases *A* for at least a hundred meters before they disappear into the bushes. *B* watches, unperturbed. With one well-timed shove, he managed to provoke aggression between *A* and *C*, perhaps increase tension between them, and gain potentially useful information about their relationship.

I was surprised when I saw this sequence on tape because I did not realize that baboons used such deliberate strategies to incite third-party aggression. Even had I detected this sequence in real time, it would constitute just one more anecdote whose details could (and should!) be questioned by people who were not there. However, because this sequence is on tape, we know exactly what happened, and different people can observe the sequence and decide whether they agree on its interpretation. In combination with dozens of other videotaped observations, events like this can comprise a database suitable for testing a hypothesis.

A second example of the value of videotaped observations concerns alliance formation in baboons. When I tried to record alliances on paper in the field, I often became frustrated and confused, because at one moment *A* and *B* were allied against *C* and then suddenly it seemed as if *B* and *C* were allied against *A*. I secretly thought that I was not a good enough observer until I examined such episodes on tape. I then discovered that, indeed, the baboons often change alliance partners so quickly that a temporary partnership could be missed in the blink of an eye. Even in slow motion, these shifts are hard to follow, but by watching a sequence over and over, one can eventually describe what happened.

The result resembles a choreographer's notation for a complex routine involving many danc-

ers, and it is not obvious what it all means. The baboons probably know exactly what such rapid shifts signify, and I hope that intelligible patterns will emerge once a large enough number of episodes are analyzed. Such shifting partnerships are to my mind the single most striking attribute of baboon alliances, and yet they have received virtually no recognition in the literature, probably because they are so hard to follow unless they are recorded on videotape.

A third example concerns the astounding degree of responsiveness to a partner's cues during greetings. When videotaped greetings are observed in slow motion, it becomes immediately apparent that the two baboons respond to each other's subtlest shifts in movement and glances with split-second timing that cannot possibly be documented, or often even perceived, in real time. After watching hundreds of greetings in slow motion, I have become convinced that at least as important as *what* each baboon does is *how* they do it, and specifically, how finely coordinated their movements are with those of the other baboon.

In slow motion, some greetings look like the awkward steps of two people first learning to dance together, whereas others look like Fred Astaire and Ginger Rogers. Preliminary analyses indicate that the latter usually involve greetings between established friends, whereas the former involve greetings between individuals who are not friends (but who may be attempting to change that). If these results hold up, they suggest that coordinated movement may be one important way animals establish reliable, trusting relationships without words (Savage Rumbaugh et al. 1993). In fact, to the extent that such fine coordination depends on a major investment of time, this method of evaluating partners may be more reliable than mere verbal commitments.

These are just a few examples of the kinds of questions that can be addressed only through videotaped observations. Such observations, in my view, hold tremendous potential for delving much more deeply into the world of animal communication and thereby, animal social cognition.

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