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**Social complexity and the information acquired during eavesdropping
by primates and other animals**

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INTRODUCTION

In many of the studies reviewed in this book, ‘eavesdropping’ takes the following
20 form: a subject has the opportunity to monitor, or eavesdrop upon, an interaction between
two other animals, A and B (Peake, this volume). The subject then uses the information
obtained through these observations to assess A’s and B’s relative dominance or
attractiveness as a mate (e.g. Mennill *et al.*, 2002). For example, Oliveira *et al.* (1998)
25 found that male fighting fish *Betta splendens* that had witnessed two other males
involved in an aggressive interaction were subsequently more likely to approach the loser
of that interaction than the winner. Subjects’ behaviour could not have been influenced
by any inherent differences between the two males, because subjects were equally likely
to approach the winner and the loser in competitive interactions they had not observed.
Similarly, Peake, *et al.* (2001) presented male great tits *Parus major* with the opportunity
30 to monitor an apparent competitive interaction between two strangers by simulating a
singing contest using two loudspeakers. The relative timing of the singing bouts (as
measured by the degree of overlap between the two songs) provided information about
each ‘contestant’s’ relative status. Following the singing interaction, one of the
‘contestants’ was introduced into the male’s territory. Males responded significantly less
35 strongly to singers that had apparently just ‘lost’ the interaction (see also McGregor &
Dabelsteen, 1996; Naguib *et al.*, 1999, and many chapters in this volume).

What information does an individual acquire when it eavesdrops on others? In
theory, an eavesdropper could acquire information of many different sorts: about A,
about B, about the relationship between A and B, or about the place of A’s and B’s
40 relationship in a larger social framework. The exact information acquired will probably
reflect the particular species’ social structure. For example, songbirds like great tits live
in communities in which six or seven neighbours surround each territory-holding male.
Males appear to benefit from the knowledge that certain individuals occupy specific areas
(e.g. Brooks & Falls, 1975), that competitive interactions between two different
45 neighbours have particular outcomes, and that these outcomes are stable over time. We
would therefore expect an eavesdropping great tit not only to learn that neighbour A was

dominant to neighbour B, for example, but also to form the expectation that A was likely to defeat B in all future encounters. More speculatively, because the outcome of territorial interactions are often site-specific (see Bradbury & Vehrencamp, 1998 for a review), we would expect eavesdropping tits to learn further that A dominates B in some areas but B dominates A in others. In contrast, the information gained from monitoring neighbours' interactions would unlikely be sufficient to allow the eavesdropper to rank all of its neighbours in a linear dominance hierarchy, because not all neighbouring males would come into contact with one another. Such information would be difficult if not impossible to acquire; it might also be of little functional value.

In contrast, species that live in large, permanent social groups have a much greater opportunity to monitor the social interactions of many different individuals simultaneously. Monkey species such as baboons *Papio cynocephalus*, for example, typically live in groups of 80 or more individuals that include several matrilineal families arranged in a stable, linear dominance rank order (Silk *et al.*, 1999). Offspring assume ranks similar to those of their mothers, and females maintain close bonds with their matrilineal kin throughout their lives. Cutting across these stable, long-term relationships based on rank and kinship are more transient bonds – for example, the temporary associations formed between unrelated females whose infants are of similar ages, and the 'friendships' formed between adult males and lactating females as an apparent adaptation against infanticide (Palombit *et al.*, 1997, 2001). In order to compete successfully within such groups, it would seem advantageous for individuals to recognize who outranks whom, who is closely bonded to whom, and who is likely to be allied to whom (Harcourt, 1988, 1992; Cheney & Seyfarth, 1990; see below). The ability to adopt a third party's perspective, and discriminate among the social relationships that exist among others, would seem to be of great selective benefit.

In this chapter we review evidence for eavesdropping in selected primate species, and we consider what sort of information is acquired when one individual observes or listens in on the interactions of others. We then compare eavesdropping by primates with eavesdropping in other animal species, focusing on both potential differences and directions for further research.

KNOWLEDGE ABOUT OTHER ANIMALS' KIN

80 Some of the first evidence that monkeys recognize other individuals' social relationships emerged as part of a relatively simple playback experiment designed to document individual vocal recognition in vervet monkeys *Cercopithecus aethiops* (Cheney & Seyfarth, 1980). We had noticed that mothers often ran to support their juvenile offspring when these individuals screamed during aggressive interactions. This
85 observation, like many others (e.g. Hansen, 1976; Gouzoules *et al.*, 1984) suggested that mothers recognized the calls of their offspring. To test this hypothesis, we designed a playback experiment in which we played the distress scream of a juvenile to a group of three adult females, one of whom was the juvenile's mother. As expected, mothers consistently looked toward the loudspeaker for longer durations than did control females.
90 Even before she had responded, however, a significant number of control females looked at the mother. In so doing, they behaved as if they recognized not only the identity of signallers unrelated to themselves but also associated those individuals with specific adult females (Cheney & Seyfarth, 1980, 1982).

 In an attempt to replicate these results, we carried out a similar set of experiments
95 on free-ranging baboons in the Okavango Delta of Botswana. In these experiments, two unrelated female subjects were played a sequence of calls that mimicked a fight between their close relatives (Fig. 1). The females' immediate responses to the playback were videotaped, and both subjects were followed for 15 minutes after the playback to determine whether their behaviour was affected by the calls they had heard. In separate
100 trials, the same two subjects also heard two control sequences of calls (Fig. 1). The first sequence mimicked a fight involving the dominant subject's relative and an individual unrelated to either female; the second mimicked a fight involving two individuals who were both unrelated to either female (for details see Cheney & Seyfarth, 1999).

 After hearing the test sequence, a significant number of subjects looked toward
105 the other female (Fig. 2), suggesting that they not only recognized the calls of unrelated individuals but also associated these individuals with their kin (or close associates). Females' responses following the test sequence differed significantly from their responses following control sequences. Following the first control sequence, when only

the dominant subject's relative appeared to be involved in the fight, only the subordinate
110 subject tended to look at her partner (Fig. 2). Following the second control sequence,
when neither of the subjects' relatives was involved, neither subject looked at the other
(Fig. 2). Finally, following a significant proportion of test sequences, the dominant
subject approached and supplanted (a mild form of aggression) the subordinate (Fig. 3).
In contrast, when the two subjects approached each other following the two control
115 sequences, the dominant rarely supplanted the subordinate (Fig. 3).

Taken together, these experiments suggest that baboons and vervet monkeys
recognize the individual identities of group members unrelated to themselves, and that
they recognize the social relationships that exist among these animals. Such knowledge
can only be acquired by observing, or eavesdropping, on social interactions in which the
120 observer is not involved, and making the appropriate deductions.

Other studies provide additional evidence of monkeys' ability to distinguish the
close associates of other individuals. For example, in an experiment performed on captive
long-tailed macaques *Macaca fascicularis*, Dasser (1988a) trained a female subject to
choose between slides of one mother-offspring pair from her social group and slides of
125 two unrelated individuals from her group. Having learned to respond to one mother-
offspring pair, the subject was then tested with 14 novel slides of familiar mothers and
offspring paired with an equal number of novel slides of familiar unrelated animals
matched for age and sex. In all tests, she correctly selected the mother-offspring pair. In
so doing, she appeared to use an abstract category to classify pairs of individuals that was
130 analogous to our concept of 'mother-child affiliation'. Dasser was able to rule out the
possibility that mothers and offspring were matched according to physical resemblance,
because subjects were unable to match unfamiliar mothers and offspring. Instead,
individuals appeared to be classified according to their degree of association. Again, such
knowledge of other individuals' close associates can only be obtained by monitoring, or
135 eavesdropping, upon their social interactions.

Under natural conditions, it is difficult to determine whether animals distinguish
among different categories of social relationships. Do monkeys recognize, for example,
that mother-offspring bonds are distinct from sibling bonds or friendships even when all
are characterized by high rates of interaction? In perhaps the only test of monkeys' ability

140 to recognize different categories of social affiliation, Dasser (1988b) trained a long-tailed
macaque to identify a pair of siblings from her social group and then tested her ability to
distinguish novel slides of familiar sibling pairs from familiar mother-offspring pairs,
familiar pairs of less closely related matrilineal kin, and familiar unrelated pairs.
Although the subject did distinguish siblings from unrelated pairs and pairs of less
145 closely related individuals, she was unable to discriminate between siblings and mothers
and offspring. This failure may have occurred because the same female had previously
been rewarded for picking the mother-offspring pair. It is also possible, however, that she
did not distinguish between different kinship categories and simply chose the pair that
was more closely affiliated.

150 Natural patterns of aggression also reflect the knowledge that monkeys have of
their group's social network. In many monkey species, an individual who has just
threatened or been threatened by another animal will often 'redirect aggression' by
threatening a third, previously uninvolved, individual. Judge (1982) was the first to note
that redirected aggression in rhesus macaques *Macaca mulatta* does not always occur at
155 random. Rather than simply threatening any nearby individual, animals will instead
specifically target a close matrilineal relative of their recent opponent. Similar kin-biased
redirected aggression occurs in Japanese macaques *Macaca fuscata* (Aureli *et al.*, 1992)
and vervets (Cheney & Seyfarth, 1986; 1989).

160 **KNOWLEDGE ABOUT OTHER ANIMALS' DOMINANCE RANKS**

Dominance ranks offer another opportunity to test whether nonhuman primates
gain information about other animals' relationships by eavesdropping on their social
interactions. Like matrilineal kinship, linear, transitive dominance relations are a
165 pervasive feature of social behaviour in groups of Old World monkeys. A linear,
transitive rank order might emerge because individuals simply recognize who is
dominant or subordinate to themselves. In this case, a linear hierarchy would occur as an
incidental outcome of paired interactions and there would be no evidence to suggest that
animals eavesdropped on others' interactions. Alternatively, a linear hierarchy might
170 emerge because individuals genuinely recognize the transitive dominance relations that

exist among others: a middle-ranking individual, for example, might know that A is dominant to B and B is dominant to C, and therefore conclude that A must be dominant to C. Like knowledge of matrilineal kin, such knowledge could only be acquired through eavesdropping on the interactions of others.

175 In many species of Old World monkeys, female dominance ranks are determined by the rank of an individual's matriline (Walters & Seyfarth, 1987; Chapais, 1988). Knowledge of another female's rank cannot, therefore, be obtained by attending to absolute attributes such as age or size; instead, it demands the monitoring of other individuals' interactions. Several observations and experiments suggest that monkeys do
180 recognize the rank relations that exist among others females in their group. For example, dominant female baboons often grunt to mothers with infants as they approach the mothers and attempt to handle or touch their infants. Grunts seem to function to facilitate social interactions by appeasing anxious mothers, because an approach accompanied by a grunt is significantly more likely to lead to subsequent friendly interaction than is an
185 approach without a grunt (Cheney *et al.*, 1995b). Occasionally, however, a mother will utter a submissive call, or 'fear bark', as a dominant female approaches. Fear barks are an unambiguous indicator of subordination; they are never given to lower-ranking females.

To test whether baboons recognize that only a more dominant animal can cause another individual to give a fear bark, we designed a playback experiment in which adult
190 females subjects were played a causally inconsistent call sequence in which a low-ranking female apparently grunted to a high-ranking female and the higher-ranking female apparently responded with fear barks. As a control, the same subjects heard the same sequence of grunts and fear barks made causally consistent by the inclusion of additional grunts from a third female who was dominant to both of the other signallers.
195 For example, if the inconsistent sequence was composed of female 6's grunts followed by female 2's fear barks, the corresponding consistent sequence might begin with female 1's grunts, followed by female 6's grunts and ending with female 2's fear barks. Some subjects were higher-ranking than the signallers; others were lower-ranking. Regardless of their own relative ranks, subjects responded significantly more strongly to the causally
200 inconsistent sequences, suggesting that they recognize not only the identities of different

signallers, but also the rank relations that exist among others in their group (Cheney *et al.*, 1995a).

Further suggestion that monkeys recognize other individuals' ranks comes from observations on competition among adult female vervet monkeys for access to a grooming partner (Seyfarth, 1980). Such competition occurs when one female approaches two that are grooming, supplants one of them, and then grooms with the female that remains. Interestingly, in those cases when a female approaches two groomers who are both subordinate to her, the lower-ranking of the two groomers typically moves away, while the higher-ranking remains (Cheney & Seyfarth, 1990). By remaining seated, the higher-ranking of the two groomers acts as if she recognizes that, although they are both lower-ranking than the approaching female, she is the higher-ranking. Though not definitive, these observations suggest that females recognize not only their own status relative to other individuals but also other individuals' status relative to each other. In other words, they appear to recognize a rank hierarchy (Cheney & Seyfarth, 1990).

The ability to rank other group members is perhaps not surprising, given the evidence that captive monkeys and apes can be taught to rank objects according to an arbitrary sequential order (D'Amato & Columbo, 1989; Treichler & van Tilberg, 1996), the amount of food contained within a container (Gillan, 1981), their size, or the number of objects contained within an array (e.g. Matsuzawa, 1985; Hauser *et al.*, 1996; Brannon & Terrace, 1998). What distinguishes the social example, however, is the fact that, even in the absence of human training, female monkeys seem able to construct a rank hierarchy and then place themselves at the appropriate location within it.

KNOWLEDGE ABOUT MORE TRANSIENT SOCIAL RELATIONSHIPS

All of the studies discussed thus far focussed on interactions among females in groups where matrilineal kin usually retain close bonds and similar ranks throughout their lives. It might seem, therefore, that an individual could simply memorize the close associates and relative ranks of other females and thereafter navigate easily through a predictable network of social relationships. Not all social and rank relationships, however, are as stable as those among matrilineal kin. Some types of social bonds are

relatively transient, and some rank relationships – particularly among adult males – change often. Nonetheless, there is evidence that nonhuman primates also recognize these more transient associations.

235 For example, under natural conditions male and female hamadryas baboons *Papio hamadryas* form close, long-term bonds that can last for a number of years. Potential rivals appear to recognize the ‘ownership’ of specific females by other males and refrain from challenging those males for their females (Kummer *et al.*, 1974). Experiments conducted in captivity have shown that rival males assess the strength of other males’
240 relationships with their females before attempting to challenge them. They do not attempt to take over a male’s female if the pair appears to have a close social bond (Bachmann & Kummer, 1980). Although similar experiments have not yet been conducted with savanna baboons, observational data suggest that these baboons, too, recognize the temporary bonds, or ‘friendships’, that are formed between males and lactating females (Palombit *et al.*, 1997). For example, Smuts (1985) observed that males who had recently been
245 threatened by another male often redirected aggression toward the female friends of their opponent (see Dunbar, 1983 for similar observations on gelada baboons *Theropithecus gelada*).

 Monkeys also seem to recognize the bonds that exist between males and particular
250 infants. In Tibetan macaques *Macaca thibetana*, males are often closely affiliated with a particular infant in the group. Competitive interactions between males are mediated by the carrying of infants, and a male will frequently carry an infant and present it to another male. In a study of such carrying (or ‘bridging’) behavior, Ogawa (1995) observed that males more frequently provided other males with those males’ affiliated infants than with
255 other, non-affiliated infants.

 Finally, there is evidence that monkeys recognize even very transient dominance relations among others. Dominance among male vervets, baboons, and macaques is determined primarily by age, fighting ability, and, in some populations, the presence of alliance partners. As a result, rank relations among males are considerably less stable
260 than they are among females (Walters & Seyfarth, 1987). In a study of a large social group of captive bonnet macaques *Macaca radiata*, Silk (1993, 1999) found that males formed linear, transitive dominance hierarchies that remained stable for only short

periods of time. As in other primate species, males occasionally attempted to recruit alliance support during aggressive interactions (roughly 12% of all aggressive encounters). Significantly, males consistently solicited allies that outranked both themselves and their opponents. Males did not simply solicit the highest-ranking individual in the group or choose allies that outranked only themselves. Instead, soliciting males seemed to recognize not only their own rank relative to a potential ally but also the rank relation between the ally and their opponent. If dominance ranks remained stable this might not have been a difficult task. However, over the course of one year, roughly half of the 16 males changed dominance rank each month (data from Silk, 1993, Table 3). The males' apparent ability to keep track of such highly transient rank relations suggests that they carefully monitored all aggressive interactions among other males, constantly updated their list of relative ranks, and placed themselves accurately into each new list.

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EAVESDROPPING BY OTHER MAMMALS

Data from dolphins *Tursiops truncatus* and hyenas *Crocuta crocuta* suggest that nonhuman primates are not the only mammals in which individuals acquire information about many different individuals' social relationships. When competing over access to females, male dolphins form dyadic and triadic alliances with selected other males, and allies with the greatest degree of partner fidelity are most successful in acquiring access to females (Connor *et al.*, 1992, 1999, 2001). The greater success of high-fidelity alliances raises the possibility that males in newly formed alliances, or in alliances that have been less stable in the past, recognize the strong bonds that exist among others and are more likely to retreat when they encounter rivals with a long history of cooperative interaction.

Like many species of Old World monkeys, hyenas live in social groups comprised of matrilineal groups in which offspring inherit their mothers' dominance ranks (Smale *et al.*, 1993; Engh *et al.*, 2000). Holekamp *et al.* (1999) played recordings of cubs' 'whoop' calls to mothers and other breeding females. As with vervet monkeys and baboons, hyena females responded more strongly to the calls of their offspring and close relatives than to the calls of unrelated cubs. In contrast to vervets and baboons, however, unrelated

295 females did not look at the cubs' mothers. One explanation for these negative results is that hyenas are unable to recognize third-party relationships, despite living in social groups that are superficially similar to those of many primates. It also remains possible, however, that hyenas are simply uninterested in the calls of unrelated cubs.

300 In fact, hyenas' patterns of alliance formation suggest that they do monitor other individuals' interactions and extrapolate information about other animals' relative ranks from their observations. During competitive interactions over meat, hyenas often solicit alliance support from other, uninvolved individuals. When choosing to join on-going skirmishes, hyenas that are dominant to both of the contestants almost always support the more dominant of the two individuals (Engh *et al.*, in press). Similarly, when the ally is intermediate in rank between the two opponents, it inevitably supports the dominant individual. These data provide the first evidence for a non-primate species that alliance partners may be chosen on the basis of both the allies' and the opponents' relative ranks (Harcourt, 1988, 1992). They are consistent with the hypothesis that hyenas are able to infer transitive rank relations among other group members.

310 **POSSIBLE DIFFERENCES BETWEEN PRIMATES AND OTHER ANIMALS**

Do primates differ from other animals in their ability to infer third party social relationships through eavesdropping? We can identify at least three competing hypotheses.

315 The first hypothesis argues that primates are in fact more intelligent than non-primates. This intelligence is reflected not only in tests of captive animals but also in primates' superior ability to keep track of complex social relationships. The difference between primates and non-primates is qualitative and fundamental, and will be corroborated by future research.

320 The second hypothesis maintains that selection has favored the ability to recognize other individuals' relationships in all species that live in large, complex social groups. According to this hypothesis, monkeys only appear to have a greater capacity to recognize third party social relationships because they have received more attention than non-primates living in similarly large groups. Once this imbalance in research has been

325 redressed, differences between primates and other animals will disappear, to be replaced
by a difference that depends primarily on group size and composition.

The third hypothesis claims that neither phylogeny nor group size and
composition have influenced animals' ability to gain information about other individuals'
social relationships. It argues, in effect, that there are no species differences in 'social
330 intelligence'. Monkeys and hyenas, for example, only appear to excel in their ability to
recognize allies' and opponents' relative ranks because their large social groups allow
them to display this knowledge. In contrast, studies of species that live in small social
groups have to date focussed primarily on observers' ability to assess the dominance of
only two individuals. Once monogamous and even solitary species have been given the
335 opportunity to reveal what they know about the social relationships of many different
individuals, they will be shown to possess a level of 'social intelligence' that is no
different from that found among animals living in large social groups.

At present, it is difficult to test among these alternative hypotheses; below we
review some information that may be relevant.

340

1. Primates have greater 'social intelligence' than other species

Primates have larger brains for their body size than other vertebrates (Martin,
1983). Dunbar (2000) argues that this arises because primate social groups are not only
larger but also more complex than those of other taxa. Primate groups are typically
345 composed of many reproductively active males and females, and individuals interact
regularly with both kin and non-kin with whom they must simultaneously cooperate and
compete for resources. Such social complexity may place strong selective pressure on the
ability to recognize other individuals' close associates.

To date, only monkeys and possibly dolphins have been shown to recognize the
350 affiliative relationships that exist among other group members. In monkey groups,
closely-bonded individuals are usually matrilineal kin, but this is not always the case. The
ability to classify other individuals into matrilineal or closely-bonded sub-groups is likely
to be relatively complex, for several reasons.

Matrilineal kin groups vary in size, and not all individuals within a kin group
355 interact at the same rate or in the same way. Moreover, no single behavioural measure

underlies the associations between individuals, and there is no threshold or defining criterion for a ‘close’ social bond. For example, in many monkey species females form the majority of their alliances with matrilineal kin, and high-ranking kin usually form alliances at higher rates than low-ranking kin (reviewed by Walters & Seyfarth, 1987; 360 Silk, 1987). There is no evidence, however, that other group members more easily recognize the kin (or close associates) of high-ranking individuals than those of low-ranking individuals. Similarly, female kin usually occupy adjacent dominance ranks. This rule of thumb, however, cannot reliably be used to classify females into kin groups, because not all adjacently-ranked females are kin. We do not yet know whether monkeys 365 discriminate among different types of social bond – whether they distinguish, for example, among the bonds formed by mothers and offspring, sisters, or friends. Moreover, the degree to which there is a quantitative or qualitative threshold for learning to recognize that two other individuals share a close bond is not known.

Furthermore, some social relationships among monkeys are transitive, while 370 others are not. For example, if infant A_1 and juvenile A_2 both associate at high rates with a particular adult female A , it is usually correct to infer that the juvenile and infant are also closely bonded. Similarly, if A is dominant to B and B is dominant to C , it is usually true that A is dominant to C . In other cases, however, transitivity cannot be assumed. If infant baboon A_1 and juvenile baboon A_2 both associate at high rates with the same adult 375 female and she associates with an adult male ‘friend’, we can infer that the male is probably also closely allied to the infant. However, it would be incorrect to assume that he is equally closely allied to the juvenile, who may instead be more closely allied to another male who was previously the mother’s friend (Seyfarth, 1978; Smuts, 1985; Palombit *et al.*, 1997). Baboon females from the same matriline often form friendships with different 380 males; conversely, the same male may form simultaneous friendships with females from two different matrilines. In the latter case, the existence of a close bond between a male and two females does not predict a close bond between the two females. In fact, their relationship is as likely to be competitive as it is friendly (Palombit *et al.*, 2001).

Finally, as group size increases, the challenge of monitoring other individuals’ 385 social relationships and dominance ranks increases exponentially. In a group of 80 animals (not an unusual size for many monkey species), each individual confronts 3,160

different possible dyadic combinations and 82,160 different triadic combinations of individual, numbers that may place considerable demands on the observer's memory and inferential abilities.

390 Preliminary evidence suggests that monkeys are able to monitor and remember the social ranks and relationships of many individuals simultaneously. Despite the lack of a consistent criterion for determining which individual is likely to be closely bonded with which others, monkeys appear to be able to distinguish the close associates of other group members. They appear to view their social groups not just in terms of the individuals that
395 comprise them but also in terms of a web of social relationships in which certain individuals are linked with several others.

Some learning experiments with captive animals support the view that primates are generally more adept than non-primates at classifying items according to their relative relations. In oddity tests, for example, a subject is presented with three objects, two of
400 which are the same and one of which is different, and asked to choose the object that is different. Monkeys and apes achieve high levels of accuracy in such tests even when tested with novel stimuli (Harlow, 1949; D'Amato *et al.*, 1985; see also reviews by Tomasello & Call, 1997; Shettleworth, 1998). Baboons and chimpanzees can also learn to make abstract discriminations about relations between relations, matching patterns
405 containing repeated samples of the same item with similar 'same' patterns (Premack, 1983; Oden *et al.*, 1988; Fagot *et al.*, 2001). In all cases, subjects' performance suggests the use of an abstract hypothesis, because concepts like 'odd' specify a relation between objects independent of their physical features. In a similar manner, the concept 'closely bonded' can be applied to any two individuals and need not be restricted to specific pairs
410 that look alike.

Judgments based on relations among items have been demonstrated more often in nonhuman primates than in other taxa, and primates seem to recognize abstract relations more readily than at least some other animals. Although it is possible, for example, to train pigeons to recognize relations such as 'same', the procedural details of the test
415 appear more critical for pigeons than they are for monkeys, and relational distinctions can easily be disrupted (Herrnstein, 1985; Wright *et al.*, 1988; Wasserman *et al.*, 1995). Rather than attending to the relations among stimuli, pigeons seem predisposed to focus

on absolute stimulus properties and to form item-specific associations (reviewed by Shettleworth, 1998). Similarly, in tests of transitive inference, monkeys and apes appear to acquire a representation of series order that allows them to rank items even when some items in the list are missing. In contrast, pigeons seem to attend primarily to the association between adjacent pairs, which limits their ability to add or delete items from a list (D'Amato & Colombo, 1989; von Fersen *et al.*, 1991; Treichler & van Tilberg, 1996; Zentall *et al.*, 1996).

425

2. Differences in 'social intelligence' are related to group size and complexity

If, as has been hypothesized, the recognition of third-party relationships confers a selective advantage because it allows individuals to remember who associates with whom, who outranks whom, and who is allied to whom, we should expect to find evidence for this ability not just in nonhuman primates but also in any animal species that lives in large social groups composed of individuals of varying degrees of dominance rank and genetic relatedness. We would also predict that selection should have acted less strongly on this ability in solitary species and species living in small, egalitarian groups that are composed primarily either of close kin or of unrelated individuals. Thus, the ability to recognize the close associates of others should be evident in non-primate species such as hyenas and lacking or less evident in some ape species, including gorillas *Gorilla gorilla* and orangutans *Pongo pygmaeus*. Although recent evidence that hyenas recognize other individuals' relative ranks lend support to this hypothesis, other comparative data are lacking. For example, no study has yet attempted to determine the extent to which any ape species is able to recognize the social relationships of other group members.

Within the Primate order, species that live in large groups have a relatively larger neocortex than those that are solitary or live in small groups (Barton & Dunbar, 1977). A similar relation is found in carnivores (Barton & Dunbar, 1997) and toothed whales (Connor *et al.*, 1998a; Marino, 1998; Connor *et al.*, 1998b), supporting the hypothesis that sociality has favored the evolution of large brains (see also Jolly, 1966; Humphrey, 1976; Cheney & Seyfarth, 1990). Indeed, differences in social complexity may exert their effect even in species that lack a cortex entirely. In paper wasps *Polistes dominulus*, for

example, there is a significant increase in the size of the antennal lobes and collar (a
450 substructure of the calyx of the mushroom body) in females that nest colonially – with
other queens – as opposed to solitary breeders (Ehmer *et al.*, 2001). This increase in
neural volume may be favoured because sociality places increased demand on the need to
discriminate between familiar and unfamiliar individuals and to monitor other females’
dominance and breeding status. Clearly, therefore, neural correlates of sociality need not
455 be restricted to higher mammals.

Further supporting this argument are data from some other laboratory studies
suggesting fewer differences between primates and other animals in the ability to make
relational distinctions. For example, the African gray parrot Alex *Psittacus erithacus* is
reported to make explicit same/different judgments about sets of objects (Pepperberg,
460 1992, this volume). Similarly, sea lions *Zalophus californianus* (Schusterman & Krieger,
1986; Schusterman & Gisener 1988) and dolphins (Herman *et al.* 1993; Mercado *et al.*
2000) have been taught to respond to terms such as ‘left’ and ‘right’ that require the
animals to assess relations among a variety of different objects. Finally, a number of
species, including parrots (Pepperberg, 1994) and rats (Church & Meck, 1984; Capaldi,
465 1993), are able to assess quantities, suggesting that relatively abstract concepts of
numerosity and transitivity may be pervasive among animals (reviewed by Shettleworth,
1998).

3. There are few differences in ‘social intelligence’ across species

470 Recent research on ‘eavesdropping’ by birds and fish indicates that even animals
living in small social groups are capable of acquiring detailed information about other
individuals’ relative dominance or attractiveness as a mate. Often, this information is of
necessity restricted to a few other individuals. For territorial species living in small
family groups, questions about the ability to track social relationships among many other
475 individuals are largely moot, because the opportunity to monitor interactions among all
possible neighbours rarely arises. Eavesdropping on the competitive singing duets of
strangers, for example, allows territorial songbirds to extract information about the two
contestants’ relative dominance. Whether these birds would also be capable of
recognizing a dominance hierarchy involving numerous individuals remains unclear.

480 Although many species of songbirds form flocks during the winter, little is known about
the social interactions that take place within such flocks, or the degree to which flock-
members recognize other individuals' relative ranks (but see Popp, 1987).

To date, few studies of birds have focused on group-living species like chickens,
where dominance hierarchies occur. There is some evidence that chickens monitor the
485 interactions of other flock members to gain information about other individuals' relative
ranks. To date, however, tests have only involved hierarchies of three individuals (Hogue
et al., 1996).

Similarly, very little is known about the ability of non-primate mammals or birds
to recognize other individuals' social relationships. Colonial white-fronted bee-eaters
490 *Merops bullockoides* offer one example of an avian society in which there would appear
to be strong selective pressure for the recognition of other individuals' kin groups.
Observational evidence suggests that bee-eaters may recognize other individuals and kin
groups, and associate these groups with specific feeding territories (Emlen *et al.*, 1995),
although this has not yet been tested experimentally.

495 Clearly, more data are needed from both natural and laboratory studies before we
can make any definitive conclusions about cognitive differences between primates and
other animals, or between species living in large as opposed to small groups. It remains
entirely possible that apparent species differences between primates and other animals in
the recognition of third party social relationships are due more to differences in the social
500 context in which eavesdropping occurs than to any cognitive differences in the ability to
monitor social interactions. Given the opportunity to evaluate the social relationships of
many different individuals, species living in small family groups and even primarily
solitary species may well be shown to have similar abilities as those living in large social
groups. It is to be hoped that future research will attempt to investigate the extent to
505 which gregarious species in taxa other than primates are capable of recognizing the close
associates and allies of other group members, and to determine the neural correlates, if
any, of this ability.

SUMMARY

510 Nonhuman primates are skilled voyeurs. By observing or listening to the
interactions of others, they acquire information about other individuals' social
relationships and learn to place these relationships within a larger social framework, such
as a group of ranked, matrilineal families. Given the large, complex societies in which
monkeys cooperate and compete, the adaptive value of such eavesdropping seems clear.
515 At present, however, we do not know whether the information acquired by eavesdropping
primates differs significantly from the information acquired by individuals in other
species. Primates (and a few other mammals) may be qualitatively different from other
species in their ability to monitor the social relationships of many other individuals.
Alternatively, the societies of birds, fish, and other non-primate species – often
520 superficially simpler than those of primates – may have led us to underestimate the
information that individuals acquire about others. Finally, both hypotheses may have
some validity. There may be qualitative differences in 'social intelligence' between
different taxonomic groups, but within each group the information acquired from
eavesdropping may increase in sophistication with increasing social complexity. The
525 chapters in this volume demonstrate that eavesdropping is widespread among animals.
They set the stage for comparative research that examines differences between species in
the information acquired about others.

530 REFERENCES

- Aureli, F., Cozzolino, R., Cordischi, C. & Scucchi, S.** 1992. Kin-oriented redirection
among Japanese macaques: an expression of a revenge system? *Animal
Behaviour*, **44**, 283-291.
- 535 **Bachmann, C. & Kummer, H.** 1980. Male assessment of female choice in hamadryas
baboons. *Behavioral Ecology & Sociobiology*, **6**, 315-321.
- Barton, R.A. & Dunbar, R.** 1997. Evolution of the social brain. In: Machiavellian
Intelligence II: Extensions and Evaluations (Ed. by A. Whiten & R.W. Byrne), pp.
240-263. Cambridge: Cambridge University Press.

- 540 **Bradbury, J.W. & Vehrencamp, S.L.** 1998. *Principles of Animal Communication*.
Sunderland, MA: Sinauer Associates.
- Brannon, E. & Terrace, H.** 1998. Ordering of the numerosities 1 to 9 by monkeys.
Science, **282**, 746-749.
- Brooks, R.J. & Falls, J.B.** 1975. Individual recognition by song in white-throated
545 sparrows. III. Song features used in individual recognition. *Canadian Journal of
Zoology*, **53**, 1749-1761.
- Capaldi, E.J.** 1993. Animal number abilities: implications for a hierarchical approach to
instrumental learning. In: *The Development of Numerical Competence* (Ed. by
S.T. Boysen & E.J. Capaldi), 191-209. Hillsdale, NJ: Lawrence Erlbaum
550 Associates.
- Chapais, B.** 1988. Rank maintenance in female Japanese macaques: Experimental
evidence for social dependency. *Behaviour*, **104**, 41-59.
- Cheney, D.L. & Seyfarth, R.M.** 1980. Vocal recognition in free-ranging vervet
monkeys. *Animal Behaviour*, **28**, 362-367.
- 555 **Cheney, D.L. & Seyfarth, R.M.** 1982. Recognition of individuals within and between
groups of free-ranging vervet monkeys. *American Zoologist*, **22**, 519-529.
- Cheney, D.L. & Seyfarth, R.M.** 1986. The recognition of social alliances among vervet
monkeys. *Animal Behaviour*, **34**, 1722-1731.
- Cheney, D.L. & Seyfarth, R.M.** 1989. Reconciliation and redirected aggression in
560 vervet monkeys. *Behaviour*, **110**, 258-275.
- Cheney, D.L. & Seyfarth, R.M.** 1990. *How Monkeys See The World: Inside the Mind of
Another Species*. Chicago: University of Chicago Press.
- Cheney, D.L. & Seyfarth, R.M.** 1999. Recognition of other individuals' social
relationships by female baboons. *Animal Behaviour*, **58**, 67-75.
- 565 **Cheney, D.L., Seyfarth, R.M. & Silk, J.B.** 1995a. The responses of female baboons
(*Papio cynocephalus ursinus*) to anomalous social interactions: evidence for
causal reasoning? *Journal of Comparative Psychology*, **109**, 134-141.
- Cheney, D.L., Seyfarth, R.M. & Silk, J.B.** 1995b. The role of grunts in reconciling
opponents and facilitating interactions among adult female baboons. *Animal
570 Behaviour*, **50**, 249-257.

- Church, R.M. & Meck, W.H.** 1984. The numerical attribute of stimuli. In: *Animal Cognition* (Ed. by H.L. Roitblat, T.G. Bever, & H.S. Terrace), 445-464. Hillsdale, NJ: Lawrence Erlbaum Associates.
- 575 **Connor, R.C., Smolker, R.A. & Richards, A.F.** 1992. Dolphin alliances and coalitions. In: *Coalitions and Alliances in Humans and other Animals* (Ed. by A.H. Harcourt & F. de Waal), 415-443. Oxford: Oxford Univ. Press.
- Connor, R.C., Mann, J., Tyack, P.L. & Whitehead, H.** 1998a. Social evolution in toothed whales. *Trends in Ecology and Evolution*, **13**, 228-232.
- 580 **Connor, R.C., Mann, J., Tyack, P.L. & Whitehead, H.** 1998b. Reply. *Trends in Ecology and Evolution*, **13**, 408.
- Connor, R.C., Heithaus, R.M. & Barre, L.M.** 1999. Superalliance of bottlenose dolphins. *Nature*, **371**, 571-572.
- Connor, R.C., Heithaus, R.M. & Barre, L.M.** 2001. Complex social structure, alliance stability, and mating access in a bottlenose dolphin 'super-alliance'. *Proceedings of the Royal Society of London, B*, **268**, 263-267.
- 585 **D'Amato, M., Salmon, P. & Colombo, M.** 1985. Extent and limits of the matching concept in monkeys (*Cebus apella*). *Journal of Experimental Psychology: Animal Behavior Processes*, **11**, 35-51.
- D'Amato, M. & Colombo, M.** 1989. Serial learning with wild card items by monkeys (590 *Cebus apella*): implications for knowledge of ordinal rank. *Journal of Comparative Psychology*, **103**, 252-261.
- Dasser, V.** 1988a. A social concept in Java monkeys. *Animal Behaviour*, **36**, 225-230.
- Dasser, V.** 1988b. Mapping social concepts in monkeys. In: *Machiavellian Intelligence: Social Expertise and the Evolution of Intellect in Monkeys, Apes, and Humans* (Ed. by R.W. Byrne and A. Whiten), 85-93. Oxford: Oxford University Press.
- 595 **Dunbar, R.** 1983. Structure of gelada baboon reproductive units. III. The male's relationship with his females. *Animal Behaviour*, **31**, 565-575.
- Dunbar, R.** 2000. Causal reasoning, mental rehearsal, and the evolution of primate cognition. In: *The Evolution of Cognition. Vienna Series in Theoretical Biology* (Ed. by C. Heyes & L. Huber), 205-219. Cambridge, MA: MIT Press.
- 600

- Ehmer, B., Reeve, H.K. & Hoy, R.R.** 2001. Comparison of brain volumes between single and multiple foundresses in the paper wasp *Polistes dominulus*. *Brain, Behavior & Evolution*, **57**, 161-168.
- Emlen, S.T., Wrege, P.H., & Demong, N.J.** 1995. Making decisions in the family: an evolutionary perspective. *American Scientist*, **83**, 148-157.
- 605 **Engh, A.L., Esch, K., Smale, L. & Holekamp, K.E.** 2000. Mechanisms of maternal rank 'inheritance' in the spotted hyaena, *Crocuta crocuta*. *Animal Behaviour*, **60**, 323-332.
- Engh, A.L., Siebert, E., Greenberg, D. & Holekamp, K.** In press. Primate-like cognition in a social carnivore.
- 610 **Fagot, J., Wasserman, E.A. & Young, M.** 2001. Discriminating the relation between relations: the role of entropy in abstract conceptualization by baboons (*Papio papio*) and humans (*Homo sapiens*). *Journal of Experimental Psychology: Animal Behavior Processes*, **27**, 316-328.
- 615 **Gillan, D.J.** 1981. Reasoning in the chimpanzee, II. Transitive inference. *Journal of Experimental Psychology : Animal Behavior Processes*, **7**, 150-164.
- Gouzoules, S., Gouzoules, H. & Marler, P.** 1984. Rhesus monkey (*Macaca mulatta*) screams: Representational signalling in the recruitment of agonistic aid. *Animal Behaviour*, **32**, 182-193.
- 620 **Harlow, H.F.** 1949. The formation of learning sets. *Psychological Review*, **56**, 51-65.
- Hansen, E.W.** 1976. Selective responding by recently separated juvenile rhesus monkeys to the calls of their mothers. *Developmental Psychobiology* **9**, 83-88.
- Harcourt, A.H.** 1988. Alliances in contests and social intelligence. In: *Machiavellian Intelligence: Social Expertise and the Evolution of Intellect in Monkeys, Apes, and Humans* (Ed. by R.W. Byrne & A. Whiten), 132-152. Oxford: Oxford University Press.
- 625 **Harcourt, A.H.** 1992. Coalitions and alliances: are primates more complex than non-primates? In: *Coalitions and Alliances in Humans and Other Animals* (Ed. by A.H. Harcourt & F. de Waal). New York: Oxford University Press.
- 630 **Hauser, M.D., MacNeilage, P. & Ware, M.** 1996. Numerical representations in primates. *Proceedings of the National Academy of Sciences*, **93**, 1514-1517.

- Herman, L.M, Pack, A.A, & Morrel-Samuels, P.** 1993. Representational and conceptual skills of dolphins. In: *Comparative Cognition and Neuroscience* (Ed. by H.L. Roitblat, L.M. Herman, & P.E. Nachtigall), 403-442. Hillsdale, NJ: Lawrence Erlbaum Associates.
- 635
- Herrnstein, R.J.** 1985. Riddles of natural categorization. *Philosophical Transactions of the Royal Society of London, B*, **308**, 129-144.
- Hogue, M.E., Beaugrand, J.P. & Laugue, P.C.** 1996. Coherent use of information by hens observing their former dominant defeating or being defeated by a stranger.
- 640 *Behavioural Processes*, 38, 241-252.
- Holekamp, K.E., Boydston, E.E., Szykman, M., Graham, I., Nutt, K.J., Birch, S., Piskiel, A. & Singh, M.** 1999. Vocal recognition in the spotted hyaena and its possible implications regarding the evolution of intelligence. *Animal Behaviour*, **58**, 383-395.
- 645 **Judge, P.** 1982. Redirection of aggression based on kinship in a captive group of pigtail macaques. *International Journal of Primatology*, **3**, 301.
- Kummer, H., Goetz, W., & Angst, W.** 1974. Triadic differentiation: an inhibitory process protecting pair bonds in baboons. *Behaviour*, **49**, 62-87.
- Marino, L.** 1988. Quantifying brain-behavior relations in cetaceans and primates. *Trends in Ecology and Evolution*, **13**, 408.
- 650 **Martin, R.D.** 1983. *Primate Origins and Evolution: A Phylogenetic Reconstruction*. Princeton: Princeton Univ. Press.
- Matsuzawa, T.** 1985. Use of numbers by a chimpanzee. *Nature*, **315**, 57-59.
- McGregor, P. K. & Dabelsteen, T.** 1996. Communication net-works. In: *Ecology and Evolution of Acoustic Communication in Birds* (Eds. D. E. Kroodsma & E. H. Miller), 409-425. New York: Cornell University Press.
- 655 **Mennill, D.J., Ratcliffe, L.M. & Boag, P.T.** 2002. Female eavesdropping on male song contests in songbirds. *Science*, **296**, 873.
- Mercado, E., Killebrew, D.A., Pack, A.A., Macha, I., & Herman, L.M.** 2000.
- 660 Generalization of 'same-different' classification abilities in bottlenosed dolphins. *Behavioural Processes*, **50**, 79-94.

- Naguib, M., Fichtel, C. & Todt, D.** 1999. Nightingales respond more strongly to vocal leaders of simulated dyadic interactions. *Proceedings of the Royal Society of London B*, **266**, 537-542.
- 665 **Oden, D. Thompson, R. & Premack, D.** 1988. Spontaneous transfer of matching by infant chimpanzees (*Pan troglodytes*). *Journal of Experimental Psychology: Animal Behavior Processes*, **14**, 140-145.
- Ogawa, H.** 1995. Recognition of social relationships in bridging behavior among Tibetan macaques (*Macaca thibetana*). *American Journal of Primatology*, **35**, 305-310.
- 670 **Oliveira, R.F., McGregor, P.K., & Latruffe, C.** 1998. Know thine enemy: fighting fish gather information from observing conspecific interactions. *Proceedings of the Royal Society of London B*, **265**, 1045-1049.
- Palombit, R.A., Seyfarth, R.M., & Cheney, D.L.** 1997. The adaptive value of “friendships” to female baboons: Experimental and observational evidence.
- 675 *Animal Behaviour*, **54**, 599-614.
- Palombit, R.A., Cheney, D.L., & Seyfarth, R.M.** 2001. Female-female competition for male “friends” in wild chacma baboons (*Papio cynocephalus ursinus*). *Animal Behaviour*, **61**, 1159-1171.
- Peake, T.M., Terry, A.M.R., McGregor, P.K. & Dabelsteen, T.** 2001. Male great tits eavesdrop on simulated male-male vocal interactions. *Proceedings of the Royal Society B*, **268**, 1183-1187.
- 680 **Pepperberg, I.M.** 1992. Proficient performance of a conjunctive, recursive task by an African gray parrot (*Psittacus erithacus*). *Journal of Comparative Psychology*, **106**, 295-305.
- 685 **Pepperberg, I.M.** 1994. Numerical competence in an African gray parrot (*Psittacus erithacus*). *Journal of Comparative Psychology*, **108**, 36-44.
- Popp, J.W.** 1987. Choice of opponents during competition for food among American goldfinches. *Ethology*, **75**, 31-36.
- Premack, D.** 1983. The codes of man and beast. *Behavioral and Brain Sciences*, **6**, 125-
690 167.
- Schusterman, R.J. & Gisiner, R.** 1988. Artificial language comprehension in dolphins and sea lions: the essential cognitive skills. *Psychological Record*, **38**, 311-348.

- 695 **Schusterman, R.J. & Krieger, K.** 1986. Artificial language comprehension and size transposition by a California sea lion (*Zalophus californianus*). *Journal of Comparative Psychology*, **100**, 348-355.
- Seyfarth, R.M.** 1978. Social relationships among adult male and female baboons. II. Behavior throughout the female reproductive cycle. *Behaviour*, **64**, 227-247.
- Shettleworth, S.** 1998. *Cognition, Evolution, and Behaviour*. Oxford: Oxford University Press.
- 700 **Silk, J.B.** 1987. Social behavior in evolutionary perspective. In: *Primate Societies* (Ed. by B.B. Smuts, D.L. Cheney, R.M. Seyfarth, R.W. Wrangham & T. Struhsaker), 318-329. Chicago : Univ. Of Chicago Press.
- Silk, J.B.** 1993. Does participation in coalitions influence dominance relationships among male bonnet macaques? *Behaviour*, **126**, 171-189.
- 705 **Silk, J.B.** 1999. Male bonnet macaques use information about third-party rank relationships to recruit allies. *Animal Behaviour*, **58**, 45-51.
- Silk, J.B., Seyfarth, R.M., & Cheney, D.L.** 1999. The structure of social relationships among female savanna baboons. *Behaviour*, **136**, 679-703.
- 710 **Smale, L., Frank, L.G., & Holekamp, K.E.** 1993. Ontogeny of dominance in free-living spotted hyaenas: Juvenile rank relations with adult females and immigrant males. *Animal Behaviour*, **46**, 467-477.
- Smuts, B.** 1985. *Sex and Friendship in Baboons*. Chicago: Aldine.
- Tomasello, M. & Call, J.** 1997. *Primate Cognition*. Oxford: Oxford University Press.
- 715 **Treichler, F. & Van Tilburg, D.** 1996. Concurrent conditional discrimination tests of transitive inference by macaque monkeys: List linking. *Journal of Experimental Psychology, Animal Behavior Processes*, **22**, 105-117.
- Von Fersen, L., Wynne, C., Delius, J. & Staddon, J.** 1991. Transitive inference formation in pigeons. *Journal of Experimental Psychology: Animal Behavior Processes*, **17**, 334-341.
- 720 **Walters, J.R. & Seyfarth, R.M.** 1987. Conflict and cooperation. In : *Primate Societies* (Ed. by B.B. Smuts, D.L. Cheney, R.M. Seyfarth, R.W. Wrangham & T. Struhsaker), 306-317. Chicago : Univ. Of Chicago Press.

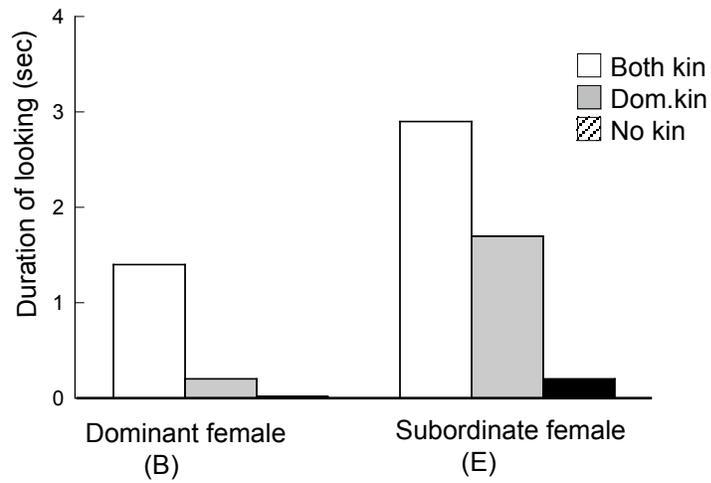
- 725 **Wasserman, E.A., Hugart, J.A., & Kirkpatrick-Steger, K.** 1995. Pigeons show same-different conceptualization after training with complex visual stimuli. *Journal of Experimental Psychology: Animal Behavior Processes*, **21**, 248-252.
- Wright, A., Cook, R., & Rivera, J.** 1988. Concept learning by pigeons: matching to sample with trial-unique video picture stimuli. *Animal Learning and Behavior*, **16**, 436-444
- 730 **Zentall, T., Weaver, J. & Sherburne, L.** 1996. Value transfer in concurrent-schedule discriminations by pigeons. *Animal Learning & Behavior*, **24**, 401-409.

FIGURES AND FIGURE LEGENDS

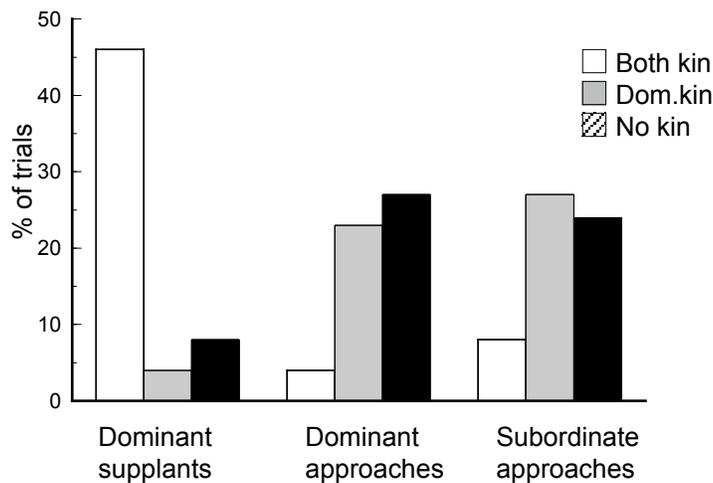
Figure 1. The protocol for playback experiments testing baboon females' recognition of other individuals' kin. B represents the more dominant of the subjects, E the more subordinate. B₁ and E₁ represent the subjects' close kin. B and D represent signallers unrelated to either subject.

	<u>Playback sequence</u>	<u>Subjects</u>
Test	B ₁ threat-grunt + E ₁ scream 	B and E
Control 1 (Dominant's kin)	B ₁ threat-grunt + D scream 	B and E
Control 2 (No kin)	A threat-grunt + C scream 	B and E

740 Figure 2. The duration that subject looked at each other following each type of playback .
sequence. Histograms show means \pm SD for 26 dyads in each of the three conditions.



745 Figure 3. The proportion of subjects' first interactions with each other that took various forms following each playback sequence. Histograms show means for 26 dyads in each condition. 'Dominant supplant': The dominant subject approached and supplanted the more subordinate subject. 'Dominant approaches': The dominant subject approached the subordinate subject without supplanting her and/or interacted with her in a friendly manner. 'Subordinate approaches': The subordinate subject approached the dominant subject and/or interacted with her in a friendly manner.



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