
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 form: a subject has the opportunity to monitor, or eavesdrop upon, an interaction between two other animals, A and B. 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; Ch. 2). For example, Oliveira *et al.* (1998) found that male fighting fish *Betta splendens* that had witnessed two other males involved in an aggressive interaction subsequently responded more strongly to 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 responded equally strongly to the winner and the loser of competitive interactions they had not observed. Similarly, Peake *et al.* (2001) presented male great tits *Parus major* with the opportunity 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 strongly to singers that had apparently just 'lost' the interaction (see also McGregor & Dabelsteen, 1996; Naguib *et al.*, 1999; Ch. 2).

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 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 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 (reviewed by Bradbury & Vehrencamp, 1998), 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, which 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.





	<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

Fig. 25.1. The protocol for playback experiments testing baboon females' recognition of other individuals' kin. B, the more dominant of the subjects; E, the more subordinate; B₁ and E₁, the subjects' close kin; A, C and D, signallers unrelated to either subject.

Knowledge about other animals' kin

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 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. 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 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. 25.1). 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 trials, the same two subjects also heard two control sequences of calls (Fig. 25.1). 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).

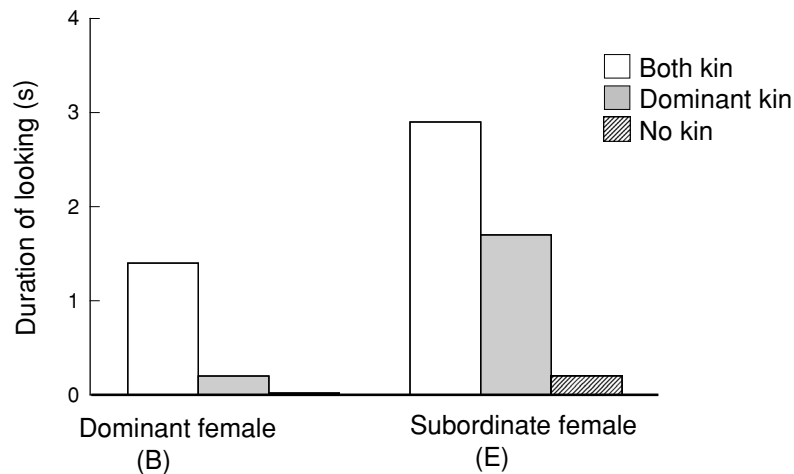


Fig. 25.2. The duration that the subject looked at the other female following each type of playback sequence. Histograms show means for 26 dyads in each of the three conditions.

After hearing the test sequence, a significant number of subjects looked toward the other female (Fig. 25.2), 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 subject tended to look at her partner (Fig. 25.2). Following the second control sequence, when neither of the subjects' relatives was involved, neither subject looked at the other (Fig. 25.2). Finally, following a significant proportion of test sequences, the dominant subject approached and supplanted (a mild form of aggression) the subordinate (Fig. 25.3). In contrast, when the two subjects approached each other following the two control sequences, the dominant rarely supplanted the subordinate (Fig. 25.3).

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 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

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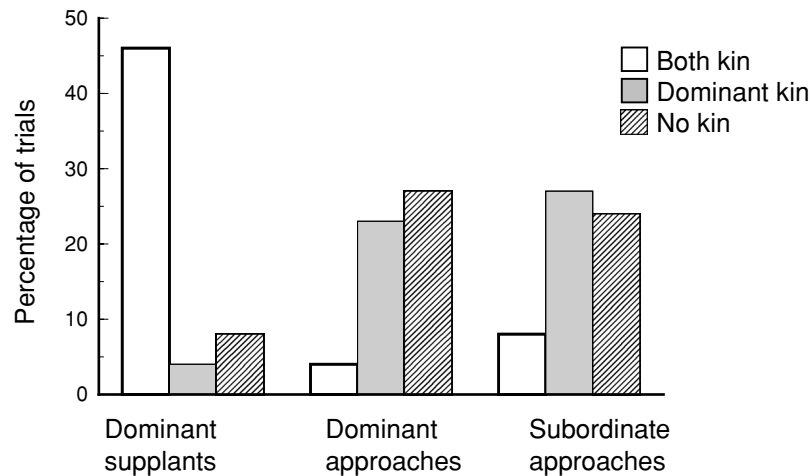


Fig. 25.3. The percentage of subjects' first interactions with each other that took various forms following each playback sequence. Histograms show means for 26 dyads in each condition. Dominant supplants indicates that the dominant subject approached and supplanted the more subordinate subject. Dominant approaches indicates that the dominant subject approached the subordinate subject without supplanting her and/or interacted with her in a friendly manner. Subordinate approaches indicates that the subordinate subject approached the dominant subject and/or interacted with her in a friendly manner.

group and slides of 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 analogous to our concept of 'mother-child affiliation'. Dasser (1988a) was able to exclude 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 eavesdropping upon, their social interactions.

Under natural conditions, it is difficult to determine whether animals distinguish between 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 to recognize different categories of social affiliation, Dasser (1988b) trained a long-tailed macaque to identify a pair of siblings from

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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-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.

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 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). Kazem & Aureli (Ch. 10) further discuss the relationship between redirected aggression and communication networks.

Knowledge about other animals' dominance ranks

Dominance ranks offer another opportunity to test whether non-human primates gain information about other animals' relationships by eavesdropping on their social interactions. Like matrilineal kinship, linear, transitive dominance relations are a 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 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.

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 recognize the rank relations that exist among other 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 approach without a grunt (Cheney *et al.*, 1995a). 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 female 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. 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 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.*, 1995b).

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.

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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 & Colombo, 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 so far focus 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 bond are relatively transient, and some rank relationships – particularly among adult males – change often. Nonetheless, there is evidence that non-human primates also recognize these more transient associations.

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' 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 savannah 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 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 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') behaviour, Ogawa (1995) observed that males more frequently provided other males with those males' affiliated infants than with 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 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 (approximately 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, approximately half of the 16 males changed dominance rank each month (data from Table 3 in Silk, 1993). 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.

Eavesdropping by other mammals

Data from dolphins *Tursiops truncatus* and hyaenas *Crocuta crocuta* suggest that non-human primates are not the only mammals in which individuals acquire information about many different individuals' social relationships (for other mammals see Chs. 17 and 18). 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, hyaenas live in social groups comprising matrilineal lines 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, hyaena females responded more strongly to the calls of their own offspring and those of close relatives than to the calls of unrelated cubs. In contrast to vervets and baboons, however, unrelated females did not look at the cubs' mothers. One explanation for these negative results is that hyaenas 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 hyaenas are simply uninterested in the calls of unrelated cubs.

In fact, hyaenas' 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, hyaenas often solicit alliance support from other, uninvolved individuals. When choosing to join ongoing skirmishes, hyaenas that are dominant to both of the contestants almost always support the more dominant of the two individuals (Engh *et al.*, 2004). Similarly, when the ally is intermediate in rank between the two opponents, it inevitably supports the dominant individual. These data provided the first evidence in 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 hyaenas are able to infer transitive rank relations among other group members.

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.

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.

The second hypothesis maintains that selection has favoured 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 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 intelligence'. Monkeys and hyaenas, for example, only appear to excel in their ability to recognize the relative ranks of allies and opponents 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 focused primarily on observers' ability to assess the dominance of only two individuals. Once monogamous and even solitary species have been given the 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 these alternative hypotheses; below we review some information that may be relevant.

Hypothesis 1: primates have greater social intelligence than other species

Primates have larger brains for their body size than other vertebrates (Martin, 1983). Dunbar (2000) argued that this arises because primate social groups are not only larger but also more complex than those of other taxa. Primate groups are typically 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 close associates of other individuals.

To date, only monkeys and possibly dolphins have been shown to recognize the 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 subgroups is likely to be relatively complex, for several reasons.

Matrilineal kin groups vary in size and not all individuals within a kin group 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, females in many monkey species 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 Silk, 1987; Walters & Seyfarth, 1987). There is no evidence, however, that other group members more easily recognize the kin (or close associates) of high-ranking individuals than the kin 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 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 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 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 males; conversely, the same male may form simultaneous friendships with females from two different matriline. 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' social relationships and dominance ranks increases exponentially. In a group of 80 animals (not an unusual size for many monkey species), each individual confronts 3160 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.

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 constitute 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 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 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' performances suggest 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 that look alike.

Judgements based on relations among items have been demonstrated more often in non-human 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 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).

Hypothesis 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 non-human 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 hyaenas and lacking or less evident in some ape species, including gorillas *Gorilla gorilla* and orangutans *Pongo pygmaeus*. Although recent evidence that hyaenas recognize other individuals' relative ranks lends 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, 1979). A similar relation is found in carnivores (Barton & Dunbar, 1997) and toothed whales (Connor *et al.*, 1998a,b; Marino, 1998), supporting the hypothesis that sociality has favoured 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 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 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, Alex, an African grey parrot *Psittacus erithacus*, is reported to make explicit same/different judgements about sets of objects (Pepperberg, 1992, Ch. 24). Similarly, sea lions *Zalophus californianus* (Schusterman & Krieger, 1986; Schusterman & Gisiner 1988) and dolphins (Herman *et al.* 1993; Mercado *et al.* 2000) have been taught to respond to terms such as 'left' and 'bright', which 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, 1993), are able to assess quantities, suggesting that relatively abstract concepts of numerosity and transitivity may be pervasive among animals (reviewed by Shettleworth, 1998).

Hypothesis 3: there are few differences in 'social intelligence' across species

Recent research on social eavesdropping (Ch. 2) 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 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. 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).

Recently, Bond *et al.* (2003) tested the prediction that socially living birds will display enhanced abilities to make transitive inferences by comparing the performance of highly social pinyon jays *Gymnorhinus cyanocephalus* with relatively non-social western scrub jays *Aphelocoma californica*. Using operant procedures, subjects were required to order a set of arbitrary stimuli by inference from a series of dyadic comparisons. Subjects of both species learned the sequence order, but pinyon jays did so more rapidly and more accurately than scrub jays. Although not conclusive, these results lend support to the hypothesis that social complexity may be correlated with superior performance in tasks involving the ranking of multiple stimuli (see also Hogue *et al.* (1996) for experiments with flock-dwelling domestic chickens *Gallus domesticus*).

As yet, very little is known about the ability of non-primate mammals or birds to recognize social relationships of other individuals. Colonial white-fronted bee-eaters *Merops bullockoides* offer one example of an avian society in which there would appear to be strong selective pressure for the recognition of the kin groups of other individuals. 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.

Clearly, more data are needed from both natural and laboratory studies before we can draw 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 result more from differences in the social context in which eavesdropping occurs than from 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 to those living in large social groups. It

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is to be hoped that future research will attempt to investigate the extent to 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

Non-human primates are skilled voyeurs. By observing or listening to the interactions of others, they acquire information about the social relationships of other individuals 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. At present, however, we do not know whether the information acquired by eavesdropping in 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 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 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.

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