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The Structure of Social Knowledge in Monkeys

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The chapters in this volume richly document the complex societies found in many animal species. In this chapter we explore the kinds of intelligence that might underlie social complexity.

Animal societies have been described as "socially complex" for many different reasons. Some, like the colonies of bees or wasps, involve thousands or even tens of thousands of individuals that behave differently toward others depending on colony membership, age, sex, caste, or reproductive state. The sheer size of these groups, and the intricate pattern of interaction among their members, have led some to describe them as "superorganisms" (Seeley 1995). Other animal societies, like those of the dolphins, whales, elephants, and primates described in this book, involve tens or hundreds of animals that recognize each other as individuals. The members of these societies behave differently toward one another depending on kinship, sex, dominance rank, reproductive condition, and their previous history of interaction. Categories cut across one another, and the social calculus required to survive and reproduce seems formidable indeed. Finally, the social behavior of monogamous and even solitary species has been described as complex because of the sophisticated ways in which individuals locate one another, and the intricate coordination and timing involved in mating and rearing offspring.

By itself, however, social complexity does not necessarily imply sophisti-

cated intelligence. Data from insects, together with experiments conducted by Schusterman and colleagues on sea lions (see Chapter 7) as well as many others, have shown clearly that complex societies and social relationships can be generated by relatively simple mechanisms. Indeed, if we have learned anything from decades of debate between behaviorists and cognitive scientists, it is that the same bit of behavior can be explained equally well in many different ways—some cognitively complex, others less so. Does a baboon that apparently knows the matrilineal kin relations of others in her group have a "social concept," as some have argued (e.g., Dasser 1988), or has the baboon simply learned to link individual A_1 with individual A_2 through a relatively simple process like associative conditioning, as others believe (e.g., Thompson 1995)? At present, the preferred explanation depends more upon the scientist's mind than upon any objective understanding of the baboon's.

As a benchmark for comparison with nonhuman species, human social intelligence is always lurking in the background. Humans have sophisticated ways of classifying each other and using these classifications to predict what others are likely to do. Somehow, during the course of human evolution, these cognitive skills were favored by natural selection. How did this occur? How might we have gotten from the relatively simple learning mechanisms proposed by Schusterman and colleagues (Chapter 7) and others to the sort of complex social intelligence we see in humans today?

We begin with a brief review of data on the recognition of social relations in monkeys. We ask: What must a monkey know, and how must its knowledge be structured, in order to account for its behavior? We then review two hypotheses derived from studies of laboratory animals—one offered to explain primate social knowledge, another not—and consider their strengths and limitations. Our goal is to uncover a model of social intelligence that both accounts for existing behavior and explains why, during the course of evolution, some cognitive strategies gained an evolutionary advantage over others.

Knowledge of Other Animals' Kin Relations

East African vervet monkeys *(Cercopithecus aethiops)* live in groups of 10–30 individuals. Each group occupies a territory that is surrounded by the territories of other vervet groups. A typical group contains three to seven adult males, together with five to eight adult females and their offspring. When young males reach adult size between five and six years of age, they emigrate to a neighboring group. Females remain in the group where they were born throughout their lives and form close, long-lasting bonds with their matrilineal relatives. Adult female vervets and their offspring can be arranged in a linear dominance hierarchy in which offspring rank immediately below their mothers. The stable core of a vervet social group, then, is a hierarchy of matrilineal families (Cheney & Seyfarth 1990).

Most affinitive social interactions, such as grooming, mutual tolerance at feeding sites, and the formation of aggressive alliances, occur within families (Seyfarth 1980; Whiten 1983; reviewed in Cheney & Seyfarth 1990). Clearly, individuals distinguish their own close matrilineal relatives from all others because their behavior toward them is so different. For a monkey to achieve a complete understanding of her society, however, she must be able to step outside her own sphere of interactions and recognize the relations that exist among others (Cheney & Seyfarth 1986; Harcourt 1988). Such knowledge can only be obtained by observing interactions in which oneself is not involved and making the appropriate inferences (Cheney & Seyfarth 1990). There is, in fact, growing evidence that monkeys do possess knowledge of other animals' social relationships and that such knowledge affects their behavior.

Evidence that vervet monkeys recognize other animals' social relations first emerged as part of a relatively simple playback experiment designed to document individual recognition by voice (Cheney & Seyfarth 1980). We had noticed that mothers often ran to support their juvenile and infant offspring when these individuals screamed during rough play. This observation, like many other studies (e.g., Hansen 1976; see also 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 two-year-old juvenile to a group of three adult females, one of whom was the juvenile's mother. As expected, mothers consistently looked toward or approached 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. They behaved as if they recognized the close social bonds that existed between particular juveniles and particular adult females (Cheney & Seyfarth 1980, 1982).

In an attempt to replicate these results, we recently carried out a similar set of experiments on free-ranging baboons *(Papio cynocephalus ursinus)* in the Okavango Delta of Botswana (for details of the study area and subjects, see Hamilton et al. 1976; Cheney et al. 1995a; Silk et al. 1999). The social orga-

nization of baboons is similar to that of vervets. In these experiments, two unrelated females were played a sequence of calls that mimicked a fight between each of their close relatives. The females' immediate responses to the playback were videotaped, and both subjects were also followed for 15 minutes after the playback to determine whether their behavior was affected by the calls they had heard. In separate trials, the same two subjects also heard two control sequences of calls. 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 the other female, suggesting that they recognized not just the calls of unrelated individuals, but also those individuals' kin (or close associates). Moreover, in the minutes following playback, dominant subjects were significantly more likely to supplant subordinate subjects, suggesting that the dominant female's behavior toward others was influenced by her perception of whether one of her own relatives and another individual's relative had recently been involved in a fight. 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 looked at her partner. Following the second control sequence, when neither of the subjects' relatives was involved, neither subject looked at the other. Finally, following both control sequences, the two subjects were significantly more likely to approach each other and interact in a friendly manner than following the test sequence.

Taken together, these experiments argue that baboons and vervet monkeys recognize the individual identities of even unrelated group members. Moreover, they appear to view their social groups not just in terms of the individuals that comprise them but also in terms of a web of social relationships in which certain individuals are linked with several others. Their behavior is influenced not only by their own recent interactions with others but also by the interactions of their close associates with other individuals' close associates.

Other studies provide additional evidence of monkeys' abilities to distinguish both their own and other individuals' close associates. For example, in a playback study using the contact calls of rhesus macaques *(Macaca mulatta)*, Rendall and colleagues (1996) found that females not only distinguish the identities of different signalers but also categorize signalers according to matrilineal kinship. Similarly, in an experiment performed on captive long-tailed macaques *(Macaca fascicularis)*, Dasser (1988) trained a female subject to choose between slides of one mother-offspring pair and slides of two unrelated individuals. Having been trained to respond to one mother-offspring pair, the subject was then tested with 14 novel slides of different mothers and offspring paired with an equal number of novel pairs of unrelated animals. In all tests, she correctly selected the mother-offspring pair. In so doing, she appeared not to rely on physical similarity (compare Parr & de Waal 1999), but instead, Dasser argued, classified individuals on the basis of an abstract category analogous to our concept of "mother-child affiliation."

In each of these studies, animals that were grouped into familial associations nonetheless retained their individual identities: a mother and her offspring, for example, were judged to be alike in belonging to the same family but still recognized as distinct individuals.

Finally, in many species of monkeys, 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 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).

Kin-biased redirected aggression also appears in more complex forms. In two different vervet groups studied over two different time periods, we found that a female was more likely to threaten another individual if one of her own close relatives and one of her opponent's close relatives had recently been involved in a fight (Figure 8.1; Cheney & Seyfarth 1986, 1989). These results support Dasser's (1988) contention that monkeys recognize that certain types of social relationships share similar characteristics. When a vervet monkey (A_2 in Figure 8.1) threatens B_2 following a fight between one of her own relatives (A_1) and one of her opponent's relatives (B_1), A_2 acts as if she recognizes that the relationship between B_2 and B_1 is in some way similar to her own relationship with A_1 (Cheney & Seyfarth 1990). In a similar manner, when a baboon female hears a playback sequence mimicking a fight be-
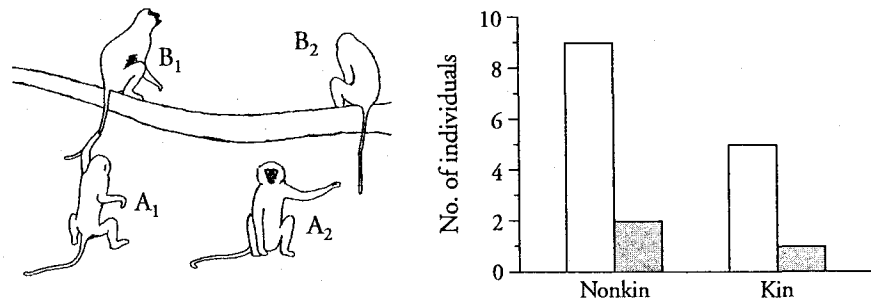
Figure 8.1. Redirected aggression in vervet monkeys. Open histograms show the number of individuals who behaved more aggressively toward an opponent after a fight between one of their own relatives and one of their opponent's relatives than during a matched control period. Shaded histograms show the number of individuals who were as likely to act aggressively after a fight as during the matched control period. Drawing by John Watanabe. From Cheney & Seyfarth (1990), with permission.

tween her own relative and the relative of another female, this temporarily increases the likelihood that her subsequent interactions with that female will be antagonistic (Cheney & Seyfarth 1999).

Knowledge of Other Animals' Dominance Ranks

Along with matrilineal kinship, linear, transitive dominance relations are a pervasive feature of social behavior in groups of Old World monkeys. And like matrilineal kin relations, dominance relations provide human observers with an opportunity to explore what monkeys know about their companions. A linear, transitive rank order might emerge because individuals can recognize the transitive dominance relations that exist among others: A is dominant to B and B is dominant to C, therefore A must be dominant to C. Alternatively, monkeys might simply recognize who is dominant or subordinate to themselves. In the latter case, a transitive, linear hierarchy would emerge as the incidental outcome of paired interactions. The hierarchy would be a product of the human mind, but not exist in the minds of the monkeys themselves.

There is evidence, however, that monkeys do recognize the rank relations that exist among others 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. The grunts seem to function to fa-

cilitate 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. 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 female subjects were played a causally inconsistent call sequence in which a lower-ranking female apparently grunted to a higher-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 others. 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. Subjects responded to all playbacks by looking toward the speaker, but did so for significantly longer durations to the causally inconsistent sequences. This consistent difference in response suggests that they recognize not only the identities of different signalers, but also the rank relations that exist among others in their group (Cheney et al. 1995a).

Further evidence that monkeys recognize other individuals' ranks comes from cases in which adult female vervet monkeys compete with one another for access to a grooming partner (Seyfarth 1980). Such competition occurs whenever one female approaches two that are grooming, supplants one of them, and then grooms with the female that remains. In a small proportion of cases, this competition takes a form that is especially interesting for our present purposes. As shown in Figure 8.2, a high-ranking female (ranked 2, for example) approaches two groomers who are both subordinate to herself (say, females ranked 4 and 5). Though 4 and 5 both rank lower than 2, they are not equally likely to depart. In a significant number of cases, the higher-ranking of the two females remains seated, while the lower-ranking of the two moves away (Cheney & Seyfarth 1990).

In so doing, the higher-ranking of the two females acts as if she recognizes that, although she is lower-ranking than the approaching female, her grooming partner is even more subordinate. In order to accomplish this ranking, a female must know not only her own status relative to other individuals but
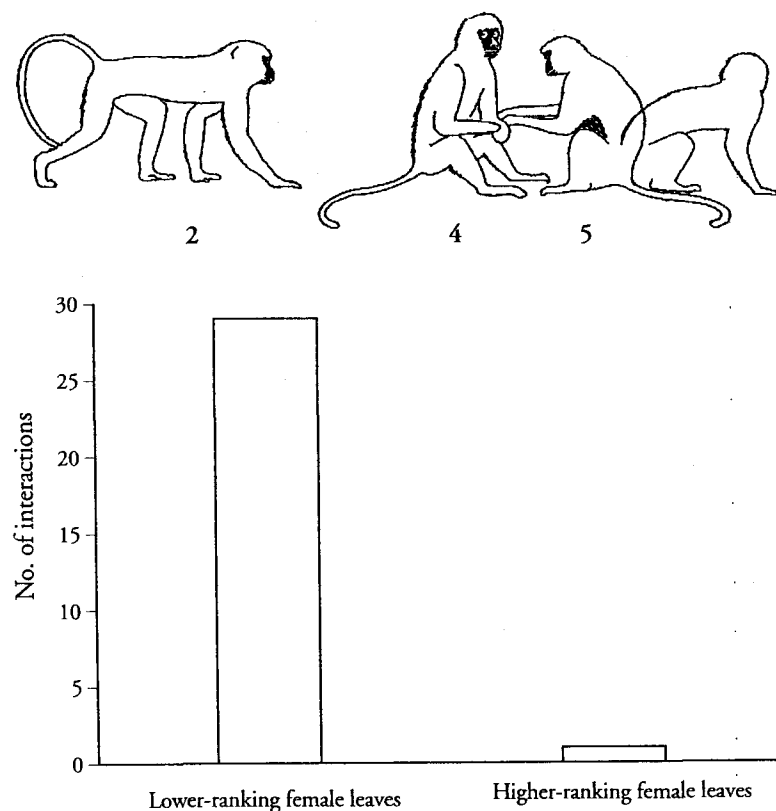
Figure 8.2. Competition over access to a grooming partner in vervet monkeys. Data are taken from all cases during 1985 and 1986 in which a high-ranking female (for example, female 2) approached two lower-ranking females (for example, females 4 and 5) and supplanted one individual and groomed the other. Drawing by John Watanabe. From Cheney & Seyfarth (1990), with permission.

also other individuals' status relative to each other. In other words, she must 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 1988), the amount of food contained within a container (Gillan 1981), their size, or the number of objects contained within an array (e.g., 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.

More Transient, Complicated Social Relations

Although male vervets, baboons, and macaques emigrate from their natal group at about the time of sexual maturity, female kin remain closely bonded throughout their lives. Similarly, dominance ranks among females and immatures are relatively unchanging, though an occasional upheaval may result in all of the members of one matriline rising in rank together (Samuels et al. 1987; Chapais 1988; Cheney & Seyfarth 1990; Gygax et al. 1997). It might seem, therefore, that an individual baboon, vervet, or macaque could simply learn her relative dominance rank early in life and thereafter navigate easily through familiar social terrain. This relatively stable social network is complicated, however, by many short-term, transient social relations that change often. These more temporary relationships cannot be ignored if an individual is to predict the behavior of others.

Male vervets, baboons, and macaques also form linear dominance hierarchies. Because dominance is determined primarily by age and fighting ability, however, rank relations are considerably less stable than they are among females (Walters & Seyfarth 1987). Nevertheless, males appear to recognize other individuals' relative ranks. For example, in a study of captive male 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 percent of all aggressive encounters). Silk found that males consistently solicited allies that outranked both themselves and their opponents. Silk's analysis ruled out simpler explanations based on the hypotheses that males chose allies that outranked themselves, or that males chose the highest-ranking individual in the group. 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 would not be a difficult task. However, during Silk's year-long study of 16 males, roughly half of the males changed dominance rank each month (data from Silk 1993, Table 3).

As a second example, consider the close bonds formed by lactating female baboons with resident adult males (Seyfarth 1978; Smuts 1985). Such "friendships" are particularly likely to occur after a new adult male has joined the group and rapidly risen to alpha status, and they typically endure until the female resumes sexual cycling. During this period, the female's friend intervenes on her behalf during aggressive encounters and also carries and protects her infant. Indirect evidence suggests that the male friend is often the infant's father (Bulger & Hamilton 1988; Palombit et al. 1997). One clear function of male-female friendships is to protect the female's infant from infanticide (Palombit et al. 1997).

Other group members seem to recognize the friendships that exist between particular females and particular males. Having been threatened by a more dominant male, for example, subordinate males will sometimes redirect aggression toward that male's female friend (Smuts 1985). In so doing, they act as if they recognize the close bond that exists between the two individuals.

Female members of the same matriline do not necessarily form friendships with the same male. A male often maintains simultaneous friendships with two females of different ranks and from different matrilines (Palombit et al. 1997, 2000). Although the definitive experiments have not yet been conducted, other baboons appear to recognize these patterns of association. A baboon who recognizes that females A_1 and A_2 associate at high rates, and that female A_2 and male X associate at high rates, does not act as if she expects female A_1 and male X also to associate at high rates. Instead, she identifies female A_1 with an entirely different male. Females A_1 and A_2, in other words, are not treated as interchangeable just because they belong to the same matrilineal kin group; instead, baboons seem to recognize that the same individual can simultaneously belong to more than one class.

Underlying Mechanisms

If the data just reviewed had come from a study of children in a nursery school, we would not hesitate to conclude that individuals divide their social companions into groups, that groups have a nested, hierarchical structure, and that the understanding of such relations is both complex and abstract.

Adult humans, for example, know that all the members of a matriarchy form a group, in the sense that they are more closely linked to one another than any one individual is to those outside the family. In their relations with others, the members of a matriarchy are in some respects interchangeable, but they also retain their own individual identities. Taken together, human family members exhibit a hierarchical structure in the sense that a parent, A_1, has a different relationship with her children $A_2 \ldots A_n$ than they do with each other, yet all parent-child relations share common properties that distinguish them from all sibling relations.

Human understanding of social relations is complex because it is not based on any one—or even a few—behavioral measures. Young children learn quickly that X and Y are friends even if they interact only rarely. And finally, human understanding of social relationships is abstract because we give names to types of relationships and can compare one type of relationship to another in a manner that is independent of the particular individuals involved. If someone mentions a sister, friend, or enemy, we immediately have some idea of her relationship with that person even if we have never met the individual involved.

Although human knowledge of social relationships is structured, complex, and abstract, there is no a priori reason to believe that the same mental operations underlie the social knowledge of monkeys and apes. In recent years, several authors (e.g., Heyes 1994; Thompson 1995; Schusterman & Kastak 1998) have argued that the complex behavior of nonhuman primates can be explained by relatively simple processes of associative learning and conditioning. Below we consider these arguments in light of the data just reviewed.

Equivalence Classes

Laboratory studies of equivalence class formation suggest that many animal species can be taught to place dissimilar stimuli into the same functional class. For example, Schusterman & Kastak (1993, 1998) taught a California sea lion, Rio, to group seemingly arbitrary stimuli into "equivalence classes." The stimuli were grouped together based on prior association, not physical similarity (for details see Chapter 7). Next, Rio was presented with one member from the A stimulus class and one from the B stimulus class, allowed to select one of the stimuli, and rewarded with food. Assuming Rio selected A_1 over B_1, she then received repeated presentations of the same stimuli, with A_1 rewarded and B_1 not rewarded, until she achieved a performance of 90 percent correct in a block of 10 consecutive trials (Schusterman &

Kastak 1993). Then Rio was tested with, for example, A_2 and B_2 (transfer test 1) or A_3 and B_3 (transfer test 2), to determine whether she had begun to treat all A stimuli as equivalent to each other and all B stimuli as equivalent to each other, at least insofar as they followed the rule "If $A_1 > B_1$ then $A_n >$ B_n." Rio performed correctly on 28 of 30 transfer tests, significantly above chance (Schusterman & Kastak 1998; see also Chapter 7).

The authors suggest that the kind of equivalence judgments demonstrated by Rio constitute a general learning process that underlies much of the social behavior of animals, including the recognition of social relationships. According to Schusterman and Kastak (1998) "both social and non-social features of the environment can become related through behavioral contingencies, becoming mutually substitutable even when sharing few or no perceptual similarities" (1998, p. 1088; see also Dube et al. 1993; Fields 1993; Heyes 1994; Sidman 1994; Wasserman & Astley 1994). Thus, for example, a baboon or vervet monkey learns to group members of the same matriline together because they share a history of common association and functional relations. And when one monkey threatens the close relative of a recent opponent, she does so because members of the same matriline have effectively become "interchangeable" (Schusterman & Kastak 1998, p. 1094). As a result of equivalence class formation, members of the same class are not only "mutually substitutable" but also exhibit "transitivity": if $A_1 > B_1$ and A_2 is a member of the same class as A_1 and B_2 is a member of the same class as B_1, then $A_2 > B_2$.

There is no doubt that associative processes provide a powerful and often accurate means for animals to assess the relationships that exist among different stimuli, including members of their own species. However, before rushing to conclude that nonhuman primate social knowledge can be explained entirely on the basis of learned behavioral contingencies (e.g., Heyes 1994), it seems worth pointing out several ways in which social relations among nonhuman primates do not conform to equivalence class relations.

No Single Behavioral Measure Underlies the Associations between Individuals

It is, of course, a truism that monkeys can learn which other individuals share a close social relationship by attending to patterns of association. Matrilineal kin, for example, almost always associate at higher rates than nonkin. But no single behavioral measure is either necessary or sufficient to recognize such associations. For example, aggression often occurs at as high a rate within families as it does between families, and different family members may groom each other and associate with each other at different rates (Cheney & Seyfarth 1986). To recognize that two individuals are closely bonded despite relatively high rates of aggression or relatively low rates of grooming, a monkey must take note of a variety of different patterns of aggression, reconciliation, grooming, and proximity. There is no threshold or defining criterion for a "close" social bond.

By contrast, the equivalence classes in Schusterman's & Kastak's (1998) experiments were established by repeatedly presenting arbitrary visual stimuli aligned in groups of three. Either spatial or temporal juxtaposition would therefore suffice as a basis for the formation of association of stimuli within an equivalence class.

As yet, we do not know if monkeys distinguish between matrilineal kin bonds and the equally strong bonds that may form between unrelated animals who interact at high rates (for example, male and female baboon "friends"). If monkeys do make such distinctions, this would argue that they assess and compare social relationships using a metric that is based on more than just patterns of association.

Class Members Are Sometimes Mutually Substitutable, Sometimes Not

In discussing the experiment in which an adult female vervet hears a juvenile's scream and then looks at the juvenile's mother (Cheney & Seyfarth 1980), Schusterman & Kastak (1998) argue "that the existing relation between the scream, the juvenile itself, and the frequent association between the infant [sic] and its mother resulted in a three-member equivalence class" (1998, p. 1093). As a result, they are treated the same—not because they have become indistinguishable (Schusterman and colleagues, Chapter 7) but because one stimulus can be substituted for another without violating the associative link that has been formed between them. But in fact the call, the juvenile, and the mother are not interchangeable in this manner. Although listeners may place these stimuli in the same class under some circumstances, the call itself is linked primarily to the juvenile and only secondarily to the mother. In habituation/dishabituation experiments on rhesus macaques, monkeys both distinguished calls from different matrilines and distinguished among the calls of different individuals within the same matriline (Rendall et al. 1996).

Some Social Relationships Are Transitive, Others Are Not

If infant A_1 and juvenile A_2 both associate at high rates with a particular adult female, it is usually correct to infer that the juvenile and infant are also closely bonded and will support one another in an aggressive dispute (e.g., Altmann et al. 1996). Similarly, if A is dominant to B and B is dominant to C, it is usually correct to infer that A is dominant to C (Cheney & Seyfarth 1990). By contrast, 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, it would be correct to assume that the male is closely allied to the infant but incorrect to assume that he is equally closely allied to the juvenile. Male baboon friends form close bonds with their female's infant but not with any other of her older offspring (Seyfarth 1978; Smuts 1985; Palombit et al. 1997). To cite another example mentioned earlier, female members of the same matriline often form friendships with different males, and, conversely, the same male may form simultaneous friendships with females from two different matrilines. In the former case, a close bond between female A_1 and female A_2, and between female A_1 and male X, does not imply that A_2 and X are closely linked. In the latter case, the existence of close bonds between male X and females A_1 and C_1 do not predict a close bond between the two females. In fact, their relationship is more likely to be competitive than friendly (Palombit et al. 2000).

Individuals May Belong to Multiple Classes Simultaneously

As the previous examples make clear, at any one time an individual monkey belongs simultaneously to many different classes. An adult female, for example, belongs to a matrilineal kin group, associates with one or more adult males, holds a particular dominance rank, and may be weakly or strongly linked to other females outside her matriline. Again, the natural situation is considerably more complex than that in Schusterman's and Kastak's experiment.

Class Membership Changes Often

Whereas female dominance rank and membership in a kin group constitute relatively stable, predictable behavioral associations, other social relationships change often and unpredictably. For example, we know from field experiments that closely related vervet monkeys groom and support one another in alliances at rates much higher than those for nonkin. Unrelated animals, however, are more attentive to another individual's recruitment call if they have recently engaged in a grooming interaction than if they have not (Seyfarth & Cheney 1984). Thus the social relations among nonkin wax and wane throughout the day, with transient periods when they resemble the bonds among kin and many other times when they do not.

Considering a slightly longer time scale, when female vervets or baboons give birth, they often become extremely attractive to other females, who groom them at high rates and attempt to interact with their infants (Seyfarth 1976, 1977, 1980; Altmann 1980; Silk et al. 1999). The change in the rate of grooming received is particularly pronounced for females of low rank, who otherwise receive little attention from higher-ranking individuals. The low-ranking mother's dominance rank, however, does not change. Moreover, as her infant matures, her attractiveness to others diminishes. Similarly, when a low-ranking female forms a close friendship with a dominant male, she gains access to feeding sites from which she might normally be excluded by higher-ranking females. This preferential access disappears, however, when the friendship is terminated (Seyfarth 1978; Smuts 1985; Palombit et al. 2000).

Finally, consider the problem faced by a male bonnet macaque who, in order to recruit the most useful allies, must keep track of transitive rank relations among 16 male companions in a group in which half of the males change rank each month (Silk 1993).

Training May Distort an Animal's Natural Method of Classification

In Schusterman's and Kastak's experiment, as in many other studies, the subject was first presented with stimuli that had links to one another (A_1, A_2, A_3) and then rewarded for choosing stimuli from one class over stimuli from another ($A_1 > B_1$). Thus trained, the subject generalized her knowledge such that, when presented with any other AB stimulus pair, she always chose A. Speaking conservatively, these results tell us only that, when presented with certain stimuli and rewarded for following a particular rule with a subset, a sea lion will generalize the rule and apply it to all of the other members of that subset. The experiment does not tell us whether, in the absence of train-

ing and reward, the sea lion would naturally recognize this particular rule, or, if she did recognize it, whether she would apply it generally beyond her immediate experience.

The distinction between learning that is rewarded in the laboratory and learning that occurs in the wild is important, because any intervention by humans that selectively rewards one kind of learning over another potentially distorts an animal's natural method of acquiring and storing information. For example, pigeons trained to match to sample with just a few stimuli are not able to transfer to novel stimuli, although monkeys and chimpanzees do so easily. However, pigeons do learn to match similar stimuli if they are trained with hundreds of exemplars over hundreds of trials. Apparently, although pigeons can acquire the abstract concept same/different, they seem predisposed to attend to absolute stimulus properties and to form item-specific associations (Wright et al. 1988; see also Wasserman et al. 1995; Shettleworth 1998). Extensive human training, therefore, leads to qualitative changes in the ways in which pigeons classify stimuli. Similarly, Tomasello and colleagues compared the performance of chimpanzees raised by humans (but without language training), chimpanzees raised by their own mothers, and two-year-old children. Human-reared chimpanzees showed more imitation (Tomasello et al. 1993), more joint attention, and were more likely to use gestures to direct the demonstrator's attention (Carpenter et al. 1995) than did chimpanzees raised by their own mothers. In another study, chimpanzees that had been trained to use tokens as symbols were able to solve match-to-sample tasks that required them to judge relations between relations. Naïve chimpanzees could perceive these relations but their knowledge seemed to remain tacit (Premack 1983; Thompson & Oden 1995). Mere exposure to humans, therefore, enhances chimpanzees' problem-solving skills, either by changing their attention and motivation or altering their cognitive abilities.

The Magnitude of the Problem

In Schusterman's and Kastak's experiment, Rio was confronted with a total of 180 dyadic comparisons. This is roughly equivalent to the number of different dyadic comparisons—but not the number of triads—that confront a monkey in a group of 18 individuals. As shown in Figure 8.3, however, the number of possible dyads and triads increases rapidly as group size increases.
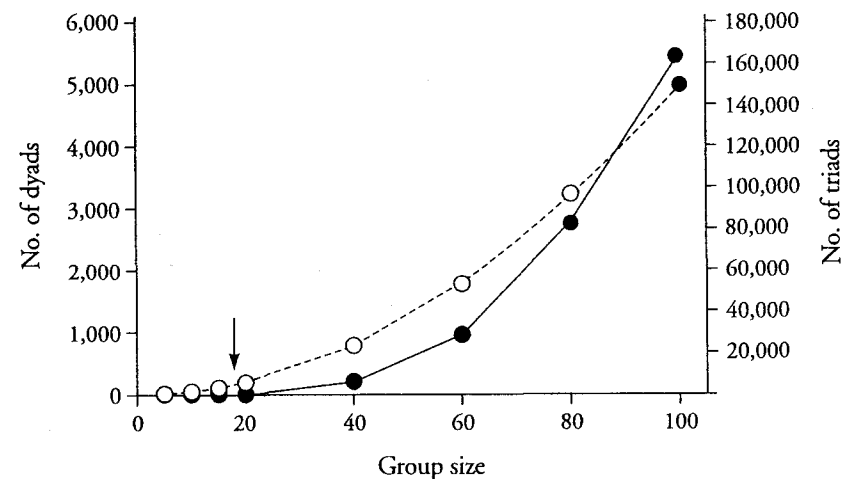
Figure 8.3. The number of different dyadic (two-individual) and triadic (three-individual) combinations possible in groups of different sizes.

In a group of 80 animals (not an unusual group size for baboons, macaques, or mangabeys), each individual confronts 3,160 different possible dyadic combinations and 82,160 different triadic combinations. Under these conditions, it seems likely that free-ranging monkeys and apes face problems in learning and memory that are not just quantitatively but also qualitatively different from those presented in the typical laboratory experiment.

Summary

In several respects the "equivalence classes" that make up nonhuman primate groups exhibit complexities not present in Schusterman's and Kastak's experiments. This is not to say that Schusterman's and Kastak's experiments, or the similar arguments offered by Heyes (1994), are completely erroneous, nor do we mean to suggest that associative learning plays no role in the development of primate social knowledge. In fact, it seems unlikely that a monkey could form a concept such as "closely bonded" without attending to social interactions and forming associations between one individual and another. To some extent, learning about other individuals' social relationships is by definition dependent on some form of conditioning. However, in order to conclude that all primate social knowledge results only from the kind of associative

processes discussed by these authors, we need empirical evidence that associative mechanisms can account for behavior as complex as that known to occur in free-ranging primate groups, not a simplified surrogate.

Chunking in Human and Animal Memory

To survive and reproduce successfully, nonhuman primates must be able to predict the behavior of others. Predicting other animals' behavior demands, in turn, that individuals memorize information about all of the dyadic and triadic relations in their group. And, as already noted, memory loads will be enormous in species with large social groups because increases in group size lead to an explosive increase in the number of dyads and triads.

Faced with the problem of remembering long strings of letters, words, or numbers, human subjects learn the string faster and remember it better if some kind of "rule" allows them to group items into "chunks" that conform to a particular rule. Chunking in humans is an adaptive strategy because it increases the capacity of short-term memory (Miller 1956; Simon 1974). It is facilitated if the stimuli to be remembered are segregated by some kind of "phrasing," like spatial or temporal separation, that corresponds to or reinforces the higher-order rule governing the formation of chunks (Restle 1972; Fountain et al. 1984). Finally, even when a chunked structure is not obvious, human subjects will work to discover one. People presented with randomly ordered lists of words will learn to remember them according to semantic categories, like food, clothing, or animals (Bousfield 1953), and in the absence of any obvious categories subjects will invent idiosyncratic relations between words to facilitate chunking and thereby improve recall (Tulving 1962; Macuda & Roberts 1995). Humans thus bring to problems in learning and memory a predisposition to search for statistical regularities in the data.

Chunking in human memory might, of course, be entirely the result of language, since humans can attach verbal labels to the categories they detect or the rules they use to identify patterns. Several recent studies involving animals, however, indicate that "chunking is a more primitive and biologically pervasive cognitive process than has been recognized previously" (Terrace 1987).

In a study that is directly relevant to research on primate social knowledge, Dallal and Meck (1990) observed the foraging behavior of rats in a 12-arm radial maze. Three different food types were hidden in four arms each, and

the baiting configuration remained constant from trial to trial. For example, arms 3, 5, 6, and 9 always contained one food type, arms 2, 7, 10, and 12 always contained another, and so on. Performance was measured by calculating the number of arms an individual needed to visit in order to obtain food from all 12 locations.

Subjects initially moved at random from arm to arm as they foraged, but they soon diverged from this pattern to one in which food was selected in a highly predictable order; specifically seed, seed, seed, seed, pellet, pellet, pellet, pellet, and rice, rice, rice, rice. Dallal and Meck (1990) argue that "Rather than manage the 12 locations independently in memory, rats . . . could organize the stable arrangement of differentiable food types/outcomes in a hierarchical fashion" and this mental organization led to improved performance.

Macuda and Roberts (1995) replicated Dallal's and Meck's results and proposed two contrasting models of spatial memory representation for a 12-arm radial maze containing three food types. In the nonchunked representation (Figure 8.4), the organization of memories is not hierarchical, chunking is absent, and each arm and its food type is independently represented in memory. In the chunked representation (Figure 8.5), organization is hierarchical. Food types now serve as higher-order nodes in a memory tree, and each food node prompts retrieval of a spatial map of the arms containing
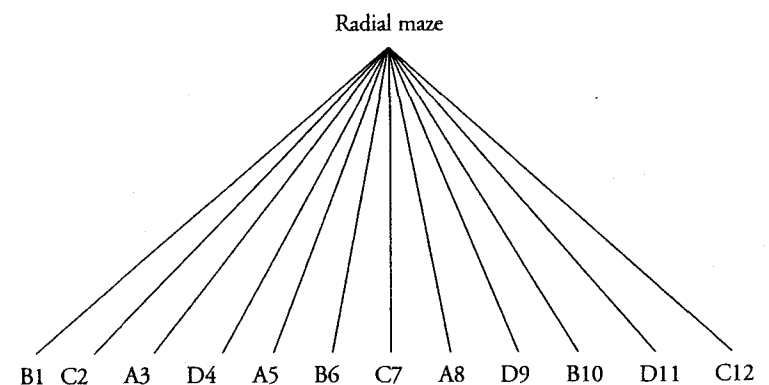

Figure 8.4. A representation of a rat's knowledge of the location of food in a 12-arm radial maze where there are four different food types (represented by the letters A–D) placed randomly among 12 arms (represented by the numbers 1–12). The drawing assumes that each arm–food type combination is remembered independently. Modified from Macuda & Roberts (1995).
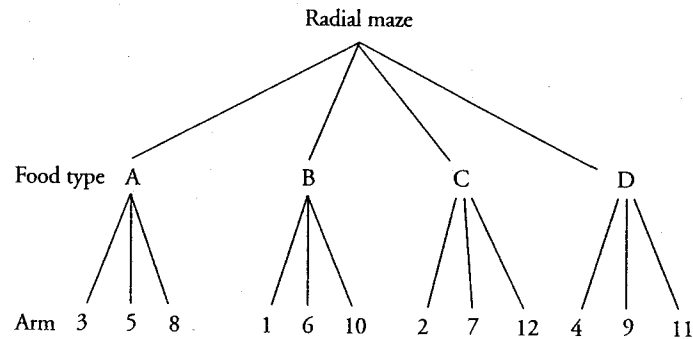
Figure 8.5. A representation of a rat's knowledge of the location of food in a 12-arm radial maze, assuming that the rat groups together, or "chunks," arms that contain similar types of food. Modified from Macuda & Roberts (1995).

that food. Hierarchical chunking reduces the load on working memory, promotes a lower error rate, and leads to the clustering of visits to arms containing the same food (Macuda & Roberts 1995, p. 21). In two experiments designed to test between these models, rats provided strong evidence that their knowledge was organized in a chunked, hierarchical fashion.

The earliest experiments on chunking in animal memory compared animals' performance on tests in which the stimuli had or had not been previously segregated by the experimenter into groups. Reviewing his results, Terrace (1987, p. 351) concluded that pigeons "can impose a self-generated organizational scheme on a series of arbitrary elements" when stimuli have already been segregated. The studies summarized above go an important step further by suggesting that rats actively organize stimuli into groups even in cases in which the experimenter has not provided any structure. They are comparable to studies of free-recall in humans, in which subjects imposed their own idiosyncratic mental structure on an otherwise unstructured dataset (Tulving 1962).

The Link with Primate Social Knowledge

Data on the social knowledge of nonhuman primates are compatible with models of knowledge acquisition based on either the formation of equivalence sets or hierarchical chunking. Both models assume that stimuli—in this case other individuals—are linked in memory through elementary asso-

ciative processes, and that associative links are structured according to one or more rules. For two reasons, however, the model based on chunking seems more relevant to studies of primate social knowledge: chunking emerges naturally, without human intervention, and chunking has known adaptive advantages over other mental strategies.

Free-Recall versus Training

In Schusterman's and Kastak's study, the subject was rewarded for behaving in a manner consistent with the formation of equivalence classes; alternative choices were not rewarded. By contrast, in the chunking studies reviewed above, subjects received no reward other than food, and this food would have been obtained even if they had not formed chunks. The fact that the rats were not specifically trained suggests that the mechanisms underlying their actions were the same as the mechanisms underlying their behavior under more natural conditions.

Perhaps more important, rats in the radial maze were presented with a world in which there was no inherent structure imposed by the experimenter, yet they imposed a structure of their own. Even in the earliest minutes after they were released into the maze, the animals appeared to search actively for a rule that would allow them to organize and remember the locations of different food (see also Fountain & Annau 1984; Fountain et al. 1984). If rats, without explicit reinforcement, organize randomly placed food locations into chunks, how much more likely is it that monkeys, confronted with a society in which there are already statistical regularities in behavior, will organize their knowledge of social companions into hierarchical groups? The hierarchical chunking model predicts that monkeys who were asked to remember the order in which they had seen pictures of their social companions would perform poorly if these pictures were presented at random. By contrast, if the pictures occurred in groups of family members and in the order of the current dominance hierarchy, the monkeys should perform well (see Swartz et al. 1991 for the beginnings of such a study).

The Adaptive Value of Structured Associations

The adaptive value of chunking is directly relevant to the problem confronting primates like baboons, macaques, or mangabeys that live in large social
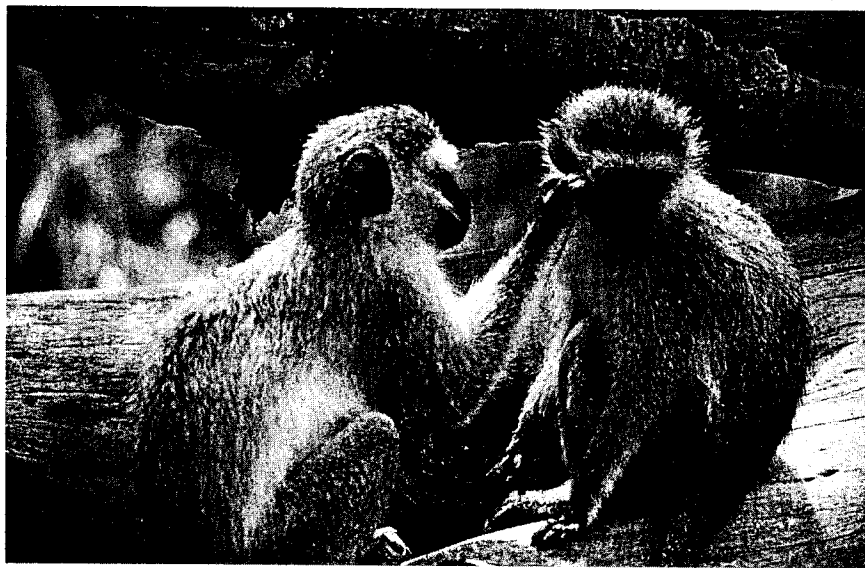
Figure 8.6. Vervet monkeys grooming.

Conclusion

To survive and reproduce, a monkey must predict the behavior of others. In nonhuman primate groups, where alliances are common, prediction demands that a monkey learn and remember all of its opponents' dyadic and triadic relations. The task is similar to the problems faced by human and animal subjects in memory experiments.

In response to these pressures, we suggest that nonhuman primates are innately predisposed to group other individuals into hierarchical classes. They actively search for ways to arrange their companions into rule-governed clusters. Once such groups are formed they somehow label the groups as higher-order nodes in a memory tree, both for ease of recall and to facilitate predictions of behavior. The formation of hierarchical classes is an adaptive social strategy, shaped by natural selection.

groups. Faced with the need to remember hundreds or even thousands of dyadic and triadic relations in order to monitor and predict other animals' behavior, it is logical to assume that monkeys, like rats in a radial maze, will actively search for any rule that decreases memory load. A monkey could organize others into groups by noting patterns of grooming, alliances, and spatial proximity (Figure 8.6). The basis for chunking could be quantitative, in the sense that other individuals would be grouped together only if they had been seen grooming for a certain minimal length of time. Alternatively, it could follow an either/or classification—a single, pivotal alliance could cause animals to be grouped together regardless of whatever else they did.

Whatever metric is used, the adaptive value of chunking as a cognitive strategy is clear, particularly when hierarchical chunking is compared with models of knowledge representation like equivalence sets, which rely on associations between stimuli but lack a hierarchical structure. As group size gets larger, equivalence sets become increasingly implausible: there are simply too many dyads and triads to store in memory (see above, Figure 8.3). By contrast, as group size gets larger a model based on chunking into hierarchical groups becomes increasingly *more* plausible because it offers a means by which individuals can overcome the limits imposed by working memory.