

The representation of social relations by monkeys*

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Abstract

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*Monkeys recognize the social relations that exist among others in their group. They know who associates with whom, for example, and other animals' relative dominance ranks. In addition, monkeys appear to compare types of social relations and make same/different judgments about them. In captivity, longtailed macaques (*Macaca fascicularis*) trained to recognize the relation between one adult female and her offspring can identify the same relation among other mother–offspring pairs, and distinguish this relation from bonds between individuals who are related in a different way. In the wild, if a vervet monkey (*Cercopithecus aethiops*) has seen a fight between a member of its own family and a member of Family X, this increases the likelihood that it will act aggressively toward another member of Family X. Vervets act as if they recognize some similarity between their own close associates and the close associates of others. To make such comparisons the monkeys must have some way of representing the properties of social relationships. We discuss the adaptive value of such representations, the information they contain, their structure, and their limitations.*

Introduction

The vervet monkeys had moved out of their sleeping trees to forage on the ground. While the adults fed, the juveniles played in a nearby bush. Macauley, the son of a low-ranking female, wrestled Carlyle, the juvenile

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daughter of the highest-ranking female, to the ground. Carlyle screamed, chased Macauley away, and then went to forage next to her mother. Apparently, however, the fight had been noticed by others, because twenty minutes later Shelley, Carlyle's sister, approached Austen, Macauley's sister, and without provocation bit her on the tail.

This anecdote sets the stage for what is by now the familiar sort of popular article on nonhuman primates. Read any description of a longterm study of monkeys and apes and you will find an account of complex kinship networks, friendships, struggles for dominance, and shifting alliances. In fact, one of the fascinations of studying monkeys and apes is that their social structure often seems as rich and complex as our own. Like the Montagues and the Capulets, monkeys apparently recognize that the relations within their own families are similar to relations in other families, and they use this knowledge to retaliate against their opponents.

But still a nagging question remains: How much do the monkeys really know about what they are doing? Do they actually make use of concepts like "kinship" or "closely bonded," or are they simply responding on the basis of associations that they have formed between other group members?

Mental representations in animals are usually considered in terms of how different species store information about their physical environment: what pigeons know about trees (Herrnstein, 1990, this issue; Herrnstein & Loveland, 1964); what ducks and fish know about the rate of return at different feeding sites (Gallistel, 1989), or what rats know about time (e.g., Church & Broadbent, 1990, this issue; Gibbon & Church, 1990, this issue). For many animals, however, the most complicated problems in survival and reproduction concern members of their own species. Nonhuman primates, for instance, live in highly social groups where animals both compete with each other for access to scarce resources and cooperate to defend a home range against other groups. As a result, an individual must maintain relations with others that are delicately balanced between competition and cooperation. Further complicating matters, within each group some individuals are close genetic relatives while others are not, some are dominant while others are subordinate, and competition frequently takes the form of temporary alliances in which two animals join together to defeat a third. Because of alliances, one individual interacting with another must predict not only what the other is likely to do but also which third parties are likely to come to his opponent's aid. In short, monkeys and apes must assess each others' social relationships. Moreover, the demands placed on individuals by life in a social group may have favored the evolution of complex cognitive processes. This paper examines what nonhuman primates know about each other, and considers the extent to which monkeys and apes might be said to form "mental

representations" of their own and other animals' social relationships.

Research on animal intelligence frequently attempts to distinguish between "knowing how" and "knowing that," a distinction first drawn by the philosopher Gilbert Ryle (1949; see also Dickinson, 1980; Whiten & Byrne, 1988a). "Knowing how" refers to the ability to perform a specific, procedural task based on recognition of a particular stimulus. Ants, for example, remove the carcasses of dead conspecifics from their nest. The function of this behavior is to rid the nest of bacteria, but ants certainly are not aware of the relation between corpses and disease; they are simply responding to the presence of oleic acid on the decaying corpse. Ants will remove anything that smells of oleic acid, regardless of whether it is dead or infected (Wilson, 1971). Even a live ant dabbed with oleic acid will be dragged, struggling, out of the nest. Similarly, a monkey mother's response to her offspring's scream might be relatively unmodifiable; she might simply run to her offspring's aid whenever she heard a vocalization with a particular set of acoustic properties.

By contrast, "knowing that" refers to "declarative representations or knowledge" (Dickinson, 1980), and implies an ability to make causal inferences about the world. Rather than simply running whenever her offspring screams, for example, the monkey mother might understand enough about the relation between dominance rank and kinship to recognize that discretion is often the greater part of valor, and that she should only intervene on her offspring's behalf when the offspring is fighting with a member of a lower-ranking matriline. In other words, because it refers to more general knowledge about things and can be divorced from a particular response, "knowing that" allows greater flexibility in behavior depending upon changes in the social and physical environment (Whiten & Byrne, 1988a).

In analyzing primate social knowledge, therefore, we must distinguish between knowledge that can be used in only a limited set of circumstances and knowledge that can be applied more broadly. A monkey may have formed an association between two members of the same matriline because the two animals are often encountered together. As a result, the monkey knows that whenever she approaches one individual she is also likely to be near the other. Such knowledge, however, might be limited to these two individuals, or to a small set of animals within the monkey's own group. It would prepare the monkey for some (indeed, many) sorts of interactions, but not for those that depended on the recognition of more differentiated relationships – for example, the difference between a relative and a "friend."

Alternatively, the monkey might have interacted with many different kin pairs and she might have inferred, on the basis of her experiences and observations, that such relationships share similar properties regardless of the particular individuals involved. The monkey might even have labels, like "closely

bonded” or “enemies,” that help order relationships into types. In this case the monkey’s knowledge would be less constrained by particular stimuli, more general, and more abstract. It could also be applied in a much wider variety of circumstances.

There is now a variety of evidence suggesting that monkeys’ and apes’ knowledge of their social environment – that is, their knowledge of each other – is declarative rather than procedural. Among baboons, macaques, and vervet monkeys, for example, adult females compete with each other to interact with the members of high-ranking families. In so doing, they act as if they recognize that some animals are useful allies, and that bonds with these individuals can potentially help to maintain or even improve their own status. But is this really so? Can we actually provide evidence that the monkeys assess each others’ relationships and classify them into types? Or are the animals just responding to a relatively narrow set of stimuli? To answer these questions we must examine more closely what monkeys actually know about social relationships and how such knowledge affects their behavior. That is the purpose of this paper.

Probing into the minds of monkeys, however, is not easy. Unlike anthropologists studying humans, or even psychologists working on captive apes, we cannot simply interview our subjects and ask them what they think about each other. Instead, we must rely on a variety of indirect methods, including observations, anecdotes and experiments, each focusing on situations in which the monkeys reveal, by their behavior, some of what they know about the principles that govern their interactions. By using different methods and drawing on data from a number of different species, we hope that conceptual or methodological weaknesses in one area can be wholly or partially overcome by work in another. As readers will quickly become aware, no single set of experiments or observations can ever provide the kind of ringing, definitive proof one would like. Instead we circle the problem, trying, from as many different angles as possible, to understand a perspective on social life that is different from our own.

Recognizing the relationships of others: Kinship, friendship and dominance rank

Knowledge about other animals’ companions

In order to understand a dominance hierarchy, or to predict which individuals are likely to form alliances with each other, a monkey must step outside its own sphere of interactions and recognize the relations that exist among

others. Such knowledge can only be obtained by observing interactions in which one is not involved and making the appropriate inferences. There is, in fact, growing evidence that monkeys do possess knowledge of other animals' social relationships, and that such knowledge affects their behavior.

Studies of hamadryas baboons (*Papio cynocephalus hamadryas*) in Ethiopia were the first to show that nonhuman primates assess the relationships that exist among others. Under natural conditions, hamadryas baboons are organized into one-male units, each of which contains one fully adult male and two to nine adult females (Kummer, 1968; Sigg, Stolba, Abegglen, & Dasser, 1982; reviewed in Stambach, 1987). One-male units frequently come into contact with single, unattached males, and a male unit leader must constantly defend himself against attempts by other males to take over his females. Experiments using captive hamadryas have shown that "rival" males assess the strength of an owner's relationship with his females before competing to acquire them. Rival males do not attempt to take over a female if they have previously seen her interact with her owner. Such "respect of possession" holds even when the rival is dominant to the owner in other contexts (Kummer, Goetz, & Angst, 1974). This phenomenon seems to be widespread. Among both geladas in Ethiopia and savanna baboons in Kenya, challenges from a rival are less likely to occur if a male has strong grooming relations with a female, and more likely to occur if grooming relations are weak (Dunbar, 1983; Smuts, 1985).

To test the hypothesis that rivals make judgments about the strength of bonds between a male and his females, Bachmann and Kummer (1980) studied six adult males and six adult females, using choice tests to determine how strongly each male preferred each female and how strongly each female preferred each male. A male-female pair was then placed in a large outdoor enclosure and allowed to interact freely. Different "rival" males were allowed to watch the pair and then given an opportunity to challenge the owner. Bachmann and Kummer found that the probability of a challenge was not correlated with either the rival's or the owner's preference for a particular female. The female's preference, however, did make a difference: If a female was with an owner she strongly preferred, this inhibited challenges from middle- and low-ranking rivals. The two highest-ranking males challenged all owners regardless of how strongly females preferred them. Although Bachmann and Kummer could not rule out the possibility that rival males were simply responding to the females' actions rather than their relationships, the experiments suggested that the males might have been able to assess the strength of the attraction between an owner and his female and to avoid challenging owners when the pair's relationship was close. This seems an adaptive strategy because aggressive challenges, which involve potential in-

jury, may be too costly if the contested female prefers to remain with her current mate.

Further evidence that monkeys recognize relations among others comes from playback experiments on vervet monkeys. In many primate species, mothers will run to their offsprings' aid when the offspring scream during a fight, suggesting that females can distinguish among the calls of different individuals. To test this hypothesis, we played the scream of a 2-year-old juvenile from a concealed loudspeaker to its mother and two control females who also had offspring in the group. We found that mothers consistently either looked toward or approached the speaker for longer durations than did control females, indicating that they recognized the voice of their offspring (Cheney & Seyfarth, 1980). This result was entirely expected, given the many studies that had already shown individual recognition by voice in primates (e.g., Hansen, 1976; Kaplan, Winship-Ball, & Sim, 1978; Waser, 1977) as well as birds and other mammals (e.g., Brooks & Falls, 1975; Emlen, 1971; Kroodsma, 1976; Petrinovich, 1974).

More interesting, however, was the behavior of control females. When the responses of control females were compared with their behavior before the scream was played, we found that playbacks significantly increased the likelihood that control females would look at the mother. By contrast, there was no change in the likelihood that control females would look at each other (Cheney & Seyfarth, 1980, 1982b). The females appeared to be able to associate particular screams with particular juveniles, and these juveniles with particular adult females. They behaved as if they recognized the kin relationships that existed among other group members.

At this point, it is important to emphasize that, whenever we speak of kin recognition in primates, we define the term operationally, as the recognition of a close social bond. The ability to recognize other animals' kin does not imply that monkeys have a concept of "kinship" or "genetic relatedness," but simply that they recognize the close associates of other group members. In most cases close associates are also kin, and this "rule of thumb" appears to be the primary mechanism underlying kin recognition in nonhuman primates (for reviews see Gouzoules, 1984; Gouzoules & Gouzoules, 1987; Waldman, Frumhoff, & Sherman, 1987). There is at present no evidence that monkeys differentiate among kin relationships that are characterized by similar rates of interaction – for example, sister as opposed to daughter – simply because the relevant tests have not yet been conducted.

Monkeys seem not only to distinguish among the screams of different juveniles, but also to differentiate among different types of aggressive interactions. In a study of maternal intervention in the semi-free-ranging population of rhesus macaques (*Macaca mulatta*) on Cayo Santiago, Puerto Rico,

Gouzoules, Gouzoules, and Marler (1984) noticed that the screams of juveniles varied systematically in their acoustic features, that different types of screams were given in different types of conflicts, and that mothers responded differently to different scream types. Mothers reacted most strongly to the screams given to higher-ranking opponents, next most strongly to screams given to lower-ranking opponents, and least strongly to screams given to relatives. Through its screams, in other words, a juvenile effectively classifies its opponents according to kinship and dominance. By her selective responses, an adult female reveals knowledge of both her offspring's voice and her offspring's network of social relationships.

For additional evidence that monkeys recognize the kin relationships (or close associates) of other group members, consider the phenomenon of redirected aggression. In many primate species, an animal that has been involved in a fight will "redirect" aggression and threaten a third, previously uninvolved individual. In rhesus macaques (Judge, 1982) and vervet monkeys (Cheney & Seyfarth, 1986, 1990a) such redirected aggression is not distributed randomly but is directed toward a close relative of the prior opponent. Vervets in Amboseli were significantly more likely to threaten unrelated individuals following a fight with those animals' close kin than during matched control periods (Cheney & Seyfarth, 1986, 1990a). This was not because fights caused a general increase in aggression toward unrelated animals. Instead, aggression seemed to be directed specifically toward the kin of prior opponents.

Similar kin-biased patterns of interaction were evident in a behavior that is the mirror image of redirected aggression, reconciliation. In many species of monkeys and apes, including vervet monkeys, animals sometimes reconcile after fights by approaching their former opponents and touching, hugging, or grooming them (e.g., longtailed macaques: Cords, 1988; rhesus macaques: de Waal & Yoshihara, 1983; stump-tail macaques: de Waal & Ren, 1988; patas monkeys: York & Rowell, 1988; chimpanzees: de Waal & Roosmalen, 1979). It is not only the primary antagonists who reconcile, however. Monkeys will also reconcile with the kin of their former opponents. Studying reconciliation among captive patas monkeys (*Erythrocebus patas*), York and Rowell (1988) found that unrelated animals contacted the kin of their former opponents almost twice as often following a fight than during matched control periods. Similarly, vervet monkeys were significantly more likely to groom or initiate a friendly interaction with an unrelated animal following a fight with that animal's kin than in the absence of such a fight (Cheney & Seyfarth, 1990a).

Interestingly, however, reconciliation among related vervet monkeys differed in two respects from reconciliation among unrelated opponents. First,

unrelated animals were more likely to reconcile with their opponents' kin than with their opponents themselves. Related animals were more likely to reconcile directly with their opponents. Second, reconciliation appeared to be a more important context for affiliative interactions among nonkin than among kin. Nonkin were significantly more likely to initiate friendly interactions both directly with their opponents and with their opponents' kin following a fight than during control periods (see also York & Rowell, 1988). In contrast, related vervet monkeys were as likely to interact with their opponents and their opponents' kin (who were also their own kin) during control periods as they were following a fight. Apparently, the generally high rates of grooming and friendly interactions among kin swamped the effect of affiliative interaction in the context of reconciliation. This result is similar to that reported by Cords (1988), who found that juvenile male longtailed macaques also reconciled at higher rates with nonkin than with kin. Relationships among unrelated animals are typically less predictable and stable than those among relatives, and Cords has suggested that post-conflict affiliative interactions may function as a repair mechanism for relationships among nonkin. Such reconciliatory interactions may be less important for kin, who interact at high rates in any case.

The fact that unrelated vervets reconciled with their opponents' kin as well as (indeed, more than) with their opponents themselves suggest that conflict resolution extends beyond individual opponents to their entire families. There is a good reason for this. Over 20% of all aggressive interactions among female vervets involved alliances by two individuals against a third, and vervets formed approximately 65% of their alliances with family members (Cheney & Seyfarth, 1987). Since an aggressive interaction with a particular individual is likely to expand to include other members of that individual's matriline, it may be as important to reconcile with the opponent's family as with the opponent herself (Judge, 1983), particularly if the opponent is a member of a higher-ranking matriline. Reconciliation with an opponent's relatives may have the added advantage of establishing affiliative contact with a relevant, yet uninvolved, individual while nevertheless avoiding the opponent (see also de Waal, 1989).

Knowledge about other animals' relationships is not limited to the recognition of matrilineal kin. Consider, for example, the pattern of redirected aggression among pairs of male-female "friends" in savanna baboons (*Papio cynocephalus anubis*, Smuts, 1983, 1985). Baboon males and females sometimes form longterm pair bonds, or "friendships," in which proximity and cooperative behavior are maintained throughout the female's reproductive cycle (e.g., Altmann, 1980; Kaufmann, 1965; Seyfarth, 1978). In some baboon groups, friendships persist for years at a time (Smuts, 1983, 1985;

Strum, 1984). In the most well documented study of friendships, Smuts (1985) found that females and males often redirected aggression against their opponents' friends. Following a fight with another male, for example, a male frequently appeared to seek out his rival's female friend and chase her. The baboons, in other words, seemed to recognize friendships.

In sum, monkeys in many different species appear to observe interactions in which they are not involved and recognize the relationships that exist among others. In this respect, monkeys make good primatologists. A male considers how strongly a female prefers her partner before he attempts to take her away; juveniles and adult females take note of their opponents' kin as they plot retaliation or reconciliation; and adult females, upon hearing a juvenile's cry for help, learn to expect a response from the mother.

Knowledge about other animal's ranks

Dominance relations in vervets and many other primates are transitive. This allows a human observer to assemble, from data on interactions in pairs of individuals, a rank hierarchy that orders the behavior of a large number of animals. The fact that we can derive such hierarchies does not, however, prove that they also exist in the minds of monkeys. It is certainly possible that monkeys attend to each others' dominance interactions and that they recognize rank orders (and transitive relations) among others in their group (e.g., Kummer, 1982). Alternatively, each monkey may simply know who is dominant and who is subordinate to itself, having derived this knowledge from personal experience. In the latter case, a dominance hierarchy would occur as an incidental outcome of paired interactions (e.g., Altmann, 1981).

A variety of observational data suggests that monkeys recognize the dominance ranks of others. When competing over grooming partners, for example, both female vervets and female baboons supplant each other, on average, most often for access to the highest-ranking individual, next most often for access to the second-highest-ranking individual, third most often for access to the third-highest-ranking individual, and so on (Seyfarth, 1976, 1980). This pattern does not occur simply because high-ranking females spend more time grooming and are therefore more likely to be available as objects of competition; females of different ranks spend roughly equal amounts of time in grooming interactions. The observed pattern, moreover, is consistent across many different individuals (Seyfarth, 1976, 1980). In other words, adult females seem not only to rank one another but also to "agree" on their ranking of the most preferred grooming partners. Similarly, in both pigtail macaques (Gouzoules, 1975) and savanna baboons (Scott, 1984) the intensity of male-male competition for mates is directly related to the rank of the female involved.

Additional hints that monkeys are able to judge the ranks of others emerge when we consider the details of social behavior when adult female vervet monkeys compete for access to grooming partners. Competition over access to a grooming partner occurs whenever one female approaches two that are grooming, supplants one of them, and then grooms or is groomed by the remaining individual. In a small proportion of all cases such competition takes a form that is especially interesting for our present purpose: A high-ranking female (ranked 2, for example, in a group of six adult females) approaches two groomers who are both lower-ranking than she is (say, females ranked 4 and 5). Though Females 4 and 5 are both subordinate to Female 2, they are not equally likely to depart. During one 8-month period in 1985–86, in 29 out of 30 interactions that took this form, the higher-ranking female (Female 4 in our generic example) did nothing, while the lower-ranking female (Female 5) moved away. This result was independent of kin relations among the individuals involved.

It is Female 4, of course, whose behavior is most interesting. She acts as if she has recognized that, even though she is subordinate to Female 2, Female 5 is more subordinate than she is. Female 4's behavior, in other words, suggests that she recognizes the ranking:

Female 2 > Female 4 > Female 5.

To do so she must not only know her own status relative to Females 2 and 5 but also their status relative to each other. In other words, she must recognize a rank hierarchy.

An alternative explanation might argue that Female 2's approach simply has a greater effect on Female 5 than it does on Female 4. If the probability of a supplant depends on the magnitude of the difference between two individuals' ranks, the result could be explained without positing that individuals know the ranks of others. Data gathered in 1985–86, however, do not support this view. For example, when dominant females approached others who ranked two, three or four steps beneath them in the hierarchy, the subordinate was supplanted in 61%, 54% and 63% of all cases, respectively ($N = 101, 61$ and 48 approaches).

It is also possible that Female 4 gave some subtle glance or shrug in Female 5's direction as Female 2 approached that was not noticeable to the human observer. Such behavior would explain the observation without requiring any knowledge of ranking on the monkeys' part. Clearly, we will never be able to exclude this possibility entirely. If these gestures do occur, however, they are extremely subtle, and do not resemble any other form of threats or supplants.

Nonhuman primates may not be the only species that rank each other.

Linear, transitive, dominance hierarchies are common, for example, in wild dogs, hyaenas, and a variety of birds (e.g., Dufty, 1986; Frame, Malcolm, Frame, & van Lawick, 1979; Frank, 1986; Rowher, 1982; Yasukawa, 1979). Studying captive goldfinches, Popp (1987) observed competitive interactions among individuals at a feeding site that contained two perches. He found that when a dominant bird flew into a site that was already occupied by two subordinate animals, it usually approached and supplanted the more subordinate of the two, as if it recognized the birds' relative ranks. As with monkeys, however, simpler explanations are possible. In this instance, rather than recognizing the other birds' relative ranks, the dominant bird may simply have distinguished individuals whose latency to fly off in past interactions was different. The subordinate birds' behavior might reveal more about goldfinches' understanding of dominance hierarchies. Did the bird that flew away recognize that it was more subordinate than the one that stayed?

In the absence of experiments designed specifically to test for animals' understanding of dominance hierarchies, no one set of data can ever prove decisively that monkeys recognize each others' ranks. For the moment, we can only conclude that a variety of data from a number of different species suggest that monkeys can rank one another. We turn now to the question of how they might do it.

Consider first some experiments by Michael D'Amato and his colleagues (D'Amato & Colombo, 1988; see also D'Amato & Salmon, 1984; D'Amato, Salmon, Loukas, & Tomie, 1985). In these tests, captive cebus monkeys were trained to respond to five stimuli (a circle, a plus sign, a dot, a vertical line and an hourglass – hereafter A,B,C,D and E) in a specified order: first AB, then ABC, then ABCD, and finally ABCDE. To test the animals' knowledge of the sequential position of each item, subjects were given pairwise tests (for example, BC or DA) and rewarded for responding only to pairs that appeared in the correct sequential order. The monkeys performed well. In addition, their latency to respond was shortest when the first item in the test series was A, longer when it was B, longer still when it was C, and so on. Their latency was also shortest when the two items in the test series were adjacently ranked, longer when they were separated by one item, and longer still when they were separated by two items. D'Amato and Colombo believe that these results demonstrate “an internal representation of the sequential order of the five items” (see also D'Amato & Colombo, *in press*).

D'Amato and colleagues argue that the representation of rank order in cebus monkeys is based on “associative transitivity,” which they contrast with “transitive inference.” In associative transitivity no inference is involved because there is nothing in the initial conditional discrimination that demands a particular pairing of stimuli on the test trials. There is no underlying rule,

in other words, that is common to the pairs AB and BC. As a result, in the absence of prior association, the subject has no way of inferring that in the test trials A should be linked with C. In many respects, the experiments test only whether monkeys are capable of ordering stimuli sequentially.

By contrast, experiments that test for transitivity in children (Bryant & Trabasso, 1971), squirrel monkeys (McGonigle & Chalmers, 1977) and chimpanzees (Gillan, 1981) have all involved identification of a relation between the training stimuli: for example, A is longer than B, B is longer than C, and so on. This may have allowed transitivity to be inferred on subsequent tests (D'Amato & Salmon, 1984). Gillan, for example, taught chimpanzees that stimulus E had more food than stimulus D, D had more food than C, C more than B and B more than A. He then tested individuals on novel nonadjacent pairs like BD, BE and CE. The animals consistently chose the stimulus in each pair that was associated with the greater amount of food. In this and other tests, subjects may have inferred the relation "greater than" and solved test problems according to this relational rule rather than according to the prior association of particular stimuli (for alternative explanations see Breslow, 1981; D'Amato & Salmon, 1984; McGonigle & Chalmers, 1977).

While socially living monkeys seem to recognize the dominance ranks of others, we know very little about how these ranks are learned, or how ranks are represented in the animals' minds. One means by which a monkey might acquire information about other animals' ranks is simply through "brute force," a method similar to D'Amato's "associative transitivity." Here a monkey simply observes and remembers all possible dyadic interactions until it is able to conclude that A is dominant to everyone, B is dominant to everyone but A, C is dominant to everyone but A and B, and so on. The brute force method does not require the ability to make transitive inferences, but it does demand that a monkey observe at least one interaction between all pairs of group members before constructing a dominance hierarchy.

In contrast, a monkey who could make transitive inferences about rank relations among other group members could construct a linear dominance hierarchy on the basis of partial information, without having to observe interactions among all pairs of individuals.

At present there are no data that allow us to choose between these alternatives, though tests on captive squirrel monkeys (McGonigle & Chalmers, 1977) and chimpanzees (Gillan, 1981) suggest that transitive inference is at least possible. In some cases, it is difficult to explain the behavior of monkeys in large groups without assuming that the animals are using the more efficient method of transitive inference. Although vervet monkeys typically live in groups of fewer than 30 individuals, many macaque and baboon groups commonly exceed 100 members. Observers often report spending months with a

group without ever seeing some individuals interact. Yet when data on social interactions within such groups are analyzed (e.g., Scott, 1984) there is still evidence that the animals construct rank orders of their fellow group members. Since these rank orders include individuals who interact only rarely, it seems probable that their places have been calculated by animals who observe a subset of dyadic interactions and make the additional assumption that all rank relations are transitive.

The representation of social relationships

Nonhuman primates classify other individuals according to their patterns of association and seem to recognize the bonds and enmities that exist among individuals other than themselves. Humans, though, go several steps further, to classify different types of relationships into superordinate categories that are independent of the particular individuals involved. If a friend mentions a sister, an uncle, or a husband, we immediately have some idea of the nature of her relationship with the other person, even if we have never met the individual in question. And if the friend tells us that her uncle wrecked her new car and her husband closed her bank account and left town, we are shocked at least in part because their behavior is at variance with what we typically expect of people in these categories. In fact, it could easily be argued that humans are overly eager to classify relationships. “The friend of my enemy is also my enemy” is, cognitively speaking, a delightfully complex concept, redolent of all sorts of inference, transitivity, and classification. It can, however, lead to awkward overgeneralizations and less than adaptive behavior. Is there any evidence that monkeys, too, classify social bonds into higher order units that allow relationships to be compared independent of the individuals involved?

Judgments about relations

Many animals appear to classify objects according to “concepts” – relatively abstract criteria that are not based on any single perceptual feature (Lea, 1984). For example, tests that demand cross-modal transfer of performance from lights to tones or the classification of objects according to relative size, hue, or shape demonstrate that animals as diverse as pigeons, parrots, sea lions, and monkeys are capable of forming abstract concepts and using them to classify objects in the external world (e.g., pigeons: Herrnstein, 1990, this issue; Herrnstein & Loveland, 1964; African grey parrot: Pepperberg, 1983; sea lions; Schusterman, 1988; squirrel monkeys: Roberts & Mazmanian,

1988; stump-tail macaques: Schrier, Angarella, & Povar, 1984; rhesus macaques: Sands, Lincoln, & Wright, 1982; Schrier & Brady, 1987; see also Premack, 1986). The precise nature of these mental representations remains elusive. It seems clear, however, that the animals are not simply responding according to perceptual similarities, since in many studies no single set of perceptual criteria was either necessary or sufficient to account for the subjects' behavior. The critical features used by pigeons and monkeys to identify animal pictures remain unknown (Medin & Smith, 1984). D'Amato and van Sant (1988) argue that such features cannot help but remain elusive, and that further efforts to identify concepts in animals through photograph discrimination may be futile.

In addition to classifying stimuli according to relatively abstract features, monkeys can readily be taught to solve problems that require recognition of a relation between objects rather than a specific physical attribute. In oddity tests, for instance, a subject is presented with three objects, two of which are the same and one of which is different. It receives a reward only if it chooses the different object. Many monkey species achieve scores of 80% to 90% correct even when new stimuli are used for each problem and each set of stimuli is presented for only one trial (e.g., Davis, Leary, Stevens, & Thompson, 1967; Strong & Hedges, 1966). Such performance suggests that animals are using an abstract hypothesis, "pick the odd object." The hypothesis is called abstract because "odd" does not refer to any specific stimulus dimension, as does "red" or "square." Instead, oddity is a concept that specifies a relation between objects independent of their specific stimulus attributes (Essock-Vitale & Seyfarth, 1987; Roitblat, 1987).

Although judgments based on relations among items have been demonstrated more often in nonhuman primates than in other taxa, there is no a priori reason to expect that this ability should be restricted to primates. Pepperberg (1987), for example, has taught an African grey parrot to make same/different judgments about the color, shape, and material of objects. Similarly, the fact that not only chimpanzees (Boysen & Berntson, 1989; Matsuzawa, 1985) but also rats (Capaldi & Miller, 1988; Church & Meck, 1984) are able to generalize numerical discriminations from training sets to novel sets composed of entirely different items suggests that many species may have a concept of numerosity that is based on relatively abstract criteria (see also discussion by Gallistel, 1989).

Premack (1983, 1986) contends that tasks like oddity tests require only judgments about relations between elements, not relations between relations. By contrast, judgments about relations between relations are involved in tasks like analogical reasoning. They are less fundamental and universal than judgments about relations between elements, and they have thus far been demonstrated only in language-trained chimpanzees.

In his study of analogical reasoning in chimpanzees, Premack (1976, 1983) trained Sarah to make same/different judgments between pairs of stimuli. Once Sarah could use these words correctly even when confronted with entirely new stimuli, she was shown two pairs of items arranged in the form A/A' and B/B'. Her task was to judge whether the relation shown on the left was the same or different from the relation shown on the right. Alternatively, Sarah was given an incomplete analogy like A/A' *same as* B/? Her task then was to complete the analogy in a way that satisfied this relation.

In the most complex test, the objects shared no obvious physical similarity. For example, Sarah was asked "lock is to key as closed paint can is to ___," with the options for completing the analogy being a can opener and a paint brush. Here the identity between two such relations is not based on physical similarity (in fact they look quite different), but on the underlying relation *opening*, which both cases instantiate. Hence it is not the stimuli themselves but this relation that must be represented in the subject's mind. To solve an analogy the chimpanzee must infer the appropriate relation for each stimulus pair and then compare these two relations to see if they are the same (Gillan, Premack, & Woodruff, 1981; Premack, 1983). In other words, she must somehow form a representation of the concept instantiated by each pair, and then compare these representations.

Premack (1983) contends that the ability to form such abstract representations is enhanced by, and may require, language training. His claim is not that chimpanzees naturally lack the ability to reason abstractly. Instead, he believes that all primates possess the potential for such skills but only chimpanzees subject to language training are able to realize this potential.

The assessment of social relationships

Premack's tests prompt one to ask whether group-living primates might use abstract criteria to make same/different judgments about social relationships. A comparable problem in the social domain might concern the judgment of relations within different kin groups: Is the relation Mother A/Infant A the same as or different from the relation Mother B/Infant B (Cheney & Seyfarth, 1982c)? Premack's analogy tests therefore bring us back to the central question of this section: Is there any evidence that primates, in their assessment of each others' behavior, ever classify relationships using criteria that are independent of the particular individuals involved?

Verena Dasser (1988a) studied social knowledge in longtailed macaques who were members of a group of 40 individuals living in a large, outdoor enclosure. After considerable effort, Dasser trained three adult females so that they could be temporarily removed from the group and placed in a small

test room to view slides of other group members. In one test that used a simultaneous discrimination procedure, the subject saw two slides. One showed a mother and her offspring, the other showed an unrelated pair of group members. The subject was rewarded for pressing a response button below the mother-offspring slide. Having been trained to respond to one mother-offspring pair (five different slides of the same mother and her juvenile daughter), the subject was tested using 14 novel slides of different mothers and offspring paired with 14 novel unrelated alternatives. The mother-offspring pairs varied widely in their physical characteristics. Some slides showed mothers and infant daughters, others showed mothers and juvenile sons or mothers and adult daughters. Nonetheless, in all 14 tests the subject correctly selected the mother-offspring pair.

In a second test that used a match-to-sample procedure, the mother was represented as the sample on a center screen, while one of her offspring and another stimulus animal of the same age and sex as the offspring were given as positive and negative alternatives, respectively. Having learned to select the offspring during training, the subject was presented with 22 novel combinations of mother, offspring, and unrelated individual. She chose correctly on 20 of 22 tests.

Finally, to test whether monkeys could recognize other categories of social affiliation, Dasser (1988b) trained a subject to identify a pair of siblings and then tested the subject's ability to distinguish novel sibling pairs from (a) mother-offspring pairs, (b) pairs of otherwise related group members, like aunts and nieces, and (c) pairs of unrelated group members. The subject correctly identified the sibling pair in 70% of tests. Seven of the eight errors occurred when she was asked to compare siblings with a mother-offspring pair; one occurred when she compared siblings with two less closely related members of the same matriline.

Data on redirected aggression and reconciliation in vervet monkeys provide additional evidence that animals classify social relationships into types, independent of the particular individuals involved. Recall that in some monkey species redirected aggression and reconciliation are kin-biased, such that animals often interact with the kin of their prior opponents. In vervet monkeys, moreover, redirected aggression and reconciliation can extend even to the previously uninvolved kin of prior opponents. Data gathered in two social groups over two different time periods showed that an animal was more likely to threaten another individual if one of its own close relatives and one of its opponent's close relatives had recently been involved in a fight (Cheney & Seyfarth, 1986, 1990a). The same was true of reconciliation. Two unrelated individuals were more likely to engage in an affiliative interaction following a fight between their close kin than during matched control periods. So, in

the example given at the beginning of this paper, the fight between Macauley and Carlyle apparently caused Shelley, Carlyle's sister, to attack Austen, Macauley's sister. Of course, the parallel is not exact: If the prior opponents were both adult females this did not necessarily mean that the subsequent opponents would both be their daughters. Vervet families are simply too small for these perfectly balanced analogies even to arise.

Bearing in mind the preliminary nature of these results, these more complex forms of redirected aggression and reconciliation support Dasser's experiments in suggesting that monkeys recognize that certain types of social relationships share similar characteristics. When a vervet monkey (say, A2) threatens an unrelated animal (B2) following a fight between one of her own relatives (A1) and one of her opponent's relatives (B1), A2 acts as if she recognizes that the relationship between B2 and B1 is in some way similar to her own relationship with A1. In other words, we may think of A2 as having been presented with a natural problem in analogical reasoning:

A1/B1 same as A2/?

A2 correctly completes the analogy by directing aggression to another member of the B family.

Definitive proof that monkeys are indeed capable of solving social analogies, and that language training is not a necessary prerequisite, can only come from laboratory tests. We can imagine, for example, an experiment in which a monkey is asked the following question about its fellow group members: Mother A is to Infant A as Mother B is to (i) Infant B, (ii) Juvenile B, or (iii) Infant C? Dasser's results and our less rigorous observational data suggest that monkeys would solve this problem with ease. The relevant tests, however, have not yet been attempted.

We have no idea how monkeys might complete these analogies, much less how they might represent social relationships in their minds. One possibility is that they use physical resemblance as a cue, since members of the same matriline often (but not always) look alike. Note, however, that vervets and longtailed macaques treat bonds between kin as similar even when they involve pairs of animals whose within-family resemblances, at least to a human observer, are markedly different. In Dasser's study, for example, subjects generalized to a diverse array of mother-offspring pairs (mothers and young black infants; mothers and juvenile sons; mothers and adult daughters) even though they had been trained with only one example from this category (Dasser, 1988a). Similarly, male and female baboon "friends" do not resemble each other, yet other baboons nevertheless recognize that certain males and females associate at high rates.

There is no hard evidence that vervets or any other monkey species recog-

nize kinship in any sense other than a close association between two individuals (e.g., Frederickson & Sackett, 1984). However, association rates do not entirely explain differential treatment of kin and nonkin, because kin do not always interact at higher rates than nonkin. Even the same types of kinship bonds are not always characterized by similar kinds and rates of interactions. Some mother-offspring pairs, for example, are close and interact at high rates, while others are more distant (e.g., Altmann, 1980; Hinde, 1974). All, however, were classified by Dasser's subjects as falling within the same category. Similarly, while bonds within matrilineal kin groups can be extremely variable (depending, for example, on the ages and sex of family members), monkeys nevertheless treat competitive interactions as pitting one family against another (Cheney & Seyfarth, 1986, 1990b; Dunbar, 1983; Walters, 1987).

In sum, monkeys seem to use a metric to classify social relationships that cannot be explained simply in terms of physical features or the number and type of interactions. Instead, their classification seems based on an abstraction that includes all of these. Results raise the possibility that monkeys recognize a distinction between members of their own matriline and members of other, unrelated families that cannot be explained entirely in terms of close behavioral association.

In addition to recognizing the difference between bonds within their own matriline and bonds in other families, monkeys also seem to recognize the similarity among kinship bonds across different families. To recognize that certain sorts of bonds share similar characteristics independent of the particular individuals involved, monkeys must compare animals not according to physical features or a specific type of interaction, but according to an underlying relation that has been abstracted from a series of interactions over time. Monkeys take note of the elements that make up a relationship (grooming, alliances and so on). They then make judgments of similarity or difference not by comparing specific elements but by comparing the different relationships that these elements instantiate.

Representing the meaning of vocalizations

The hypothesis that monkeys classify relationships into relatively abstract categories receives additional support from experiments suggesting that vervets also classify their vocalizations into referential categories. Vervets give acoustically different alarm calls to at least five different predators, including leopards, eagles, and snakes. Each alarm call elicits a different response from other monkeys nearby, suggesting that the calls have different referents

(Seyfarth, Cheney, & Marler, 1980). By contrast, other calls in the vervets' repertoire, though acoustically distinct, have broadly similar referents. For example, vervets give two acoustically distinct calls – “wrrs” and “chutters” – at the approach of a neighboring group. Wrrs are usually given when another group has first been spotted, while chutters occur primarily when groups come together and the encounter escalates to include aggressive threats, chases, or even physical contact (Cheney & Seyfarth, 1988). Though wrrs and chutters are given under slightly different circumstances, therefore, they both occur only in the general context of an intergroup interaction.

To test the hypothesis that vervet monkeys classify vocalizations according to their referents rather than simply their acoustic properties, we repeatedly played subjects a call (for example, an intergroup wrr or a leopard alarm call) given by a specific individual in their group. Subjects rapidly habituated, and soon ceased responding to this vocalization. We then played subjects either a call with the same referent but different acoustic properties (an intergroup chutter, for example) or a call with a different referent and different acoustic properties (an eagle alarm call, for example).

Results provided clear evidence that vervet monkeys compare different calls on the basis of their referents, and not just their acoustic properties. If an animal had habituated to Individual X's intergroup wrr, she transferred habituation and also ceased responding to X's intergroup chutter. In contrast, subjects who had habituated to repeated playback of, for example, X's leopard alarm call did not transfer habituation to X's eagle alarm call (Cheney & Seyfarth, 1988).

In sum, when presented with two different vocalizations that have different acoustic properties, vervet monkeys judge them to be similar if the calls have similar referents and are given by the same individual. Just as they seem to classify social relationships into types independent of the particular animals involved, the monkeys make same/different judgments about vocalizations according to the things for which they stand, not just their acoustic properties. To make such comparisons, individuals must be able to represent, in their minds, the objects and events denoted by a vocalization, and then compare calls on the basis of these representations.

Discussion

Representing social relationships

Nonhuman primates make good primatologists. On the basis of their observations, they not only recognize the relations that exist among others but also

compare *types* of social relationships and make same/different judgments about them. Longtailed macaques trained to recognize the relation between one adult female and her offspring can identify the same relation among other mother-offspring pairs, and distinguish this relation from bonds between individuals who are related in a different way. If a vervet monkey has seen a fight between a member of its own family and a member of Family X, this increases the likelihood that it will act aggressively toward another member of Family X. Vervets act as if they recognize some similarity between their own close associates and the close associates of others. In both cases, the monkeys' judgments depend not on the particular individuals involved but on the *relationships* that exist between them. Mother-offspring pairs are judged to be similar regardless of whether the offspring are old or young, male or female; relations within families are judged to be similar regardless of whether the animals in question are sisters, brothers or parents and offspring.

To make such comparisons the monkeys must have some way of representing the properties of social relationships. This representation is not explicit: We have no evidence, for example, that monkeys have labels to describe mothers and offspring or closely bonded individuals. Nevertheless, it seems clear that the social complexity of nonhuman primate groups is based, at least in part, on processes that go beyond the formation of associations between individuals. Monkeys observe who associates with whom and then infer distinct types of relationships. These relationships may be relatively independent of the individuals that instantiate them.

Why monkeys need mental representations

Throughout this paper we have adopted a functional, evolutionary approach to the study of primate intelligence. If representations of certain aspects of the world exist in the minds of monkeys, we assume that they do so because they confer a selective advantage on those who make use of them. We also assume that what is represented, as well as the structure of information contained within a representation, will be determined by the relative utility of one sort of mental operation as opposed to another.

Groups of monkeys and apes are composed of many shifting alliances among related and unrelated animals. In order to gain a social (and reproductive) advantage over others, an individual must be able not only to predict other animals' behavior, but also to assess other animals' relationships. It is not enough to know who is dominant or subordinate to oneself; one must also know who is allied to whom and who is likely to come to an opponent's aid. For this reason, we should expect knowledge of other animals' relation-

ships to appear in any animal society where alliances are common (Harcourt, 1988).

The notion that monkeys might need representations of social relationships is buttressed by the experience of those who study them. Primatologists have long recognized that in order to explain and predict the behavior of their subjects, they cannot simply describe or list who does what to whom and how often. Instead, they must step back from the minutiae of social behavior and identify, at a more abstract level, social relationships and the general principles that underlie them. Hinde (1976, 1983), for example, defines a relationship “in terms of the content, quality and patterning of interactions” between two individuals over time. By this definition, a relationship cannot be described by any single interaction, nor is it enough simply to list what two individuals did with one another during a particular period (for example, that they groomed three times, hugged each other once, fought once and spent 23% of observation time together). What matters – and what defines a relationship – is not simply the behaviors themselves but also the temporal relations among behaviors and the way each activity is carried out. Some pairs of animals groom whenever they are together, others groom only briefly; some separate after a fight, others reconcile; for some a hug is perfunctory while for others it is a lengthy embrace. The point is: If either we (as observers) or the monkeys (as participants) want to explain or predict social behavior, we must change our unit of analysis from a set of interactions that is simple and concrete to a relationship that is more complex and abstract.

The ability to represent social relationships may have evolved because it offers the most accurate means of predicting the behavior of others (see also Humphrey, 1976, 1980; Whiten & Byrne, 1988b). There are also other advantages. Because relationships conceived in this way are abstractions, they can be more parsimonious and simpler than absolute judgments, which require learning the characteristics of every interaction (Allen, 1989; Dasser, 1985; Kummer, 1982; Premack, 1983). If a monkey can assess the relationships of others – rather than having to observe and remember all their interactions – he may be able to predict what opponents will do next even when he has seen them interact only once or twice. In other words, a monkey would be a much better social strategist if he had some way of representing different types of social relationship.

The content of representations, and their limitations

When we talk of monkeys recognizing a close association between two other animals, it is important to distinguish between “association” as referring

strictly to an observable fact – that two animals are often together – and “association” as referring to a more structured and differentiated representation of a social relationship. Monkeys are undoubtedly capable of recognizing that certain other individuals interact at high rates, and their comparison of different relationships are probably often based on differences in rates of interaction. However, an association that is based solely on interaction rates cannot incorporate any other qualities of a relationship. If a monkey learns to associate other animals solely on the basis of the rate at which they interact, he will be unable to distinguish between two different types of relationship when both involve similar rates of interaction. There will be no way for him to distinguish, for example, a female’s relationship with a juvenile male (her son) and the same female’s relationship with an adult male (her “friend” or longterm mate).

It seems probable, however, that monkeys are sensitive to more than just interaction rates when assessing other animals’ social relationships. They also appear to attend to subtler distinctions, including the types and quality of interactions, the age and sex of the participants, their dominance ranks, their past history of behavior, and so on (see, for example, Hinde, 1983). Recall, for example, that Dasser’s (1988a) longtailed macaques correctly identified numerous mother–offspring pairs despite marked variation in the ages, sex, and interaction rates of the individuals involved. Similarly, vervet monkeys reconciled primarily with their opponents’ kin following fights with unrelated animals, but with their opponents themselves following fights with members of their own matriline. This suggests that vervets distinguished their own close associates from the close associates of others, despite similarly high rates of interaction within all matrilineal kin groups. To give one final example, numerous studies of baboons, macaques, and vervets have shown that high-ranking females are more attractive grooming and alliance partners than low-ranking females, regardless of the rate at which they reciprocate (reviewed in Walters & Seyfarth, 1987). This observation suggests that females assess the benefits of social relationships not just in terms of the frequency of interactions, but also according to the potential benefits that different individuals can offer.

We may hypothesize, therefore, that the primate mind is predisposed to organize data on social behavior according to both the individuals involved and the content, quality and pattern of their interactions, since information about all of these features must be incorporated if an individual is to predict other animals’ behavior. The resulting representation has an abstract component because it is more than the sum of its parts. A social relationship cannot be described simply in terms of the participants’ physical resemblance, identities, or any single measure of activity like time spent grooming or the pro-

portion of fights followed by a reconciliation. Instead, it must incorporate information on all of these features.

If future investigations support the hypothesis that monkeys' representations of social relationships are not based solely on association rates, two further related issues will deserve particular attention. First, how many kinds of relationships are recognized? Is "mother" different from "sister"; is a "friend" of the same sex different from a "friend" of the opposite sex? At the moment, no empirical data address this issue, because no studies have examined whether monkeys can discriminate among relationships in which interaction rates are similar. Second, what are the consequences of having different representations for different types of relationships? How might they give one individual a selective advantage over others?

Even if monkeys do distinguish among different types of social relationships, however, it remains possible that their ability to assess these relationships is relatively inflexible and limited to circumstances in which the individuals involved are familiar. In all of the studies described to date, subjects have of necessity been tested only with the social companions that make up their group. As a result, we cannot state conclusively that a monkey confronted with an entirely new set of individuals – a young male transferring into a new group, for example – would be predisposed to look for close bonds among matrilineal kin, linear dominance relations, and so on. More to the point, how long would it take for a vervet or baboon to learn that not all primate species have the same patterns of social interaction? If a vervet male transferred into a gorilla group, where females are seldom closely related (Stewart & Harcourt, 1987), how long would it take for the male to cease expecting the females to interact at high rates? Would he ever?

There is no doubt that monkeys can learn to adjust to novel patterns of behavior, as Kummer, Goetz, and Angst (1970) demonstrated when they experimentally transferred females between groups of hamadryas and savannah baboons in Ethiopia. Unlike savannah baboons, who live in large, multi-male groups, hamadryas baboons form small, relatively stable one-male units. The spatial integrity of these units is strictly enforced by the males who lead them, and male unit leaders herd and threaten their females whenever the females stray from their units (Kummer, 1968). When Kummer and his colleagues artificially introduced female savannah baboons into hamadryas groups, the females learned within an hour to follow the specific males who had chosen them as their own. In particular, the females learned to approach males who threatened them, rather than to flee from them as they normally would have done in a savannah baboon group. Similarly, female hamadryas baboons who were introduced into a savannah baboon group soon learned to cease following males and formed no particular attachments with any individuals.

Interestingly, males who were transferred from one species to another failed to modify their behavior. Male savannah baboons who were introduced into hamadryas groups, for example, never learned to herd females as hamadryas males did.

Did the females' ability to adjust to their adopted groups involve any hypothesis about the nature of social structure and relationships in these groups? Was their rapid learning due entirely to the experience of being attacked or did it also involve observation and deduction? We simply do not know the mechanisms that underlie a monkey's understanding of its social environment. While a monkey's conception of social relationships may be abstract and independent of the particular individuals involved, it may also be relatively stimulus-bound and limited to the general types of bonds to which the monkey has been exposed (see also D'Amato, Salmon, & Colombo, 1985). It remains possible, in short, that monkeys are primatologists who have spent too much time studying a single species, or living in the same group.

Monkeys' representations of social relationships may be limited in at least two other respects. First, while the animals may be able to represent social relationships in their minds, we do not know if they ever make use of such representations in reasoning or computation. Consider, for instance, the different ways in which human primatologists on the one hand and monkeys on the other deal with the simultaneous existence of close bonds among kin and the attractiveness of high rank. Humans can readily see that these two principles will be additive for high-ranking families and counteractive for low-ranking families. We deduce, therefore, that high-ranking families will be more cohesive than low-ranking families, a prediction that is borne out by data (Cheney & Seyfarth, 1990b; Seyfarth, 1980). At present, however, we have no evidence that the monkeys themselves recognize this difference: no evidence, for example, that a middle-ranking female distinguishes the relations that exist in high-ranking matriline from the relations that exist in low-ranking matriline. More important, even if such data were to emerge, it would be essential to distinguish between information that the middle-ranking female had acquired through observation and experience (high-ranking mothers, for instance, support their offspring in alliances at higher rates than do low-ranking mothers) and information that the middle-ranking female had acquired through deduction. Indeed, with the exception of data on the recognition of other animals' dominance ranks, we presently have no evidence that computation plays a major role either in the monkeys' representations of social relationships or in their representations of word meaning. In this respect, representations of social phenomena may differ fundamentally from the representations of rate, time, and space used by birds and other animals

when computing and comparing feeding returns at alternative food patches (see also Gallistel, 1990 for reviews).

Second, as noted earlier, we have no evidence that monkeys can label social relationships or give names to the criteria they use in classifying them. While certain primate vocalizations do function in a manner that effectively labels different predators (Seyfarth, Cheney, & Marler, 1980) or different classes of conspecifics (e.g., Cheney & Seyfarth, 1982a; Gouzoules, Gouzoules, & Marler, 1984), monkeys apparently have no calls referring to "close partners," "friends," "enemies" or "strangers" that could be used to classify relationships. Whether they could learn such terms under the appropriate conditions remains an open question: None of the ape language studies has ever asked subjects about each others' relationships.

Among adult humans, accurate use of a word like "friend" implies that we recognize the necessary and sufficient characteristics for membership in this category, and hence that we can apply the category's label correctly in novel situations. If the presence or absence of a label is some measure of an individual's awareness of classes and of relations between classes, then the ability of monkeys to compare relationships and generalize to novel situations may be severely limited.

The apparent lack of vocalizations to describe different types of relationships may be symptomatic of a larger problem: The monkeys are unaware of their own knowledge. In Paul Rozin's (1976) terms, a monkey's knowledge of social relationships or word meaning may be "inaccessible." While the monkey can classify familiar relationships into types and even compare social relationships involving different individuals, he may not be able to examine his own knowledge, label it, apply it to new stimuli, or use it to deduce new knowledge. In addition, perhaps because the monkey cannot reflect on what he knows about others, he may be unable to attribute motives and hence understand why some relationships are alike and others are quite different.

We have argued that in order to succeed socially monkeys must be able to predict the behavior of others. To do this well they cannot rely on memorizing single interactions but must instead deal in abstractions, comparing the relationships that exist among others. For humans, the quest to predict behavior prompts us to search still further, for the factors that cause some relations to be different from others. A monkey that can compare social relationships is better able to predict the behavior of others than one who simply memorizes all the interactions he has observed. Vastly more powerful abilities to interpret other animals' behavior accrue to the individual who can attribute motives to others and classify relationships on the basis of these motives (Humphrey, 1980; Whiten & Byrne, 1988a, 1988b).

There are hints that nonhuman primates might occasionally attribute mo-

tives to one another (e.g., Byrne & Whiten, 1988; de Waal, 1982; Kummer, 1982; Premack & Woodruff, 1978). Most examples, however, are anecdotal, and they are largely restricted to chimpanzees. Whether monkeys ever attribute states of mind to each other and whether they recognize that different states of mind are the cause of different social relationships, is an open question. In most cases, it is as easy to explain the behavior of monkeys in terms of learned behavioral contingencies as in terms of the attribution of mental states (see Cheney & Seyfarth, 1990b for a review). We have good evidence that monkeys are adept at understanding each others' behavior and relationships; what remains to be determined is whether they are also adept at understanding each others' *minds*.

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