



Kin Selection in Primate Groups

Joan B. Silk¹

Received February 8, 2001; accepted April 23, 2001

Altruism poses a problem for evolutionary biologists because natural selection is not expected to favor behaviors that are beneficial to recipients, but costly to actors. The theory of kin selection, first articulated by Hamilton (1964), provides a solution to the problem. Hamilton's well-known rule ($br > c$) provides a simple algorithm for the evolution of altruism via kin selection. Because kin recognition is a crucial requirement of kin selection, it is important to know whether and how primates can recognize their relatives. While conventional wisdom has been that primates can recognize maternal kin, but not paternal kin, this view is being challenged by new findings. The ability to recognize kin implies that kin selection may shape altruistic behavior in primate groups. I focus on two cases in which kin selection is tightly woven into the fabric of social life. For female baboons, macaques, and vervets maternal kinship is an important axis of social networks, coalitionary activity, and dominance relationships. Detailed studies of the patterning of altruistic interactions within these species illustrate the extent and limits of nepotism in their social lives. Carefully integrated analyses of behavior, demography, and genetics among red howlers provide an independent example of how kin selection shapes social organization and behavior. In red howlers, kin bonds shape the life histories and reproductive performance of both males and female. The two cases demonstrate that kin selection can be a powerful source of altruistic activity within primate groups. However, to fully assess the role of kin selection in primate groups, we need more information about the effects of kinship on the patterning of behavior across the Primates and accurate information about paternal kin relationships.

KEY WORDS: altruism; kinship; kin selection; reciprocity.

¹Department of Anthropology, University of California – Los Angeles, Los Angeles, California 90095; e-mail: Jsilk@anthro.ucla.edu.

THE PROBLEM OF ALTRUISM

Since Darwin's day biologists have been aware that animals perform some behaviors that enhance the fitness of others, but not themselves. In *The Descent of Man, and Selection in Relation to Sex*, Darwin (1871, p. 75) wrote:

"Social animals perform many little services for each other: horses nibble, and cows lick each other, on any spot which itches: monkeys search for each other's external parasites; and Brehm states that after a troop of the Cercopithecus griseo-viridus has rushed through a thorny brake, each monkey stretches itself on a branch, and another monkey sitting by "conscientiously" examines its fur and extracts every thorn or burr.

Animals also render more important services to each other: thus wolves and some other beasts of prey hunt in packs, and aid each other in attacking their victims. Pelicans fish in concert. The Hamadryas baboons turn over stones to find insects, and when they come to a large one, as many as can stand round, turn it over together and share the booty . . ."

These examples intrigued, but troubled, Darwin because he realized that they contradicted the general logic of his theory of evolution by natural selection (Richards, 1987). Concurrently, however, he was convinced that the social instincts that produced behaviors like these played a fundamental role in social life and the evolution of moral sensibilities in modern humans (Darwin, 1871).

Eventually, Darwin worked out a solution to the problem. He suggested that "With strictly social animals, natural selection sometimes acts indirectly on the individual, through the preservation of variations which are beneficial only to the community. A community including a number of well-endowed individuals increases in number and is victorious over other and less well-endowed communities; although each separate member may gain no advantage over the other members of the same community" (Darwin, 1871: 155).

Although this solution relieved Darwin's anxiety about the viability of his theory, we now know that his intuition misled him. Traits that confer advantages to the group do not persist unless certain conditions are met. To see where Darwin went wrong, imagine a hypothetical species of monkeys in which there is a genetically-inherited tendency to give alarm calls. Monkeys are distributed into groups at random with respect to the trait. Thus, the distribution of the trait in each group will be, on average, the same as the distribution in the population at large. Animals that inherit the alarm calling trait are inclined to give alarm calls when they are the first to spot predators (callers) while ones that do not inherit the trait are inclined to remain silent when they sight predators (noncallers). Callers make themselves conspicuous to predators and increase their own vulnerability, while animals that are

alerted by alarm calls are more likely to escape attack. Thus, calling is costly to the actor and beneficial to the recipients.

Natural selection will favor the evolution of calling if callers have higher fitness on average than noncallers. Imagine a situation in which a caller is the first to spot the predator. She calls, allowing all the other members of the group to flee to safety and thereby gain a fitness advantage. Now imagine another group in which a noncaller sees the predator first, but does not alert the group. This reduces their chance of escaping the predator, and therefore reduces the fitness of all group members. Even though the members of the caller's group are better off on average than members of the noncaller's group, calling is not favored because calling is costly to the caller herself. Thus, the average fitness of callers will be lower than the average fitness of noncallers, and the trait will become less common in the population. In situations like these, alarm calling will not be favored by natural selection even if the costs of calling are small and the benefits of calling for other group members are quite substantial.

Solutions to Darwin's Problem

The first cogent explanation for the evolution of behaviors like alarm calling was provided by Hamilton (1964), who recognized that any process that would cause callers to interact selectively with other callers could facilitate the evolution of alarm calling behavior. More specifically, he suggested that selective interaction among kin, which are descended from a common ancestor, could promote the evolution of traits like alarm calling. He called the process kin selection. If callers live in groups composed of kin, then they enhance the fitness of others that are likely to carry copies of the same genes. Even though the caller reduces her own fitness, her call increases the fitness of her relatives, which may be callers themselves. In this situation, callers are more likely to benefit from calling than noncallers, so calling alters the relative fitness of callers and noncallers. At the same time, because kin aggregate together, noncallers are less likely to find themselves in groups with callers than expected by chance alone. The same logic can be applied to any form of behavior that is costly to the actor and beneficial to the recipient.

Selective interaction with other altruists is a necessary, but insufficient, condition for the evolution of behaviors like alarm calling. In the hypothetical situation, calling will only evolve if the benefits of calling sufficiently outweigh the costs of becoming more conspicuous to predators. The adaptive value of an alarm call or other altruistic act depends on the fitness costs to the donor and the benefits conferred on the recipient. Hamilton (1964) demonstrated that behaviors like alarm calling will be favored by selection if the costs of performing the behavior (c) are less than the benefits (b)

discounted by the coefficient of relatedness between actor and recipient (r). The coefficient of relatedness is the average probability that two individuals acquire the same allele through descent from a common ancestor. This can be expressed simply in Hamilton's rule: $br > c$.

Hamilton's Rule generates two general predictions about the evolution of altruistic behavior via kin selection. First, altruism should be limited to kin, because the inequality can only be satisfied when $r > 0$. Second, costly altruism should be restricted to close kin. When $r = 0.5$, the degree of relatedness between parents and offspring, the benefits must exceed just twice the costs to the actor in order to satisfy the inequality. But when $r = 0.125$, as it is among first cousins, the benefits must exceed 8 times the cost. Thus, close kinship facilitates costly altruism.

Kin selection plays a fundamental role in the organization of behavior in a variety of animal taxa. Perhaps the most obvious example of kin selection comes from studies of social insects, particularly eusocial species (Bourke, 1997 and Seger, 1991). In cooperatively breeding birds, kinship influences the likelihood of becoming a helper and the distribution of help given to group members (Emlen, 1991, 1997; Jaisson, 1991; Ligon, 1991). Similar patterns occur in eusocial naked mole rats (Jarvis *et al.*, 1994), cooperatively breeding lions (Packer and Pusey, 1997), brown hyenas (Owen and Owen, 1984), and dwarf mongooses (Creel *et al.*, 1991). In other social mammals, kinship influences the distribution of altruistic behaviors such as alarm calling in ground squirrels (Sherman, 1977) and allomaternal behavior in elephants (Lee, 1987).

Although kin selection is a powerful mechanism to generate altruism in nature, it is not the only possible means. Altruism can also evolve via reciprocal altruism if pairs of individuals balance the benefits and costs of altruistic acts over time (Axelrod and Hamilton, 1981; Dugatkin, 1997; Trivers, 1971). Reciprocal altruism works because individuals selectively aid reciprocating partners, and altruism is therefore restricted to reciprocators. Thus, kin selection and reciprocal altruism both rely on Hamilton's (1964) insight that altruistic behaviors can only evolve if there is some mechanism that causes altruists to interact selectively with other altruists.

Problems of Definition and Measurement

Behaviors like alarm calling are considered to be altruistic because they are costly to actors and beneficial to recipients. Some workers have complained about use of the word altruism in this context because behaviors that evolve through kin selection are phenotypically (or self-) sacrificing, but genotypically selfish (Alexander, 1974). This contradicts the common English usage of the word altruism, which connotes unselfish, self-sacrificial

acts (Fletcher, 1987). Alexander (1974) and Fletcher (1987) suggested that we use nepotism to refer to behavior that evolved via kin selection. However, this creates at least one new semantic problem. Nepotism implies preferential treatment of kin, but is silent about the nature of the effects on the actor. Thus, I use the term altruism to describe any behavior that reduces the fitness of the actor and increases the fitness of the recipients ($b > c$) and nepotism to describe preferential treatment of kin, regardless of the relative magnitude of b and c .

Practical difficulties arise when we try to test predictions derived from Hamilton's rule in nature. It is rarely possible to quantify the effects of a behavioral act or social interaction on lifetime fitness, particularly in long-lived animals like primates, and thus difficult actually to measure b and c . Testing predictions derived from Hamilton's Rule also requires information about genetic relatedness. Until recently, primatologists have relied on demographic data for this information. Thus, observers record births to known females and construct geneologies from them. This is a slow and painstaking task and still provides only half the information that is necessary to measure relatedness. Geneologies derived from demographic data trace relatedness through maternal lines. Thus, most studies that examine the effects of kinship on social behavior actually evaluate the effects of maternal kinship on behavior. This would not matter if monkeys were unable to recognize paternal kin, but it does matter if they can. Although new genetic techniques allow primatologists to identify paternity and to obtain more accurate measurements of relatedness, relatively few behavioral studies incorporating these kinds of data have been published.

How can we study kin selection if we can't measure the relevant parameters? This problem is common to almost all studies of the adaptive function of social behavior in animals. We rely on the phenotypic gambit (Grafen, 1991): the assumption that the short-term benefits that individuals derive from social interactions are ultimately translated into long-term differences in fitness. Animals that are regularly supported in agonistic confrontations, protected from harassment, or allowed to share access to desirable resources are expected to gain short-term benefits that are ultimately translated into fitness gains.

ASSESSING THE ROLE OF KIN SELECTION IN PRIMATE GROUPS

A review of the role of kin selection in the evolution of social behavior among primates should be carefully balanced across taxa and should cover the full range of relevant behavioral phenomena. Unfortunately, the

empirical record is biased. We know much more about behavioral patterns in Old World monkeys than we do about the behavior of New World monkeys and prosimians. Few studies on New World monkeys or prosimians have continued long enough to construct the kinds of genealogies that are necessary to examine the effects of kinship on social behavior. Modern molecular genetic techniques shorten the time required to do this, but studies that include these sorts of data are limited in number and scope. This means that most of what we currently know about the effects of kinship on social behavior comes from a relatively small number of species and is limited to maternal kin.

To assess the role of kin selection we would also need to gauge the importance of kin selection across the full range of altruistic behaviors that occur in nature. However, the empirical record is uneven. We know much more about the distribution of relatively common behaviors like grooming and coalition formation than we do about less common behaviors like alarm calling and food sharing (Bernstein, 1991; Gouzoules and Gouzoules, 1987; Silk, 1987; Walters, 1987a). For example, I located only one primate study on the effects of kinship on the likelihood of giving alarm calls (Cheney and Seyfarth, 1985).

Consequently, I rely on a relatively limited set of behaviors in a relatively small number of species. I have deliberately chosen to focus on cases in which kin selection plays a crucial role because they illuminate how kin selection can shape the evolution of social organization, reproductive strategies, and social behavior. Moreover, by studying a small number of examples in depth we can get a better sense of how kinship is woven into the fabric of social life.

Kin Recognition

"In general, . . . finding of ability to discriminate [kin], even if uses made of it are still obscure is prima facie suggestion of the importance that kin selection is likely to have in nature" (Hamilton, 1987).

The coefficient of relatedness, r , is the critical element to determine an adaptive course of action in social interactions (Hamilton, 1987). In order to meet the conditions of Hamilton's rule, animals must limit altruistic behavior to their kin ($r > 0$). For species in which kin are clustered in discrete locations, such as in burrows or nests, spatial location may provide sufficient information for kin discrimination (Blaustein *et al.*, 1987). However, for other animals the problem is more complicated. The ability to discriminate kin is expected to be most fully developed in species that live in social groups, when there are opportunities for costly fitness-reducing behaviors, such as egg dumping, and when simple cues for distinguishing kin from nonkin (such as location) are not likely to be effective (Hamilton, 1987).

Primates fit all three of these conditions. Most primates live in large, relatively stable social groups (Smuts *et al.*, 1987). Even the most solitary primates, like orangutans and galagos, have regular interactions with familiar conspecifics (Bearder, 1987; Delgado and van Schaik, 2000; Galdikas, 1988). Primates engage in a variety of fitness-reducing behaviors, including infanticide (van Schaik and Janson, 2000); severe intragroup aggression (Crockett, 1984; McGrew and McLuckie, 1986; Sauther *et al.*, 1999; Silk *et al.*, 1981; Vick and Pereira, 1989); and intense feeding competition (Dittus, 1979, 1988). Most primates live for extended periods of time in groups that include both relatives and nonrelatives, so context-driven mechanisms for distinguishing kin are likely to be of limited use. Thus, primates are expected to exhibit finely developed kin recognition abilities.

Several different perceptual mechanisms underlie kin recognition (Sherman *et al.*, 1997). For example, sea squirts are able to recognize other sea squirts that carry the same allele on the hypervariable histocompatibility locus (Pfennig and Sherman, 1995). Some animals learn to identify their relatives during development, drawing cues about kinship from patterns of association and interactions. This is thought to be the most common mechanism for kin recognition, particularly among mothers and offspring (Holmes and Sherman, 1983).

Close association early in life is generally thought to be the basis for kin recognition in primate groups (Bernstein, 1991; Walters, 1987a). Early association may provide an efficient mechanism to learn to recognize maternal kin, but not for identifying paternal kin. This is because close associations between males and females are uncommon in many primate species, limiting infants' abilities to identify their paternal kin. Moreover, there may be considerable uncertainty about paternity in most primate species. Even in pair-bonded species, like gibbons and titis, females sometimes mate with males outside their groups (Mason, 1966; Palombit, 1994; Reichard, 1995). In some species that form one-male groups, such as patas and blue monkeys, incursions by nonresident males may occur during the mating season (Cords, 1987). In multimale species, male rank is often correlated with reproductive success, but the association is imperfect.

If primates rely on early association to identify their relatives and associations between males and infants are unreliable cues of paternity, then paternal kin recognition would have to be based on the ability to recognize familial alleles or phenotypic matching. Wu *et al.* (1980) caused a minor sensation when they reported that juvenile monkeys showed behavioral preferences for unfamiliar half-siblings over unfamiliar nonrelatives. This was a striking result, but subsequent efforts to replicate it were unsuccessful (Fredrickson and Sackett, 1984; Sackett and Fredrickson, 1987). Small and Smith (1981) reported that mothers were more tolerant of infant handling

by their infants' paternal half siblings than by unrelated juveniles, which would imply that monkeys could identify paternal kin (Walters, 1987a). However, Bernstein (1991) found that Small and Smith's statistical analysis is flawed, and the effect they reported disappeared when he reanalyzed the data.

Subsequent studies have examined the independent effects of familiarity and kinship on interaction patterns among young monkeys (Erhart *et al.*, 1997; MacKenzie *et al.*, 1985; Welker *et al.*, 1987). In all 3 studies, monkeys showed clear preferences for familiar conspecifics over unfamiliar conspecifics. In 2 of the studies, monkeys did not discriminate among kin and nonkin when familiarity was held constant (Erhart *et al.*, 1997; Welker *et al.*, 1987). The results of the third study are anomalous: monkeys seemed to prefer paternal kin over unfamiliar nonkin when familiarity and rearing conditions were controlled, but showed no preference for familiar maternal kin (MacKenzie *et al.*, 1985). Several other researchers who examined the effects of kinship on mating preferences in captive populations reported strong inhibitions of mating with maternal kin, but no inhibition against mating with paternal kin (Inouye *et al.*, 1990; Kuester *et al.*, 1994; Smith, 1986).

Thus, most researchers have become convinced that primates rely on familiarity to distinguish kin from nonkin and therefore cannot recognize paternal kin. For example, in a review of the role of kinship in primate societies, Gouzoules and Gouzoules (1987, p. 304) concluded that available evidence from studies of baboons and macaques "cast considerable doubt on the ability of males to recognize their own infants independent of close behavioral association." Later, Chapais (1995, p. 117) wrote "Relatedness through the father, although of significant importance due to the prevalence of polygyny is not recognized in macaques: paternal half-siblings cannot recognize each other." And Mitani *et al.* (2000) reasoned, "... internal fertilization coupled with a promiscuous mating system... render it doubtful that male chimpanzees possess an ability to recognize paternal relatives."

Recent evidence suggests that the conventional wisdom may need to be reconsidered; nonhuman primates apparently recognize their own paternal kin in some situations. Widdig and her colleagues (Widdig *et al.*, 2001, in press) compared the rate and pattern of social interactions among maternal half-sisters, paternal half-sisters, and unrelated females among rhesus macaques on Cayo Santiago. Females showed strong affinities for maternal half-sisters, as expected. However, they also showed strong affinities for their paternal half-sisters, spending more time grooming and in close proximity to them than to unrelated females. Age may be a good proxy for paternal kinship as high-ranking males monopolize access to females andagemates are therefore likely to be paternal half-siblings (Altmann, 1979).

This means that monkeys might use age similarity as a context-dependent mechanism to distinguish kin from nonkin. In Widdig *et al.*'s study, females generally preferred agemates over others. Dunbar and Dunbar (1975), Pereira and Altmann (1985) and Walters (1987a,b) obtained similar results. However, Widdig and her colleagues found that female macaques also distinguished among their agemates, preferring paternal halfsiblings over nonkin.

These results are consistent with more limited evidence from a study of consort behavior among baboons in Amboseli, Kenya (Alberts, 1999). Although male dispersal typically limits opportunities for consortships among siblings, dispersal was delayed in one garbage-feeding group. Alberts (1999) found that consortships among agemates were typically less cohesive than consortships among nonagemates. However, the 3 pairs of agemates that were also paternal halfsiblings had the least cohesive consorts of all pairs of agemates, while the pairs of agemates with the most cohesive consorts were unrelated.

In Amboseli, adult female baboons also show affinities for age mates and preferences for paternal kin over unrelated individuals (Smith, 2000). Taken together, these studies suggest that cercopithecine females may use two rules of thumb to assess kinship: (a) treat as kin individuals known since birth, and (b) treat as kin individuals that bear familial cues (Smith, 2000).

Finally, there is tentative, but intriguing, evidence that primates may be able to recognize kinship from visual cues alone. Parr and de Waal (1999) found that chimpanzee females are able to match digitized photographs of unfamiliar females with their sons, but not with their daughters. Since the chimpanzees were unfamiliar with the individuals in the photographs and had no physical, auditory, or olfactory contact with them, their ability to identify mother-son pairs suggests that chimpanzees use visual cues to assess similarity. If the chimpanzee success in matching mothers and sons together is based on the ability to detect similarities in facial features, then it is possible that chimpanzees might also be able to match other kin pairs, such as fathers and sons, siblings, and so on. Of course, the chimpanzee inability to match mothers and daughters together raises some doubt about the likelihood that they can do so consistently. Moreover, it is not clear whether the chimpanzees that matched mothers and sons categorized them as kin.

Case 1: Nepotism in Macaques, Baboons and Vervets

In macaques, baboons, and vervets matrilineal kinship underlies a suite of features, including female philopatry, well-differentiated relationships

among females, matrilineal social networks, and stable matrilineal dominance hierarchies. This constellation of characteristics apparently evolved in the common ancestor of contemporary Old World monkey species and has been conserved subsequently in descendant species, even though they have radiated into diverse ecological niches throughout Africa and Asia (Di Fiore and Rendall, 1994; Rendall and Di Fiore, 1995). Thus, there are many similarities in the social structure of extant macaques, baboons, and vervets.

Matrilineal kinship bonds have a profound impact on the lives of female macaques, baboons, and vervets. Females, which remain in their natal groups throughout their lives, spend much of their time with their maternal kin, sitting near them while resting and feeding, grooming them, and handling their infants (Altmann, 1980; Chapais, 1983; Cheney, 1978; DeFler, 1978; Gouzoules, 1984; Gouzoules and Gouzoules, 1987; Kapsalis and Berman, 1996a; Kurland, 1977; Missakian, 1974; Sade, 1965; Saunders, 1988; Silk, 1982, 1999; Silk *et al.*, 1981, 1999; Walters, 1981). They are also more likely to provide coalitionary support to members of their matriline than to support others (Berman, 1983a,b,c; Bernstein and Ehardt, 1985, 1986; Chapais, 1983a; Cheney, 1983; Datta, 1983a,b; de Waal, 1977; Kaplan, 1977, 1978; Kurland, 1977; Massey, 1977; Silk, 1982; Walters, 1981).

Although several studies indicate that female macaques are more tolerant of kin than nonkin during feeding (Belisle and Chapais, 2001; de Waal, 1986; Furiuchi, 1983; Imakawa, 1988), nepotism apparently does not extend to active food-sharing. Schaub (1996) examined female long-tailed macaques' willingness to forego feeding in order to provide food to related and unrelated group members. Females gained access to food by pulling on a counter-weighted bar. When females pulled the bar toward themselves, they simultaneously denied access to their partner. When females released the bar, they allowed their partner to feed. Schaub (1996) found that most females did not differentiate between kin and nonkin, giving them equal access to food. The significance of these results is difficult to evaluate because active food sharing is not part of their normal behavioral repertoire. Females in the experimental group showed nepotistic biases in other domains, such as grooming (Schaub, 1996).

Surprisingly, kinship provides little protection against aggression, as rates of aggression are as high or higher among maternal kin than among members of different matriline (Bernstein and Ehardt, 1985, 1986; Kurland, 1977; Silk *et al.*, 1981). Bernstein (1991) suggested that the disruptive effects of aggression on social relationships among kin may be limited because monkeys are more likely to reconcile with maternal kin than with members of other matriline. This interpretation relies on the widely held assumption that reconciliation mends relationships that are damaged by conflict (Aureli and de Waal, 1999; *cf.* Silk, 1997).

Following Hamilton's Rule

Several lines of evidence suggest that macaques, baboons, and vervets are discriminating altruists, taking into account each of the parameters in Hamilton's rule. They seem to adjust their behavior in relation to the degree of relatedness between themselves and their partners. Thus, rhesus and Japanese macaques spend more time near close kin than near more distant kin and nonkin and groom and support close kin at higher rates than more distant kin and nonkin (Kapsalis and Berman, 1996a; Kurland, 1977). Macaques are more likely to intervene on behalf of close kin than distant kin (Chapais *et al.*, 1997; Datta, 1983c; Kapsalis and Berman, 1996a; Kurland, 1977; Massey, 1977) and are also more tolerant of close kin than distant kin while feeding (Belisle and Chapais, 2001).

Several studies have demonstrated that altruism becomes less common as the degree of relatedness between actors and recipients declines (Belisle and Chapais, 2001; Berman, 1982; Chapais *et al.*, 1997, 2001; Kurland, 1977; Kapsalis and Berman, 1996a). Experimental and observational data suggest that macaques do not consistently discriminate between kin and nonkin when the degree of relatedness drops to <0.125 (Belisle and Chapais, 2001; Chapais *et al.*, 2001; Kapsalis and Berman, 1996a).

It is not clear whether the relatedness threshold reflects the fact that macaques do not recognize more distant relatives as kin (Kapsalis and Berman, 1996a) or that support for distant kin fails to meet the criteria for altruism specified by Hamilton's rule (Belisle and Chapais, 2001; Silk, 2000). The fact that Japanese macaques apparently apply a single criterion across several different behaviors that might have different benefit-cost structures—coalition formation, co-feeding, avoidance of homosexual interactions—suggests that the threshold is a function of kin recognition. This interpretation is also consistent with the finding that monkeys behave differently toward direct kin (great-grandmother-great-grandoffspring) and collateral kin (aunt-nephews), even though the degree of relatedness is the same ($r = 0.125$; Chapais *et al.*, 2001).

Studies of coalition formation provide further evidence that macaques are sensitive to variation in the parameters in Hamilton's Rule. Coalitions provide "the clearest evidence of primates engaging in behavior that benefits another at some risk and/or cost to self" (Bernstein, 1991), but not all agonistic encounters pose equal risks for potential allies and not all acts of support are likely to provide equal benefits to recipients (Prud'homme and Chapais, 1996; Silk, 1992; Widdig, 2000).

Females take greater risks and absorb higher costs on behalf of close kin than distant kin or nonkin. Monkeys are more likely to intervene on behalf of close kin against individuals that are higher-ranking than themselves

(and therefore likely to launch counterattacks on allies) than on behalf of distant kin (Chapais *et al.*, 1997; Datta, 1983c). Moreover, when the risks to themselves are low, monkeys are more likely to intervene. Thus, members of high-ranking lineages, whose maternal kin are relatively invulnerable to retaliatory attacks, are supported by their relatives at higher rates than members of low-ranking lineages are (Berman, 1980; Chapais *et al.*, 1991; Cheney, 1977; Datta, 1983c; Horrocks and Hunte, 1983; Netto and van Hooff, 1986).

Careful studies of the process of rank acquisition in Japanese macaques suggest that even young females are sensitive to variation in cost-benefit ratios. As in other macaque species, young Japanese macaque females commonly rise in rank over their older sisters. This process is sometimes contentious, and younger sisters target their older sisters for rank reversals (Chapais *et al.*, 1994). When females intervene in disputes involving their older sisters and subordinate nonkin, they are as likely to intervene against their sisters as they are to support them. In contrast, when females intervene in conflicts involving kin that are not targeted for rank reversals, females are much more likely to intervene on behalf of their relatives than their opponents (Chapais *et al.*, 1994). Thus, females “apparently solve the conflict of interest between egotism and nepotism by maximizing their own rank among their kin on the one hand, and by maximizing the rank of their kin in relation to non-kin on the other” (Chapais, 1995, p. 129).

Nepotism Shapes Social Structure

Matrilineal biases in the construction and development of social networks and the patterning of support have a direct impact on the acquisition of dominance rank in macaques, baboons, and vervets (Chapais, 1992). Infants are protected and supported by their mothers and other close kin when they are threatened by other group members, particularly females lower-ranking than their own mothers (Berman, 1980; Datta, 1983a; de Waal, 1977; de Waal and Luttrell, 1985; Paul and Kuester, 1987; Walters, 1980). As they grow older, young juveniles receive support when they challenge peers whose mothers are lower-ranking than their own mothers and when they challenge adults that are subordinate to their own mothers. Initially, juveniles can defeat older and larger juveniles only when their own mothers are nearby (Datta, 1983a,b; Horrocks and Hunte, 1983). Later, they are able to defeat all group members that are subordinate to their own mothers, even when their mothers are not in the vicinity. Since juveniles are able to defeat everyone that their own mothers can defeat, but not their mothers themselves, offspring acquire ranks just below their mothers. The same process, repeated over generations and across families, generates corporate matrilineal

dominance hierarchies. Thus, daughters acquire ranks below their mothers, which in turn occupy ranks below their own mothers. This means that all members of the same matriline occupy contiguous ranks. Moreover, all members of a given matriline rank above or below all the members of other matriline. Matrilineal dominance hierarchies have been documented in ≥ 7 species of macaques (Chapais, 1992), savanna baboons (Hausfater *et al.*, 1982; Johnson, 1987; Lee and Oliver, 1979; Moore, 1978; Silk *et al.*, 1999), and vervets (Bramblett *et al.*, 1982; Fairbanks and McGuire, 1986; Horrocks and Hunte, 1983; Lee, 1983).

The matrilineal dominance hierarchies that characterize macaque, baboon, and vervet groups have 3 striking properties. They are transitive, linear, and very stable. Nearly all encounters between a particular pair of females have predictable outcomes: the higher-ranking female wins. Their dominance hierarchies are also very stable over time. Even though dominance hierarchies are sometimes disrupted by radical upheavals (Ehardt and Bernstein, 1986; Samuels *et al.*, 1987; Samuels and Henrickson, 1983), long periods with few changes are common (Bramblett *et al.*, 1982; Chapais, 1992; Hausfater *et al.*, 1982; Samuels *et al.*, 1987; Silk, 1988).

Female dominance rank has important fitness consequences for females. In some groups, high-ranking females mature at earlier ages, give birth to healthier infants, and have shorter interbirth intervals than low-ranking females do (Harcourt, 1987; van Noordwijk and van Schaik, 1999; Silk, 1987). Although statistically significant associations between dominance rank and all reproductive parameters are not evident in every group (Altmann *et al.*, 1988; Cheney *et al.*, 1988; Gouzoules *et al.*, 1982; Packer *et al.*, 1995), there is little evidence that being low-ranking is advantageous.

The relationship between dominance rank and reproductive success may also contribute to the stability of dominance hierarchies over time. The power of a matrilineage is likely to be related to its size because larger lineages are able to muster more allies than smaller lineages can. Accordingly, differential reproductive success among females of different ranks will perpetuate power differences among matriline. All other things being equal, high-ranking lineages are likely to become larger and more powerful, and to reproduce more successfully over time, while low-ranking lineages are likely to become smaller and less powerful, and to reproduce less successfully.

Although maternal kinship plays a central role in the daily lives of female macaques, baboons, and vervets, the extent of nepotism varies across species and groups (Cheney, 1992; Silk *et al.*, 1999; Thierry, 2000), within social groups over time (Kapsalis and Berman, 1996a), and among lineages within groups (Chapais and Primi, 1991; Cheney, 1977; Horrocks and Hunte, 1983; Kapsalis and Berman, 1996a; Netto and van Hooff, 1986; Silk, 1982; Silk *et al.*, 1999). For example, among female baboons in Botswana, members

of high-ranking lineages devoted a greater fraction of grooming to maternal kin than members of lower-ranking lineages did. The basis for this variation is not well-established, though ecological (Cheney, 1992), demographic (Kapsalis and Berman, 1996b), and phylogenetic factors (Thierry, 2000) may all play a role.

Kin Selection is Not the Only Force at Work

There is no reason to expect kin selection to be the only force shaping female social relationships in baboons, macaques, and vervets. In fact, females sometimes groom reciprocally (Barrett *et al.*, 2000; Henzi and Barrett, 1999; Muroyama, 1991; Silk *et al.*, 1999) or exchange grooming for other benefits. Thus, low-ranking monkeys sometimes exchange grooming for coalitionary support from high-ranking individuals (Hemelrijk, 1994; Perry, 1996; Seyfarth, 1977, 1980; Seyfarth and Cheney, 1984; Silk, 1992a,b), though this pattern does not occur in all groups (Fairbanks, 1980; Kapsalis and Berman, 1996b; Silk, 1982). Grooming might also be exchanged for tolerance at feeding sites (Cords, 1997; de Waal, 1991; Kapsalis and Berman, 1996b), access to newborn infants (Henzi, 2001; Muroyama, 1994), or reduced aggression (Silk, 1982).

Moreover, behaviors that might be altruistic in one context may not be altruistic in other contexts. For example, when Japanese macaques intervene in ongoing disputes among members of other matrilineal groups, there is a strong tendency to support the higher-ranking of the two opponents (Chapais *et al.*, 1991; Prud'homme and Chapais, 1996). This kind of conservative support, which is also common among male bonnet and Barbary macaques (Silk, 1992b, 1993; Widdig *et al.*, 2000), may reinforce existing dominance relationships and enhance the status of the ally. If both allies and recipients benefit, support may be mutualistic, not altruistic.

In some cases, the ally may be the only party that benefits from intervention and support may actually be selfish. Prud'homme and Chapais (1996) argued that this is often the case when juvenile Japanese macaques intervene in ongoing disputes. Juvenile females are considerably more likely to defeat older and larger juveniles when they intervene in ongoing disputes than when they act alone. The costs of such intervention to the ally are relatively low because counterattacks are uncommon. Moreover, interventions do not necessarily help the recipients: juvenile females were as likely to intervene on behalf of monkeys that had already defeated their opponents, and presumably did not need additional help, as they were to intervene on behalf of monkeys that had not defeated their opponents. Prud'homme and Chapais (1996) noted that juvenile females are equally likely to intervene against kin

and nonkin and suggested that females place their own interests above those of others.

Some researchers have suggested that the strong bonds among maternal kin may reflect strong attraction to females of similar rank, not to females that share genes through common descent. Seyfarth (1977, 1983) first applied this idea to females, and he hypothesized that females would be attracted to high-ranking females because they provided the most effective coalitionary support. Competition over access to high-ranking females would force females to settle for partners of their own rank, producing high rates of interaction among females of adjacent rank. Later, de Waal (1991; de Waal and Luttrell, 1986) suggested that females will be attracted to others that most closely resemble them in rank, age, and kinship because they are the ones with which exchange relationships are most likely to be profitable. In both these models, reciprocal altruism is the selective force guiding the formation of social relationships among females.

Efforts to evaluate the relative importance of maternal kinship and rank distance in female relationships have been complicated by the fact that maternal kin usually occupy adjacent ranks, confounding the effects of maternal kinship and rank distance. One approach is to compare affinities between kin and unrelated females that occupy adjacent ranks. Female baboons and bonnet macaques show clear preferences for maternal kin over unrelated females that occupy adjacent ranks (Silk, 1982; Silk *et al.*, 1999). Using matrix correlation techniques, Kapsalis and Berman (1996b) untangled the effects of maternal kinship and rank distance on social relationships among female rhesus macaques. Their analysis suggests that maternal kinship is the primary organizing principle underlying female social relationships. Kin biases are complemented by a weaker and less consistent attraction to females of similar rank and in some years by an attraction to females of higher rank. Their data provide no support for predictions derived from the similarity model.

Case 2: Red Howlers

The second case study is drawn from studies of free-ranging red howlers (*Alouatta seniculus*). Red howlers represent an independent case for analysis because Old and New World primates diverged from a common ancestor ≥ 40 ma (Rosenberger, 1992). Red howlers have been studied at several different sites in Venezuela, producing a unique body of behavioral, ecological, demographic, and genetic data.

Red howlers form groups of 2–5 adult females, 1–3 adult males, and their offspring. Members of both sexes disperse, but the pattern of dispersal

depends on sex and local demographic conditions. In most cases, females disperse at earlier ages and over longer distances than males do. Red howlers are fiercely territorial, and both sexes respond aggressively to incursions by strangers (Crockett and Pope, 1988, 1993). Females almost never join established groups, but male strategies are more variable. Males may attempt to take over established groups and to oust resident males or join migrating females as they establish new groups.

New groups are formed when unrelated, solitary migrating females meet, form social bonds, attract males, manage to establish a territory from which they exclude outsiders, and begin to reproduce (Pope, 2000a). Once females begin to reproduce within a group, they do not disperse again unless the group dissolves (Pope, 2000b). The number of females in red howler groups is confined within narrow limits. Groups with too few females are unable to defend their territories, while groups with too many females cannot secure access to adequate resources and become more attractive targets for male takeovers (Pope, 2000a). This means that female dispersal strategies are linked to the number of adult females present. Thus, in groups with 2 adult females, 50% of natal females disperse. In groups with 3 adult females, 90% disperse, while in groups with 4 adult females all natal females disperse (Crockett and Pope, 1993; Pope, 1998).

Dispersal is extremely costly for females, particularly when habitats are saturated and available territories are very limited. In these situations, females are forced to disperse over long distances and face uncertain prospects. This is reflected in female reproductive careers. Females that mature and breed in their natal groups have higher quality diets and give birth at earlier ages than ones that emigrate from their natal groups (Crockett and Pope, 1993). Even though females leave their natal groups when they are 2 or 3 years old, they do not produce their first infant until they are 7 years old (Crockett, 1984; Crockett and Pope, 1993). Females that remain in natal groups to breed give birth to their first infants when they are only 5 years old (Crockett and Pope, 1993).

The high costs of dispersal generate intense competition among females over recruitment opportunities for their daughters. Adult females actively harass maturing females in an effort to force them to emigrate. In most cases, "only the daughters of a single presumably dominant adult female are successful at remaining to breed" (Pope, 2000b). Females actively intervene on behalf of their daughters in these contests (Crockett, 1984; Crockett and Pope, 1993).

Females emigrate alone, but may join up with migrants from other groups. Migrants that form new groups are initially unrelated ($r \approx 0$). Non-random recruitment of breeding females eventually leads to an increase in the average degree of relatedness among breeding females. Thus, in

long-established groups, females represent a single matrilineage and the average degree of relatedness approaches that of mothers and daughters ($r \approx 0.43$; Pope, 1998, 2000a,b).

For females, membership in an established group is essential to achieve reproductive success. Females are often sexually active before they establish territories, but they never produce offspring until they have done so. This may reflect nutritional advantages enjoyed by females in established territories; the diets of solitary females are deficient in nutrients that limit reproduction (Pope, 2000b). There are further advantages gained from belonging to a group that contains closely related females. Females in newly-established groups have fewer surviving infants per year than females in well-established groups do (Pope, 2000a). Differences in reproductive success of females living in these groups may be due to differences in territory quality or differences in the availability of allomothers or both (Pope, 2000a). Whatever the cause, female reproductive success is correlated with the degree of relatedness within their groups (Pope, 2000a).

Males gain access to breeding females in a variety of ways. Males may join up with migrant, extragroup females and help them establish new territories. Once such groups are established, resident males must defend their positions and their progeny from alien males. Infanticidal attacks are a frequent element of both successful and unsuccessful takeover attempts, and account for nearly half of all infant mortality in some red howler populations (Crockett and Janson, 2000; Pope, 2000b).

As habitats become more saturated, male reproductive options change. First, males can only gain access to breeding females by taking over established groups and evicting male residents. Males that pursue this strategy gain immediate reproductive opportunities, but face serious risks. Males are often injured in takeover attempts, sometimes suffering debilitating or even lethal wounds (Crockett and Pope, 1988). Second, as habitats become more saturated and dispersal opportunities become more limited, males tend to remain in their groups longer (Pope, 2000b). Maturing natal males help their fathers defend their groups against takeover attempts. This makes it much harder for single males to succeed in takeover attempts.

When habitats are saturated, single males are at a distinct disadvantage in obtaining and maintaining access to breeding females. As a consequence, males form coalitions and cooperate in efforts to evict residents. After they have established residence, males collectively defend the group against incursions by extragroup males. Collective defense is crucial to males' success because single males are unable to defend groups against incursions by rival males.

The long tenure of male coalitions is remarkable because behavioral and genetic data demonstrate that only one male succeeds in siring offspring

within the group. Thus, cooperation among males involves clear fitness costs. Not surprisingly, kinship influences the duration and stability of male coalitions. Coalitions that are made up of related males last on average 8.2 years, while coalitions among unrelated males last only 2.3 years (Pope, 1990). Coalitions composed of kin are also less likely to experience dominance changes than coalitions composed of unrelated males (Pope, 1990).

Pope's (1998, 2000) genetic analyses demonstrate that demographic conditions that influence the extent of intrasexual competition among both sexes also influence the opportunities for kin selection to operate. Kin selection relies on the nonrandom distribution of altruistic behavior to other altruists and the differential success of altruists over nonaltruists. For red howlers, the extent of genetic differentiation among groups within populations is partly a function of population density. When the density of local populations is low, and opportunities for dispersing females to establish new breeding opportunities are available, the average degree of relatedness within groups and the extent of genetic variation among groups in local populations are both low. But as groups mature, selective recruitment of breeding females leads to an increase in the degree of relatedness among breeding females. Moreover, as population density rises, and opportunities to establish new breeding groups decline, most groups become socially mature, producing higher variance in relatedness among groups. In red howler groups, female reproductive success increases as the degree of relatedness among them increases, and groups that recruit more daughters produce more offspring (Pope, 2000a). These are the conditions required for kin selection to favor the evolution of cooperative behavior, and behavioral data indicate that cooperative interactions among females directly influence both these outcomes. Thus, theory and behavior converge neatly in red howlers.

CONCLUSIONS

There is persuasive evidence that primates can recognize their kin, which suggests that kin selection plays an important role (Hamilton, 1987). In the two case studies that I reviewed, monkeys conform closely to predictions derived from Hamilton's rule, reserving altruism mainly for close kin and responding as predicted to variation in cost/benefit ratios and relatedness. These cases are instructive because they demonstrate the power of kin selection in shaping social organization and influencing reproductive strategies of individuals over the course of their lives.

This does not mean that kin selection is the only force that shapes the evolution of cooperative behavior in these primate species or in other

primate groups; no behavior that is classified as altruistic is strictly limited to kin. For example, grooming is directed toward kin and reciprocating partners, even in the species that are most nepotistic. Grooming may also be traded for access to valuable commodities, including mating partners, preferred food items, and attractive neonates; or used to appease dominants (Silk, 1982) or to placate subordinates (Altmann *et al.*, 1998). The relative importance of kin selection and other forces may depend on local demographic conditions (Pope, 1998, 2000a), the availability of kin (Kapsalis and Berman, 1996b), the power of kin groups (Silk *et al.*, 1999), or the extent of intergroup competition (Cheney, 1992).

It is also important to remember that kin selection does not imply that animals will always behave altruistically toward their relatives. Even in nepotistic species, like macaques, individuals sometimes behave selfishly (Prud'homme and Chapais, 1996), and kinship does not seem to dampen rates of aggression (Bernstein, 1991). In callitrichid groups, females typically suppress reproductive activities by subordinate females (Garber, 1997), even when they are closely related (Nievergelt *et al.*, 2000). Lemurs limit the size of social groups by evicting maturing females, and do not spare their own daughters from this fate (Digby, 1999; Vick and Pereira, 1989). Although severe aggression toward daughters and suppression of daughters' reproductive activities seems quite inconsistent with Hamilton's rule, mothers are only expected to allow their daughters to breed when the benefits to daughters of breeding in their natal groups, weighted by the degree of relatedness between mothers and daughters, are less than the costs to the mother herself. If ecological pressures limit group size, recruitment of daughters may not be favored.

One of the major limitations in assessing the role of kin selection in shaping the evolution of behavior in primate groups is that most analyses have been limited to what we know about maternal kinship. If primates can recognize paternal kin, as new data on baboons and macaques suggest, then our analyses of the effects of maternal kinship on social relationships may be seriously incomplete. For example, the conclusion that kin selection does not influence the evolution of cooperation among male chimpanzees (Mitani *et al.*, 2000) might have to be revised if we discover that male chimpanzees can recognize paternal kin and practice nepotism with a patrilineal bias. Moreover, evidence of affinities among agemates may be the product of kin selection in groups in which a single male sires all the offspring of a given cohort. Work on the role of paternal kinship in the structure of social relationships is badly needed, and the availability of new genetic techniques make such work feasible.

Another factor that limits efforts to assess the role of kin selection is that knowledge of social behavior is not evenly distributed across the primate order. We know much more about kinship relationships and social behavior

of terrestrial Old World primates than arboreal Old World primates and most New World primates. Male-biased dispersal strategies are relatively uncommon among New World primates (Strier, 2000), and this may alter the dynamics of female relationships and the potential for kin selection to operate within these groups. We clearly need more information about the patterning of social behavior in groups with well-established geneologies in a broader range of taxa.

Future work can fill existing gaps in our understanding of how kin selection shapes social organization and behavior in primates. Using the tools of molecular genetics, we can obtain accurate measures of genetic relatedness to assess the effects of kinship on behavior. Researchers making use of this technology can make an important contribution to our understanding of the mechanisms underlying kin recognition in primates, document the threshold for nepotism, and assess the relative importance of kinship and reciprocity in shaping social networks. We can extend our knowledge of social organization and behavior to a wider range of taxa and gather data on a wider range of behaviors. It would be useful to be able to compare the extent of nepotism in behavior of female-bonded and male-bonded groups, to examine the relative importance of kinship and reciprocity in taxa that vary in encephalization, and to examine thresholds for nepotism across behaviors with very different cost-benefit structures. Long-term population-level studies, like those conducted on red howlers, can illuminate the connections between behavior, demographic processes, and genetics. In the laboratory we can conduct carefully designed experiments to probe knowledge of kin relationships and to measure sensitivity to variation in the parameters in Hamilton's rule. These kinds of studies will broaden and deepen our understanding of the role of kin selection in the evolution of primate social behavior.

ACKNOWLEDGMENTS

I thank Peter Kappeler and Dario Maestripieri for their invitation to write this paper and for their helpful suggestions on the text. I also thank Bernard Chapais and an anonymous reviewer for their constructive comments on the manuscript.

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