VIVAMUS

Dispersal, Nepotism, and Primate Social Behavior

Jim Moore[1]

High degrees of relatedness within primate social groups are thought to promote the evolution of altruistic behavior via kin selection. Dispersal, for whatever reason, should limit opportunities for nepotistic behaviors. Conversely, emigration is usually attributed to the avoidance of inbreeding depression. Actual dispersal patterns may result from a balance of these forces. Systematic behavioral differences are expected between taxa that differ in such patterns. In fact, comparisons of (a) colobines vs. cercopithecines, (b) bonnet, stumptailed, and Barbary macaques vs. Japanese and rhesus macaques, and (c) red vs. mantled howler monkeys yield a perplexing blend of unexplained differences and unmet theoretical expectations. Kin selection may be less important than generally believed, and/or methodological standardization more so.

INTRODUCTION

Patterns of dispersal and nepotism are inextricably linked, for the simple reason that nepotism—kin-directed beneficence—cannot be directed toward kin if one has dispersed away from them. More importantly, it is unlikely that any inclination toward nepotism directed at rarely encountered kin would evolve (Sherman, 1981). This nepotism–dispersal link is explored by Gouzoules (1984) in much greater depth than is attempted here.

Instead, this paper focuses on examples of the sorts of questions that are involved with the dispersal–nepotism linkage, emphasizing the problems

[1]Anthropology Department, University of California At San Diego, La Jolla, California 92093.

that can arise when the linkage is seen as a causal one [i.e., that individuals disperse (or not) in order to avoid (or remain with) close kin].

Prevailing views about the nature of the relationship between dispersal and nepotism in primates come largely from a faulty scenario, based on the combination of two correct models about social systems, plus an observation. The first correct model is Hamilton's (1964) explanation for the evolution of nepotistic behaviors through kin selection. Nepotism, the behavior of acting with apparent altruism toward kin, is familiar to all animal behaviorists and has, in many cases, become the null hypothesis—individuals behaving nicely to each other are assumed to be kin (Walters, 1981). The second model is Wrangham's (1980) explanation for the evolution of female-bonded primate groups, in which the distribution of a species' key resources is such that if they can be defended, stable troops of matrilineally related females should be favored. This corresponds roughly to a predicted association between female transfer and folivory, since confirmed (Moore, 1984). Wrangham's model has been enormously successful in explaining the ecological distribution of nepotism and has played an important role in shaping the field of primate socioecology over the last decade.

The observation is that inbreeding depression exists; in captivity the mating of close or moderately close relatives produces lowered viability in the offspring of a variety of primate and nonprimate species (Thornhill, in press).

Combined, these observations have led to the following popular scenario: in all but a few exceptional species, primate troops are formed of matrilineally related females which cooperatively defend their feeding range and/or guard each other against predators. Since inbreeding depression is a potentially serious problem, inbreeding must be avoided. The easiest way to do this is by differential dispersal from the natal group. Since females are staying, males have to go. Accordingly male-biased dispersal, placing limits on possibilities for male nepotism, is the predicted consequence of female nepotism plus inbreeding depression. The scenario is popular because male-biased dispersal is indeed nearly universal among mammals (Greenwood, 1980). Then-recognized exceptions, such as chimpanzees, are explicable by Wrangham's model: in these species, females seem to be "the dispersing sex," and since females disperse for ecological reasons, males presumably are not required to leave in order to avoid inbreeding and so can form male-bonded social groups.

The significance of this scenario is hard to overstate. The idea that if one sex disperses, the other does not need to (and so does not) is pervasive (e.g., Maynard Smith, 1984; Packer, 1985; Pusey, 1987; for discussion see Clutton-Brock, 1989; Moore, 1991). Colvin (1986, p. 131) summarized mammalian demography thus: "In primates, *as in other mammals*, it is

males that emigrate, while females remain with their natal group throughout their lives (emphasis added)."

There are two empirical problems with this proposition. First, it is fairly clear that some species, such as mantled howler monkeys, show appreciable rates of dispersal and transfer by both sexes (Glander, 1980; Moore, 1984); no individual is taking advantage of the situation to remain nepotistically at home. Second, in principle, both sexes can enjoy the benefits of nepotism and moderate outbreeding, without dispersal.

Killer whales (orcas, *Orcinus orca*) are highly social mammals that live in stable pods of ≈10–50 individuals, at least among the coastal "resident" populations of Puget Sound, where they have been studied for >20 years (Kirkevold and Lockard, 1986). These pods may be the most stable social units known for any mammal. Given their long lifespans [estimates range to 80 years for females in Puget Sound (Bigg *et al.*, 1987)] any statements about dispersal based on only 10–20 years of observation are somewhat preliminary. However, the best evidence available from these longitudinally studied pods suggests that both males and females normally remain in their natal pods for life (Bain, 1989; Balcomb and Bigg, 1986; Bigg *et al.*, 1987; Heimlich-Boran, 1986).

The extent of beneficent or cooperative behavior among orcas is uncertain (not surprising, given the difficulty of observing them), but it may be substantial. Lopez and Lopez (1985) describe cooperative hunting of seals and sea lions by orcas off Punta Norte, Patagonia, and note observations of adult males apparently teaching juveniles how to capture sea lions from the beach by surfing in on waves and temporarily stranding themselves as they grab their prey. "Teaching" took the form of either waiting offshore while the juvenile made repeated solo attempts or making simultaneous attempts. "Several times, an adult flung a captured live sea lion toward a juvenile which had not caught its own prey, and the juvenile pushed the prey with its head or body, or captured it in its mouth" (Lopez and Lopez, 1985, p. 182).

What sets this apart from a cat teaching its young to play with mice,[2] for example, is that males were observed doing the teaching. Orca pods are typically multimale (Balcomb and Bigg, 1986) and Lopez and Lopez

---

[2]Mother cats (*Felis catus*) exhibit a "characteristic sequence of exposing their kittens to prey. First they bring dead prey to the kittens and eat it in front of them. Then they bring in prey but do not eat it. Next they bring live prey to the kittens and allow them to play with it, but recapture it if it escapes. Finally they take little part in the prey catching process at all, merely moving toward the prey initially while their now experienced young dispatch it efficiently" (Caro, 1980, pp. 29–30); this type of experience has demonstrable positive effects on the kittens' subsequent predatory behavior (Caro, 1980). Whatever the learning mechanism employed by the kittens (Pallaud, 1984), it seems fair to say that the mother is in some real sense "teaching" her young.

(1985) report 6 adult males and 5 adult females among the ca. 30 whales observed at Punta Norte. While their breeding system is not known, paternity certainty seems unlikely to be great. Such high-investment behavior by males in large multimale groups is almost nonexistent among primates, with the significant exception of the Barbary macaque.

It is tempting to think that these two unusual attributes—lack of dispersal and indications of unusually high degrees of beneficent behavior—are connected; that because they do not disperse they must be highly inbred and consequently nepotistic. In fact, genetic evidence suggests high levels of inbreeding in the Puget Sound population (Hoelzel and Dover, 1991). However, behavioral observations suggest that they do something else highly unusual—the social group may not be the mating system. When pods meet, instead of fighting in territorial battles, they copulate (Osborne, 1986), thereby providing a means to reduce close inbreeding without dispersal. These reports are preliminary, and much remains to be done to document the breeding system of killer whales, particularly the nature of interactions between communities, but apparently they would rather copulate than switch.

Understanding how behavior and social systems evolve depends completely on the discovery of *successful* dispersal systems—i.e., how gametes are dispersed (Shields, 1987). As killer whales seem to illustrate, the dispersal of gametes and the dispersal of individuals from their natal social groups are not necessarily linked, and/or high levels of inbreeding are not necessarily to be avoided by dispersal. Dispersal—long-term change of one's social group—is not *needed* for an "adequate" degree of outbreeding to be obtained [where "adequate" is determined by the breeding history of the population (Templeton, 1987)].

Adherence to a one sex goes; one sex stays paradigm blinds us to a variety of interesting problems and may block efforts to understand other recognized puzzles. This paper reviews several such primatological puzzles, emphasizing, in each case, the way in which knowledge of dispersal can help to interpret what is going on and how it evolved.

LANGUR MALE BANDS

(There Is Always Another Theory Consistent with Partial Data)

The first puzzle is a conceptually simple problem—the basis for coalitions among male gray langurs (*Presbytis entellus*). Gray langurs have been studied at more than 20 sites throughout South Asia, in a wide variety of habitats. At intermediate population densities, most of the troops at a site

are likely to be unimale most of the time; a single resident male aggressively expels all other males, who unite to form all-male bands. These all-male bands live in home ranges which are aggressively defended against other male bands and which overlap the ranges of approximately three to seven bisexual troops; within bands, males may form coalitions, the members of which support each other during intraband agonism (Moore, 1982, 1985). In what has become a "classic scenario," the male bands either challenge healthy residents or wait until a resident vanishes (e.g., is killed by a predator) and then invade. Having invaded, males typically fight among themselves; if a single winner emerges, he expels all other males, perhaps commits infanticide, and settles into his role as the new resident. Alternatively, no single winner emerges and the troop remains multimale (Hrdy, 1977; Newton 1988; Sommer and Rajpurohit, 1989).

Langurs thus exhibit at least three levels of interest: individual, coalition, and band. What is the basis for coalitional alliances, given that many male replacements end with only a single male attaining resident status?

Within the single multicoalition band studied to data (Moore, 1985), the three adult coalitions appeared to be age-graded. Each male was assigned a score based on observable injuries (number of scars, broken digits, and teeth) and on the development of his ischial pads. Totals ranged from 0 ("young") to 8.5 ("old"); rankings correlated strongly with more subjective assessments of age (cf. Hrdy, 1977, pp. 72–76). The three six-member coalitions differed significantly from each other in "age" scores, with median scores of 0.5, 2, and 6 (Moore, 1985). The question is, Why do males form coalitions with like-aged males?

Nepotism among cohorts of brothers is an obvious first choice (Altmann, 1979), exactly analogous to the coalitions Bertram (1976) has described among male lions. However, the predictions of kin selection and game theory are remarkably similar in such a context (Packer and Pusey, 1982). If the resource (here, a troop of female langurs) is rich enough to attract multiple competitors, competitors who form coalitions may be favored. Kin selection theory suggests that relatives should be chosen. However, if kin are of widely differing ages (and age is correlated with fighting ability), a postprime male might do better for himself by joining a group of other postprimes, where he has a reasonable chance of mating, instead of accepting nomating status with a group of younger kin (cf. Appleby, 1983). Clearly, the relevant parameters include his probability of mating and the degree to which his participation in an aggressive coalition would help his relatives retain a troop; I have not tried to formalize these because we have little realistic chance of measuring such variables.

So either nepotistic or nonkin coalitions fit comfortably within existing paradigms for explaining the ultimate basis of such age-graded coalitions,

and "which is more important" can be answered only with data on the distribution of kinship within a large sample of langur male bands. Without assessment of actual relatedness among coalition members, the question appears unanswerable. [See Packer et al. (1991) for such an assessment in lions.]

THE "NICE" MACAQUES

(Dispersal Patterns Place Bounds on Interpretations of Psychological Differences Among Species.)

The second example is somewhat more complex and deals very directly with the interaction of our expectations regarding inbreeding avoidance and data on dispersal. It also involves what I think will be a major direction of primate socioecology in the next decade: the investigation of ecological bases for what have been called "temperament" or "style" differences among species. The question is, what makes Barbary, bonnet, and stumptail macaques so much "nicer" (e.g., less aggressive to conspecifics and to humans, less rigidly hierarchical) than rhesus, pigtail, or Japanese macaques? Barbary macaques (*Macaca sylvanus*), bonnets (*M. radiata*), and stumptails (*M. arctoides*) form a natural grouping on at least two grounds. Males are single-mount ejaculators, and intragroup relationships are characterized as more "easygoing" than those of other macaques (Shively *et al.*, 1982).

Bonnet macaques have been compared with a number of species in laboratory settings and are consistently found to be more affiliative and/or less aggressive, at least in intrasexual relationships (Caldecott, 1986); as Small (1982) notes, this depends to some degree on how "affiliative" is defined, emphasizing the need to be explicit in descriptions of such traits. Clarke and Mason (1988) compared female bonnet, rhesus (*M. mulatta*), and crab-eating (*M. fascicularis*) macaque responses to a novel and very useful test paradigm: the investigator simply sat in front of individually caged monkeys, avoiding eye contact or any other overt interaction, and recorded the occurrence of a variety of agonistic and affiliative behaviors. As Clarke and Mason emphasize, the standardized nature of the stimulus allows one to conclude that consistent differences among the species are due to differences in temperament. Given the relative ease and replicability of the test method, as well as the obvious adaptability to tests with conspecifics behind one-way glass, this technique seems to have great promise for assessing selected aspects of primate personalities.

As shown in Fig. 1, rhesus reacted with little unambiguous fear (grimace, alarm, and screech) and much hostility to the observer (threat, bark,
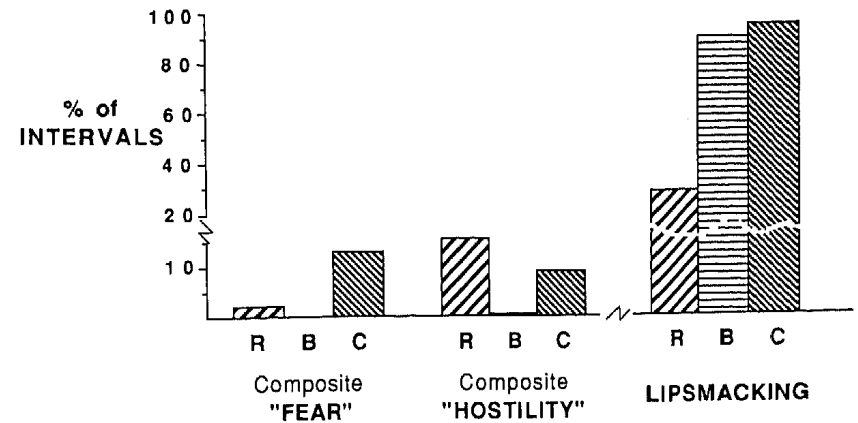

Fig. 1. Rhesus (R), bonnet (B), and crab-eating (C) macaque responsiveness to an observer. Data for the figure were calculated from Clarke and Mason (1988, Table 1) and are percentages of 1/0 scores for 15 sec intervals. Data come from seven adolescent females of each species; N for each subject = 150 intervals collected over 15 days. Clarke and Mason include lipsmacking in their "composite fear" category, but this behavior is separated here in recognition of its ambiguous behavioral significance ("placating" vs fearful; p. 360). Only data from their Condition 1 (initial habituation) are used here, as interactions between initial responsiveness and responsiveness following habituation are complex.

lunge, cage shake); crab-eating macaques showed the opposite pattern. Bonnet macaques showed neither; instead, they lipsmacked—which can be interpreted as either fear or appeasement, but certainly not aggression (Clarke and Mason, 1988, pp. 359-360).

de Waal and Luttrell (1989) compared the dominance "styles" of stumptail and rhesus macaques, based on data collected on captive social groups over a period of 8 years. They found that stumptails "[exhibit] a looser, more relaxed dominance style than the rhesus monkeys" (de Waal and Luttrell, 1989, p. 100) and that, while aggression is even more frequent in stumptails, they escalate rarely and show much more active reconciliation (Fig. 2).

I am unaware of comparable direct quantitative comparison of Barbary macaques with other species and strongly agree with de Waal and Luttrell (1989, p. 85) that the goal of documenting social dispositions among primates "can be achieved only if the results from various sites and investigators can be combined—a long-term coordinated effort requiring that 1) investigators agree on standardized measures and 2) primatological journals accept papers that in themselves may not shed much light on macaque socioecology but contribute to the pool of comparative information."

Individual mean % score
10　　20　　30　　40　　50

GROOMING
　Stumptail
　Rhesus

CONCILIATORY
　Stumptail
　Rhesus

Mean events per hour:
1　　2　　3　　4

THREAT FREQUENCY
　Stumptail
　Rhesus

FIERCE BITING
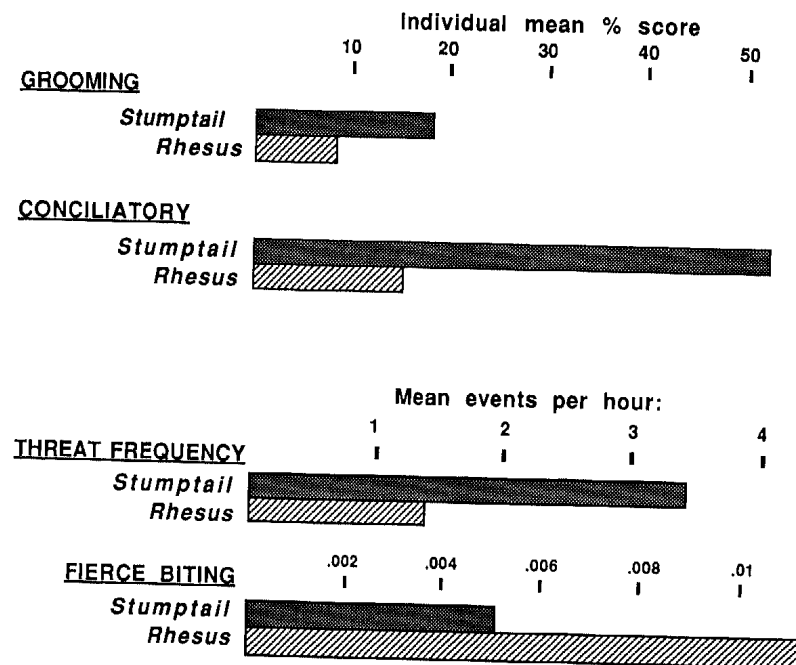.002　.004　.006　.008　.01
　Stumptail
　Rhesus

Fig. 2. Stumptail and rhesus macaque dominance styles calculated from "all partners" data in Table 1 of de Waal and Luttrell (1989). For rhesus monkeys, I used the arithmetic mean of measures for the two groups observed. *Grooming*: Percentage of scan samples allogrooming. *Conciliatory*: Individuals were considered "conciliatory" if they "engage[d] in nonagonistic body contact during the 10 min postconflict observation only, or earlier during this observation than during the matched control observation" (p. 89). This figure shows the percentage of 10-min intervals following a conflict. *Threat frequency*: threats per focal hour. *Fierce biting*: Bitting incidents, all occurrence sampling. Percentage scores shown are derived measures.

Despite the lack of formally comparative data, it is clear from the statements of researchers who have worked with them that Barbary macaques are less aggressive than is typical of rhesus, pigtail, or probably Japanese macaques (Fa, 1984; Kuester and Paul, 1986; Taub, 1980).

It is remarkable that nearly every discussion of the unusual degree of beneficent behavior observed in these monkeys alludes to the likelihood either that it is the result of higher levels of relatedness due to lack of male migration and consequent inbreeding—i.e., that it *reflects* nepotism (Taub, 1980)—or that these relaxed relationships, especially among males, make it possible for males to stay in their natal groups and so *result in* inbreeding (Deag, 1980). In either scenario, the observed beneficence is hypothesized to correlate with higher levels of genetic relatedness within the troops, due entirely to reduced male dispersal. If they are nice, they

must be nepotistic; low male migration rates and beneficent behavior are seen as causally related (Caldecott, 1986; Shively *et al.,* 1982; Wade, 1979).

This is in direct contrast to what is written about Barbary and bonnet macaques in the context of dispersal (little is known about stumptail dispersal patterns). Wrangham (1980) considers both bonnet and Barbary macaques to be female bonded (which he suggests is associated with male dispersal). More recently, Pusey (1988, p. 146) states that "there is little evidence that Barbary macaques ... differ greatly from other species of their genus in dispersal patterns," basing her opinion on the "relatively short duration" of field studies of these and bonnet macaques (Pusey and Packer, 1987, p. 253). Such statements indicate that male dispersal and female philopatry have come to be default expectations, which is problematic since there is no accepted procedure for rejecting such "null hypotheses" (Moore, 1984, 1988).

Without acceptable data *and* generally accepted ways to evaluate the importance of observed dispersal rates, we will not know whether the observed behavioral differences could be related to nepotism because we will not know if the males are in fact inbred or close kin.

Dispersal tactics among Barbary macaques are *especially* intriguing, as there is reason to think that in the wild they have hit on the same solution to the inbreeding depression/nepotism conundrum that killer whales seem to have done. Mehlman (1986) reports seeing males temporarily join troops and copulate with resident females and has found tracks of solitary males literally miles from the nearest troop. And yet he saw no indication of permanent transfer by either males or females in any of the four troops whose composition he monitored for at least 5 months. Apparently, some males wander off during the breeding season and copulate on the periphery of other troops, then return to their natal troops. It is such a simple strategy of having one's cake and eating it too. So why do no other primates employ it? [Two possible answers are as follows: perhaps more do, as illustrated by Sprague's (1992) discussion of copulation by "visitor" males in Japanese macaques (*M. fuscata*), or the artificial scarcity of predators in Morocco (and Japan) may greatly reduce the cost of such wandering for members of these two species].

This is probably the real reason for being so interested in the personality quirks of these three macaque species. Caldecott (1986) has pulled together a variety of physiological, ecological and behavioral threads to present an ingenious ultimate explanation for why these three macaque species might be different. He suggests that most macaques live in relatively poor habitats such as dipterocarp forests; consequently, evolution has favored female sexual behavior that increases intermale aggression, which in turn promotes the expulsion of "extra" males, which are nonessential mouths from the females' point of view. The result is observable demographically

in adult male:female ratios of, e.g., 1:8 for pigtailed macaques (*M. neme-strina*) (Fig. 3) (Caldecott, 1986).

Caldecott argues that bonnet, stumptail, and, historically, Barbary macaques live in richer habitats than the others, so feeding competition is less significant for these species, which favors female sexual behavior that reduces intermale sexual competition: promiscuity and short consort periods. Reduced sexual competition permits the retention of males in the group (yielding observed M:F ratios of ca. 1:1 for Barbary and bonnet macaques; data are lacking for stumptails). Once some males are retained, paternity becomes blurred by inclusive fitness effects, nepotism is favored, and male aggression is even less advantageous.

There is a final feature of this cluster of species worth mentioning. It may or may not be coincidence that both Barbary macaques and stumptails are known for exhibiting highly ritualized behaviors that seem to function to regulate agonistic behavior. Among Barbary macaques, males carry infants during interactions with other males, a behavior termed "agonistic buffering" that has been argued over in the literature for nearly 20 years (Kuester and Paul, 1986, and references therein). Stumptails employ ritualized biting apparently as a means of formally acknowledging status differences among both males and females; both dominant and subordinate

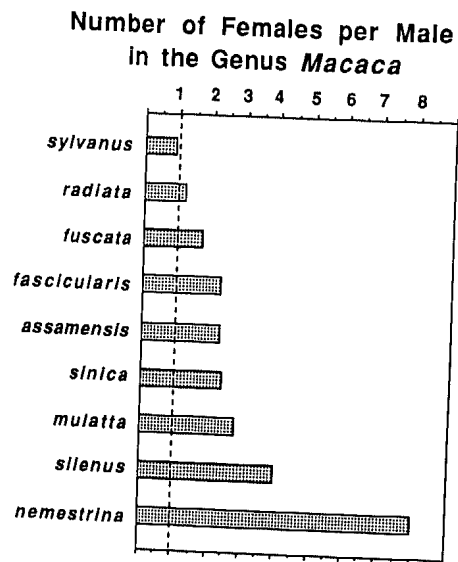### Number of Females per Male in the Genus *Macaca*

Fig. 3. Number of females per male in the genus *Macaca*. Data are from Caldecott (1986, Table II) and are based on average numbers of adult females and males per troop in nonhunted, nonprovisioned troops.

in such interactions are active participants (Demaria and Thierry, 1990; de Waal, 1989).

These ritualized—or stereotyped—behaviors introduce a host of interesting questions. Which came first, the behaviors regulating intermale tension (Deag, 1980), or the retention of related males in the group (Taub, 1984)? If the absence of such formalized gestures among bonnet macaques demonstrates that they are not necessary for the regulation of agonistic behavior among kin (and it is not obvious why they would be), then why do stumptails and Barbary macaques have them at all? Here is a situation in which dispersal, nepotism, highly elaborated "ritual," and, if Caldecott is right, ecology all come together, with three replicates to compare. [Perhaps *M. tonkeana* represents a fourth (Thierry, 1990; de Waal, 1989, p. 168).] In an important paper, Thierry (1990) discusses the role of epigenetic processes in the development of personality traits and social structure in "despotic" and "egalitarian" macaque species, rejecting explanations based on current adaptationist ecological and genetic theories. Knowledge of dispersal and relatedness patterns among the males of these species represents the missing piece that will allow us to bridge the gap between these explanations and to form a truly integrated picture of the evolution of macaque social systems and psyches.

THE NATURE AND DISTRIBUTION OF ALLOPARENTING

(Expectations Based on Belief in a "Dispersing Sex" May Lead to Mistaken Assumptions)

The next example is at a higher taxonomic level. Interest in infants other than one's own is widespread among primates, but in most species mothers resist yielding up their infants. In some, however, individuals other than the mother (alloparents) are allowed to take even neonates for (usually) short periods (Hrdy, 1976). The importance of understanding dispersal patterns for interpreting such behavior is well recognized: Clutton-Brock and Harvey (1984, p. 7) compare *Colobus guereza*, which allomother, to *C. badius*, which do not; "[t]he adaptive significance of the difference was unknown until long-term studies in Uganda showed that while female black-and-white colobus usually remained in their natal group, female red colobus usually moved to another troop and females belonging to the same troop were seldom related to each other." No fewer than 10 distinct hypotheses have been advanced to explain allomothering, with no single hypothesis adequately accounting for all observations within even a single species (Vogel, 1984). Some hypotheses assume beneficence (e.g., the alloparent is literally "aunting," helping a related female care for her infant),

while others argue that alloparents are practicing sublethal harassment of their own offsprings' future competitors (Wasser and Barash, 1981). Presumably the alloparent obtains some net benefit (else why initiate the interactions), and the net effect on the mother's fitness cannot be very negative or she would presumably not permit the behavior; beyond that rather tepid analysis, the phenomenon remains a puzzle (Nicolson, 1987).

A further puzzle concerning alloparenting is its taxonomic distribution. Alloparenting is much more common among colobines than among cercopithecines (Kohda, 1985; McKenna, 1979), suggesting that the answer to the question "Why alloparent?" may be linked in some way to a second, "Why is alloparenting so prominently a *colobine* trait?" Two proposed answers to this question differ in their assumptions about nepotism and dispersal patterns in this group.

Grouzoules (1984) argues that colobines are more prone to allomothering because females within a colobine troop are more likely to be more closely related to each other than cercopithecine females are. This is because of an association between diet and troop size. Folivorous primates tend to live in smaller troops, which can be monopolized by a single breeding male. Because only a single male is breeding in the group for years at a time, in the absence of female transfer, females born in the troop will be related both matrilineally *and* patrilineally. This is in obvious contrast to probable kinship patterns in multimale baboon and macaque troops, where less-related females cannot be trusted with young infants (Shopland and Altmann, 1987).

Gouzoules' hypothesis nicely ties together assumed dispersal patterns and kin selection theory to explain the distribution of an intriguing social behavior. By associating the taxonomic distributions of alloparenting and opportunities for nepotism, the hypothesis also effectively eliminates "selfish alloparent" explanations from consideration—a strategy of sublethal harassment of infants seems unlikely to evolve precisely in those taxa in which average intragroup relatedness is *highest*.

However, her assumption of no female transfer is problematic. There are strong indications that dispersal by females is more common among colobines than among cercopithecines, with slightly weaker evidence suggesting that intergroup transfer (as opposed to founding new troops or death) is also more typical of colobines (Moore, 1984, in press). This suggests that colobine troops are more likely to contain *un*related, instead of more closely related, females. Of course, given the almost total absence of female transfer among many cercopithecines (Pusey and Packer, 1987), a higher rate among colobines might still be negligible relative to the effects of colobine breeding structure on which Gouzoules' model is based. Unfortunately, we do not have enough data on dispersal among most primate

species to establish accurate rates; nor do we have theoretical guidelines for estimating what a "negligible" rate might be (Moore, 1988).

There is a second hypothesis to explain the distribution of allomothering between colobines and cercopithecines, one that reverses the relative importance of nepotism in the two taxa. McKenna (1979) approaches the problem by devaluing the competitive stakes. He argues that intragroup feeding competition is low among folivores such as colobines, so individuals can forage next to one another without aggression. That feeding competition is less important among colobines than among cercopithecines is supported by (1) generally low rates of observed fighting among colobines, (2) the presence of cheek pouches in cercopithecines, and (3) the close proximity in which colobines routinely feed. Given low feeding competition, McKenna suggests that dominance hierarchies are less rigidly defined and hence that social relationships are more relaxed among colobines; this reduced competition among colobines reduces the possible benefits of harming a distantly related or unrelated infant, and so the main obstacle to alloparenting—the potential for abuse of one's infant by a competitor—is removed.

Coupled with Wrangham's model for female-bonded groups, such a lowering of feeding competition would be consistent with a comparative lack of concern about relatedness and, hence, with nonnepotistic troops and (tentatively observed) prevalence of female intergroup transfer relative to cercopithecines. This is emphatically not to say that nepotism should not occur in these species, but only that their troops are not predicted to be structured to provide opportunities for nepotism.

So here is a widely known and puzzling phenomenon, with hypotheses apparently in conflict over the importance of kinship and competition in the groups being compared. *If* average relatedness among females is on average lower in colobine groups, as suggested by available observations of female dispersal, then Gouzoules' hypothesis is disproven and selfish allomother hypotheses receive some indirect support. To understand either the function of allomothering within a species or the distribution of the behavior among taxa, knowledge of patterns of relatedness—nearly synonymous with dispersal—is necessary.

RED AND MANTLED HOWLING MONKEYS

(The Limits to Nepotism May Be Closer than We Think)

The howler case reverses the somewhat repetitive theme of "without knowing more about dispersal we cannot interpret the behavior" estab-

lished above. We know a great deal about howler (*Alouatta* spp.) dispersal, but we cannot seem to find the behavioral correlates that ought to be there.

Howling monkeys are relatively inactive and live at high population densities, making it possible to collect long-term demographic data on dozens of groups at some sites. Consequently, mantled (*A. palliata*) and red (*A. seniculus*) howlers are demographically far better known than most other primates (Crockett and Eisenberg, 1987; Glander, 1980, 1992). Both males and females routinely emigrate in both species. But, among red howlers, they generally appear to found new troops or die (Crockett, 1984), while mantled howler females regularly immigrate into existing troops (Jones, 1980; Glander, 1992). This suggests that most red howler troops should be matrilines, and since most are unimale, individuals within them should be related patrilineally as well as matrilineally (Gouzoules, 1984; Pope, 1990). On the other hand, mantled howler troops regularly contain unrelated females and are often multimale; the distribution of kinship within such troops should be uneven and generally low. Kin selection theory would seem to predict major differences between the two howler species in behaviors potentially involving nepotism.

Such differences have not been discovered (Crockett and Eisenberg, 1987). At least three explanations are possible. First, newly formed red howler troops may be composed of unrelated females (Crockett and Eisenberg, 1987), and perhaps the need for cooperation among nonrelatives in such (relatively rare?) circumstances has hindered the evolution of nepotistic behaviors, thereby reducing potential differences between red and mantled howler behavior. Second, perhaps relevant behavioral differences exist but are not detectable in published reports due to methodological differences among researchers (de Waal and Luttrell, 1989). Third, perhaps nepotism is simply not so important in some demographic and/or ecological circumstances (Crockett and Eisenberg, 1987, p. 68).

If red and mantled howler monkeys do not differ in the rate or degree of expression of beneficent behavior, then substantial differences in patterns of relatedness have not produced the behavioral differences that theory predicts—a finding which seems to diminish the importance of kin selection in the evolution of primate behavior. If they differ, our failure to detect such differences during years of observation is alarming and strikingly illustrates the need to standardize observational techniques (Moore, 1984, in press).

CONCLUSION

Kin selection theory forges a conceptual link between patterns of dispersal and beneficent behavior among primates (and other animals), since dispersal patterns constrain opportunities for the evolution of nepotism and create situations promoting selfishness (Sherman, 1981; Gouzoules, 1984). Despite widespread recognition of the importance of dispersal, comparatively few primates are as demographically well-known as those discussed in this symposium. The political, financial, and personal difficulties of conducting long-term field research do not need elaboration.

Direct assessments of genetic relatedness conceivably may provide a shortcut to data on dispersal, especially successful dispersal (*sensu* Shields, 1987), among primate groups. Genetic studies, employing blood samples from trapped or darted animals, are yielding important insights, e.g., into the roles of male and female dispersal in structuring rhesus macaque populations (Melnick and Hoelzer, 1992). Techniques for using the polymerase chain reaction (PCR) to amplify DNA from hair follicles and feeding remains are currently being developed at several laboratories (Takasaki and Takenaka, 1991; Morin and Woodruff, 1992). Since shed hairs need almost no field curation for use and, in principle, may be collected without capturing animals, eventual refinement of the method should significantly increase our ability to address questions such as What is the ultimate explanation for the comparative friendliness of bonnet macaques?

Whether technological shortcuts or lengthy years in the field following individual dispersers provide the information, data on, not expectations about, dispersal are essential for understanding primate social behavior.

ACKNOWLEDGMENTS

REFERENCES

Altmann, J. (1979). Age cohorts as paternal sibships. *Behav. Ecol. Sociobiol.* 6: 161-164.

Appleby, M. C. (1983). Competition in a red deer stag social group: Rank, age and relatedness of opponents. *Anim. Behav.* 31: 913-918.

Bain, D. E. (1989). Dispersal patterns in birds and mammals—insights gained from a non-dispersing species, the killer whale (*Orcinus orca*). Poster presented at the 8th Biennial Conference on the Biology of Marine Mammals, Pacific Grove (CA).

Balcomb, K. C. and Bigg, M. A. (1986). Population biology of the three resident killer whale pods in Puget Sound and off southern Vancouver Island. in Kirkevold, B., and Lockard, J. S. (eds.), *Behavioral Biology of Killer Whales*, Alan R. Liss, New York, pp. 85-95.

Bertram, B. C. R. (1976). Kin selection in lions and in evolution. in Bateson, P. P. G., and Hinde, R. A. (eds.), *Growing Points in Ethology*, Cambridge University Press, Cambridge, pp. 281-301.

Bigg, M. A., Ellis, G. M., Ford, J. K. B., and Balcomb, K. C. (1987). *Killer Whales*, Phantom Press, Nanaimo (BC).

Caldecott, J. O. (1986). Mating patterns, societies and the ecogeography of macaques. *Anim. Behav.* 34: 208-220.

Caro, T. M. (1980). Effects of the mother, object play, and adult experience on predation in cats. *Behav. Neural Biol.* 29: 29-51.

Clarke, A. S., and Mason, W. A. (1988). Differences among three macaque species in responsiveness to an observer. *Int. J. Primatol.* 9: 347-364.

Clutton-Brock, T. H. (1989). Female transfer and inbreeding avoidance in social mammals. *Nature* 337: 70-72.

Clutton-Brock, T. H., and Harvey, P. H. (1984). Comparative approaches to investigating adaptation. In Krebs, J. R., and Davies, N. B. (eds.), *Behavioural Ecology: An Evolutionary Approach, 2nd ed.*, Blackwell Scientific, Oxford, pp. 7-29.

Colvin, J. D. (1986). Proximate causes of male emigration at puberty in rhesus macaques. In Rawlins, R. G., and Kessler, M. J. (eds.), *The Cayo Santiago Macaques*, SUNY Press, Albany, pp. 131-158.

Crockett, C. M. (1984). Emigration by female red howler monkeys and the case for female competition. In Small, M. F. (ed.), *Female Primates: Studies by Women Primatologists*, Alan R. Liss, New York, pp. 159-173.

Crockett, C. M. and Eisenberg, J. F. (1987). Howlers: Variations in group size and demography. In Smuts, B. B., Cheney, D. L., Seyfarth, R. M., Struhsaker, T. T., and Wrangham, R. W. (eds.), *Primate Societies*, University of Chicago Press, Chicago, pp. 54-68.

Deag, J. M. (1980). Interactions between males and unweaned Barbary macaques: Testing the agonistic buffering hypothesis. *Behaviour* 75: 54-81.

Demaria, C., and Thierry, B. (1990). Formal biting in stumptailed macaques. *Am. J. Primatol.* 20: 133-140.

de Waal, F. B. M. (1989). *Peacemaking Among Primates*, Harvard University Press, Cambridge, Mass.

de Waal, F. B. M., and Luttrell, L. M. (1989). Toward a comparative socioecology of the genus *Macaca*: Different dominance styles in rhesus and stumptail monkeys. *Am. J. Primatol.* 19: 83-109.

Fa, J. E. (1984). The barbary macaque. In Fa, J. E. (ed.), *The Barbary Macaque: A Case Study in Conservation*, Plenum, New York, pp. 3-15.

Glander, K. E. (1980). Reproduction and population growth in free-ranging mantled howling monkeys. *Am. J. Phys. Anthropol.* 53: 25-36.

Glander; K. E. (1992). Dispersal patterns in Costa Rican mantled howling monkeys. *Int. J. Primatol.* 3: 415-436.

Gouzoules, S. (1984). Primate mating systems, kin associations, and cooperative behavior: Evidence for kin recognition? *Ybk. Phys. Anthropol.* 27: 99-134.

Greenwood, P. J. (1980). Mating systems, philopatry and dispersal in birds and mammals. *Anim. Behav.* 28: 1140-1162.

Hamilton, W. D. (1964). The genetical evolution of social behaviour I, II. *J. Theoret. Biol.* 7: 1-52.

Heimlich-Boran, S. L. (1986). Cohesive relationships among Puget Sound killer whales. In Kirkevold, B. C., and Lockard, J. D. (eds.), *Behavioral Biology of Killer Whales*, Alan R. Liss, New York, pp. 251-284.

Hoelzel, A. R., and Dover, G. A. (1991). Genetic differentiation between sympatric killer whale populations. *Heredity.* 66: 191-195.

Hrdy, S. B. (1976). Care and exploitation of nonhuman primate infants by conspecifics other than the mother. In Rosenblatt, J. Hinde, R. A., Shaw, E., and Beer, C. (eds.), *Advances in the Study of Behavior, Vol. 6*, Academic Press, New York, pp. 101-158.

Hrdy, S. B. (1977). *The Langurs of Abu*, Harvard University Press, Cambridge, Mass.

Jones, C. B. (1980). The functions of status in the mantled howler monkey, *Alouatta palliata* Gray: Intraspecific competition for group membership in a folivorous neoptroical primate. *Primates.* 21: 389-405.

Kirkevold, B. C., and Lockard, J. S. (1986). *Behavioral Biology of Killer Whales*, Alan R. Liss, New York.

Kohda, M. (1985). Allomothering behaviour of New and Old World monkeys. *Primates* 26: 28-44.

Kuester, J., and Paul, A. (1986). Male-infant relationships in semifree-ranging Barbary macaques (*Macaca sylvanus*) of Affenberg Salem/FRG: Testing the "male care" hypothesis. *Am. J. Primatol.* 10: 315-327.

Lopez, J. C., and Lopez, D. (1985). Killer whales (*Orcinus orca*) of Patagonia, and their behavior of intentional stranding while hunting nearshore. *J. Mamm.* 66: 181-183.

Maynard Smith, J. (1984). The ecology of sex. In Krebs, J. R., and Davies, N. B. (eds.), *Behavioural Ecology: An Evolutionary Approach*, Blackwell Scientific, Oxford, pp. 201-221.

McKenna, J. J. (1979). The evolution of allomothering behavior among colobine monkeys: Function and opportunism in evolution. *Am. Anthropol.* 81: 818-840.

Mehlman, P. (1986). Male intergroup mobility in a wild population of the Barbary macaque (*Macaca sylvanus*), Ghomaran Rif Mountains, Morocco. *Am. J. Primatol.* 10: 67-81.

Melnick D. and Hoelzer, G. A. (1992). Differences in male and female macaque dispersal lead to contrasting distributions of nuclear and mitochondrial DNA variation. *Int. J. Primatol.* 13: 379-393.

Moore, J. (1982). Coalitions in langur all-male bands. *Int. J. Primatol.* 3: 314.

Moore, J. (1984). Female transfer in primates. *Int. J. Primatol.* 5: 537-589.

Moore, J. (1985). *Demography and Sociality in Primates*, Ph.D. thesis, Harvard University, Cambridge, Mass.

Moore, J. (1988). Primate dispersal (letter). *TREE* 3: 144-145.

Moore, J. (1993). Inbreeding and outbreeding in primates: What's wrong with "the dispersing sex"? In Thornhill, N. W. (ed.), *The Natural History of Inbreeding and Outbreeding: Theoretical and Empirical Perspectives*, University of Chicago Press, Chicago, (in press).

Morin, P. A., and Woodruff, D. S. (1992). Paternity exclusion using multiple hypervariable microsatellite loci amplified from nuclear DNA of hair cells. pp. 63-81 In Martin, R. D., Dixson, A. F., and Wickings, E. J. (eds.), *Paternity in Primates: Genetic Tests and Theories.* Karger, Basel.

Newton, P. N. (1988). The variable social organization of hanuman langurs (*Presbytis entellus*), infanticide, and the monopolization of females. *Int. J. Primatol.* 9: 59-77.

Osborne, R. W. (1986). A behavioral budget of Puget Sound killer whales. In Kirkevold, B. C., and Lockard, J. S. (eds.), *Behavioral Biology of Killer Whales*, Alan R. Liss, New York, pp. 211-249.

Packer, C. (1985). Dispersal and inbreeding avoidance. *Anim. Behav.* 33: 676-678.

Packer, C., and Pusey, A. E. (1982). Cooperation and competition within coalitions of male lions: Kin selection or game theory? *Nature* 296: 740-742.

Packer, C., Gilbert, D.A., Pusey, A.E., and O'Brien, S. J. (1991). A molecular genetic analysis of kinship and cooperation in African lions. *Nature* (351): 562-565.

Pallaud, B. (1984). Hypotheses on mechanisms underlying observational learning in animals. *Behav. Proc.* 9: 381-394.

Pope, T. (1990). the reproductive consequences of male cooperation in the red howler monkey: Paternity exclusion in multi-male and single-male troops using genetic markers. *Behav. Ecol. Sociobiol.* 27: 439-446.

Pusey, A. E. (1987). Sex-biased dispersal and inbreeding avoidance in birds and mammals. *TREE* 2: 295-299.

Pusey, A. E. (1988). Primate dispersal (reply to Moore). *TREE* 3: 145-146.

Pusey, A. E., and Packer, C. (1987). Dispersal and philopatry. In Smuts, B. B., Cheney, D. L., Seyfarth, R. M., Struhsaker, T. T., and Wrangham, R. W. (eds.), *Primate Societies*, University of Chicago Press, Chicago, pp. 250-266.

Sherman, P. W. (1981). Kinships, demography, and Belding's ground squirrel nepotism. *Behav. Ecol. Sociobiol.* 8: 251-259.

Shields, W. M. (1987). Dispersal and mating systems: Investigating their causal connections. In Chepko-Sade, B. D., and Halpin, Z. T. (eds.), *Mammalian Dispersal Patterns*, University of Chicago Press, Chicago, pp. 3-24.

Shively, C., Clarke, S., King, N., Schapiro, S., and Mitchell, G. (1982). Patterns of sexual behavior in male macaques. *Am. J. Primatol.* 2: 373-384.

Shopland, J. M., and Altmann, J. (1987). Fatal intragroup kidnapping in yellow baboons. *Am. J. Primatol.* 13: 61-65.

Small, M. (1982). Comparative social behavior of adult female rhesus macaques and bonnet macaques. *Z. Tierpsychol.* 59: 1-6.

Sommer, V. (1988). Male competition and coalitions in langurs (*Presbytis entellus*) at Jodhpur, Rajasthan, India. *Hum. Evol.* 3: 261-278.

Sommer, V., and Rajpurohit, L. S. (1989). Male reproductive success in harem troops of Hanuman langurs (*Presbytis entellus*). *Int. J. Primatol.* 10: 293-317.

Sprague, D. S. (1992). Life history and male intertroop mobility among Japanese macaques (*Macaca fuscata*). *Int. J. Primatol.* 13: 437-454.

Takasaki, H., and Takenaka, O. (1991). Paternity testing in chimpanzees with DNA amplification from hairs and buccal cells in wadges: A preliminary note. In Ehara, A., Kimura, T., Takenaka, O., and Iwamoto, M. (eds.), *Primatology Today*, Elsevier, Amsterdam, pp. 613-616.

Taub, D. (1980). Testing the "agonistic buffering" hypothesis. I. The dynamics of participation in the triadic interactions. *Behav. Ecol. Sociobiol.* 6: 187-197.

Taub, D. M. (1984). Male caretaking behavior among wild Barbary macaques (*Macaca sylvanus*). In Taub, D. M. (ed.), *Primate Paternalism*, Van Nostrand Reinhold, New York, pp. 20-55.

Templeton, A. R. (1987). Inferences on natural population structure from genetic studies on captive mammalian populations. In Chepko-Sade, B. D., and Halpin, Z. T. (eds.), *Mammalian Dispersal Patterns*, University of Chicago Press, Chicago, pp. 257-272.

Thierry, B. (1990). Feedback loop between kinship and dominance: The macaque model. *J. Theor. Biol.* 145: 511-521.

Thornhill, N. W. (1993). *The Natural History of Inbreeding and Outbreeding: Theoretical and Empirical Perspectives*, University of Chicago Press, Chicago (in press).

Vogel C. (1984). Patterns of infant-transfer within two troops of common langurs (*Presbytis entellus*) near Jodhpur: Testing hypotheses concerning the benefits and risks. In Roonwal, M. L., Mohnot, S. M., and Rathore, N. S. (eds.), *Current Primate Researches*. Jodhpur University, Jodhpur, pp. 361-379.

Wade, T. D. (1979). Inbreeding, kin selection, and primate social evolution. *Primates.* 20: 355-370.

Walters, J. R. (1981). Inferring kinship from behavior: Maternity determinations in yellow baboons. *Anim. Behav.* 29: 126-136.

Wasser, S. K., and Barash, D. P. (1981). The selfish "allomother": A comment on Scollay and Debold (1980). *Ethol. Sociobiol.* 2: 91-93.

Wrangham, R. W. (1980). An ecological model of female-bonded primate groups. *Behaviour* 75: 262-299.