

Colobine Socioecology and Female-bonded Models of Primate Social Structure Craig B. Stanford

Ecological models of primate social systems have been used extensively to explain the variations found in social organization among living primates and to account for primate sociality itself. Recent attempts to characterize primate social systems as either "female-bonded" or "non-female-bonded" establish a typology that does not fully consider the variation in patterns of sex-biased dispersal seen in the Primate order. This paper uses as its example the Old World monkey subfamily Colobinae to show that ecological models are based primarily on frugivorous, territorial primates. The models are inadequate to explain patterns of intergroup competition and should not be used for setting general rules for primate societies. A preliminary alternative view of sex-biased dispersal that is based on frequency dependence is offered.

INTRODUCTION

Trivers (1972) and Emlen and Oring (1977) outlined the hypothesis that females and males have been selected to invest their lifetime energies differently: females in maintaining access to maintenance and growth resources, in order to invest most in their offspring; and males in a reproductive strategy that maximizes access to females, investing relatively little in offspring. In short, females should compete for food, and males should compete for females. Wrangham extended the logic of ranking evolutionary pressures on social systems in this way to nonhuman primate societies, first to explain ape social systems (1979) and later to explain primate societies in general (1980, 1987). His female-bonded model of the evolution of primate social structure observed that most primate species are found in groups of related females accompanied by males, and hypothesized that this grouping pattern is the product of the competing costs and benefits of living and foraging socially rather than singly (Wrangham 1980, 1987).

This paper examines the applicability of this theory to the Old World monkey subfamily Colobinae and argues that ecological models of female-bonded primate groups fail to explain the range of social adaptation found in this large primate taxon. While acknowledging that a male/female asymmetry in mating strategies should be expected, I will argue that the evidence supporting both intergroup feeding competition and sex-biased dispersal is weak, and that using field data from colobine studies to test the model leads to conclusions quite different from those of the female-bonded model. By implication, the model is held insufficient as a unitary explanation for the evolution of primate societies.

The female-bonded model characterizes primate societies as either female or non-female

bonded according to each species' typical pattern of sex-biased dispersal. Males are assumed to have a greater lifetime reproductive potential than females, and in most species they invest less in offspring than do females (Trivers 1972). Since food intake for an individual female primate is maximized by feeding singly, the evolution of primate sociality suggests that there is some benefit accruing to females who forage as a group. Wrangham (1980) considered this benefit, which outweighs the costs of intra-group competition, to be the ability of females in groups to displace and defend high-quality food patches from other groups. Because the joint defense of food patches requires females to act in unison for individual reward, kin selection theory was invoked to account for the fitness advantages of female kin cooperation. Other corollaries of the model are that in female-bonded species, females should take an active role in territorial defense and are expected to influence the timing and direction of group travel (Wrangham 1980).

The model thus depends on certain ecological conditions, such as discreetly located patches of food which are large enough to accommodate a group of females and are defensible by them. In order to explain the evolution of the social systems of primate species that cannot be considered "female-bonded", one or more of these ecological conditions must not be true. Common chimpanzees (*Pan troglodytes*), mountain gorillas (*Gorilla gorilla beringei*), hamadryas baboons (*Papio hamadryas*) and red colobus monkeys (*Procolobus badius*) are four species labelled "non-female-bonded". They are considered to live predominantly in male kin groups with female dispersal for the ecological reason given above, unlike female-bonded, male-dispersal species. The rest of this paper considers whether this dichotomy is warranted.

NON-FEMALE-BONDED SPECIES

Of the four primate species identified as non-female-bonded or female transfer, the hamadryas baboon should probably be considered a special case in that female transfers occur almost exclusively between higher level strata of the social organization ("clans") and thus, females may not be permanently leaving the local breeding pool. In mountain gorillas and common chimpanzees, females do not have affiliative relationships, and females of both species may emigrate from their natal groups, although in common chimpanzees the transfer may be more of a "visit" with a later return to the natal group than a permanent emigration for reproductive purposes. The fourth species, the red colobus monkey, seems to be highly variable in social structure, and the same population may show quite different interannual levels of female emigration (Marsh 1979; Smith pers. comm.). The incidence of intensive predation on some red colobus populations by chimpanzees adds to the difficulty in establishing functional bases for social structure; the male-bonded kin groups at the core of some red colobus populations may be the evolutionary result of advantages of male cooperation against attacking chimps. The relative effectiveness of predator mobbing by related males versus single-male anti-predator attacks has not been tested.

COLOBINE SOCIOECOLOGY

The anthropoid subfamily Colobinae consists of approximately 35 species of African and Asian monkeys. The range of social and mating systems found in this group varies from monogamy (*Presbytis potenziani*) to multi-male groups with female dispersal (some red colobus populations) to territorial one-male groups (most *Presbytis* spp.), with some species displaying great intraspecific variation (*Presbytis entellus*). The group is characterized by a specialized gut anatomy that is able to break down plant cell wall materials and, using symbiotic gut flora, digest mature leaf material that is typically avoided or indigestible by other primates (Bauchop 1978). This adaptation has led to an unwarranted generalization that the colobines are leaf-eaters. Although clearly adapted to coping with a seasonally poor diet, a diversity of diets from seed-eating (*Presbytis rubicunda*, Davies 1984; *Colobus satanus*, McKey and Waterman 1982) to unripe fruit (*Procolobus badius*, Struhsaker 1975) and even ripe fruit (*Presbytis pileata*, Stanford 1989) have been reported. This probably indicates that colobines, while able to respond to

local ecologies, tend to subsist on a diet that is low in mature leaves but switch to preferred fruit and leaf flush whenever possible. It also suggests that the colobine digestive adaptation may vary among species in form and function rather than be a uniform suite of morphological and physiological traits that aid in the digestion of low-quality foods.

Most colobines live in territorial one-male groups (Table 1). Males disperse from these groups at or before sexual maturity, or are driven off by the resident male, though exceptions exist in which subadults remain in their natal groups to breed. Females transfer between groups in many species; the earlier view of social units that are essentially closed except for the dispersal of young males and invasions by outside males is almost certainly simplistic. Little data exist on female dominance relationships and where they have been documented dominance is most often simply labelled "strong" or "weak". Female dominance relations, or the lack of them in most colobines, are important because they may be related to the relatively high rates of female emigration observed among colobines (Stanford in preparation). McKenna (1979) viewed the relationships between female colobines to be strongly influenced by the uniform distribution of their leafy diets, which minimized intragroup competition and allowed a weakening of the dominance hierarchy. The assumption that colobines use leaves as a year-round staple diet has been questioned, however, and such a dietary basis for dominance is not clear (Stanford 1989).

As field data accumulate on more colobine species, most species living in one-male groups have been reported to have a regular if unknown rate of female transfer (Stanford 1989; Moore and Ali 1984; Davies 1987; Bennett 1983). It is therefore probably incorrect to classify the social systems of this subfamily as either "female-bonded" or "female-transfer". Although Wrangham (1980) allows for a "restricted" amount of transfer by females in female-bonded groups, there is a continuum of female transfer rates. For example, some red colobus populations have 100% female dispersal (Kanyawara, Kibale, Uganda; Struhsaker 1975), while others are characterized by a much lower and perhaps variable frequency (Tana River, Kenya; Marsh 1979; Smith pers. comm.). Despite numerous field studies and thousands of observer hours female transfer has rarely been reported in Hanuman langurs. Thus, there appears to be wide variation in the pattern and frequency of female transfer among members of the Colobinae. The implications of both this inter- and intra-specific variation will be discussed below.

Table 1. Summary of ecology and mating systems of colobines for which field data are available.

SPECIES	PRINCIPAL DIET	FEMALE DOMINANCE HIERARCHY?	TERRITORIAL?	TRAVEL LEADERSHIP	MATING SYSTEM	SOURCE
Capped Langur (<i>Prestbytis pileolata</i>)	wet season-fruit dry season-leaves	no	no	female	1-male groups, female transfer, all-male bands	Stanford 1989
Nilgiri Langur (<i>P. johnii</i>)	young leaves	yes	yes	female	1-male groups, some female transfer	Poirier 1970 Oates <i>et. al.</i> 1980
Hanuman Langur (<i>P. entellus</i>)	fruit/leaves	weak	yes	male	multi-male groups lone males	Jay 1965, Curtin 1975 Sugiyama 1976
Hanuman Langur (<i>P. entellus</i>)	fruit/leaves	yes	yes	male	1-male groups, all-male bands	Sommer 1988 Newton 1987, Hrdy 1977
Red Leaf-Monkey (<i>P. rubicunda</i>)	seeds, young leaves	?	yes	male	1- & 2-male groups, some female transfer	Davies 1984, 1987
Banded Leaf-Monkey (<i>P. melalophos</i>)	fruit	yes	yes	male	1-male groups, some female transfer	Curtin 1976 Bennett 1983
Purple-faced Leaf-Monkey (<i>P. vetulus</i>)	leaves	?	yes	?	1-male groups, all-male bands, some female transfer	Hladik 1977 Rudran 1973
Silver Leaf-Monkey (<i>P. cristata</i>)	leaves	?	yes	?	1-male groups, some female transfer	Wolf & Fleagle 1977 Bernstein 1968
Dusky Leaf-Monkey (<i>P. obscura</i>)	leaves	no	yes	?	1- & 2-male groups	Curtin 1976
Phayre's Leaf-Monkey (<i>P. phayrei</i>)	leaves	no	yes	?	1- & 2-male groups	Mukherjee 1982 Stanford unpublished
Sunda Island Leaf-Monkey (<i>P. comata</i>)	fruit	?	yes	?	1- & 2-male groups	Ruhayat 1983
Thomas' Leaf-Monkey (<i>P. thomasi</i>)	fruit	?	yes	?	1-male groups	Gurmaya 1986
Red Colobus (<i>Procolobus badius</i>)	young leaves	yes	no	male	multi-male groups, female transfer	Struhsaker 1975
Red Colobus (<i>P. badius</i>)	young leaves	?	yes	?	1- & 2-male groups, female and male transfer, lone males	Marsh 1979
Black-and-White Colobus (<i>Colobus guereza</i>)	leaves	no	yes	female	1- & 2-male groups	Oates 1974 Dunbar & Dunbar 1976

The dietary categories in Table 1 are necessarily vague, as a monkey that feeds heavily on leaves during one or two seasons may be highly frugivorous or a seed specialist in other parts of the year. Since the time span over which primates balance their diets and energy budgets is unknown, the potential importance of seasonal variation in diet for analyzing both feeding ecology and evolutionary and ecological influences on the social system is presently unmeasurable. Travel leadership is presented for those species for which it has been systematically reported; unlike the literature on baboon behavior, where the determination of the timing and direction of group movement has been studied (Sigg and Stolba 1981; Rhine and Westlund 1981), patterns of group travel in arboreal forest monkeys are poorly known. The significance of female leadership, discussed below, is hard to establish because it is often unobservable in dense foliage or rapidly moving groups and sub-groups, and when it is observable, fieldworkers have failed to record it systematically.

The Capped Langur

The capped langur (*Presbytis pileata*, Figure 1) is found in the eastern portion of the Indian

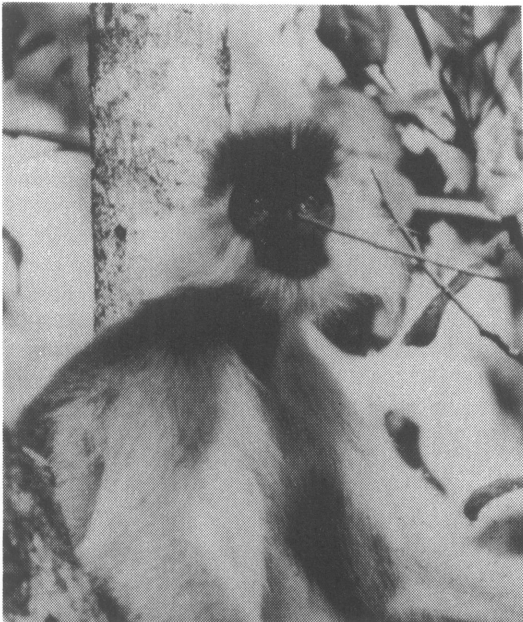


Figure 1. Capped langur monkey (*Presbytis pileata durga*) in Madhupur National Park, Bangladesh.

subcontinent. It lives exclusively in one-male groups of four to thirteen animals. During 1400 hours of observation over 15 months, three adult females immigrated into five study groups, and these immigrations were accompanied by female solicitation of and copulation with the resident male. No male changes were observed, and at least one resident male maintained his tenure for at least 26 months. Capped langur groups occupy widely overlapping home ranges, no part of which were ever observed to be defended against other groups. Food trees were also undefended. During the rainy season, capped langurs at Madhupur switched their dietary habits from predominantly mature leaves to ripe and unripe fruit. Although feeding competition theory predicts that widely dispersed fruit sources should be competed for more intensely than abundant leaves, capped langur groups showed no greater rates of aggressive displays during intergroup encounters when they fed heavily on fruit than when they ate mainly leaves. Groups encountered one another an average of about once per day in the Madhupur forest. The response upon meeting was one of mutual attention and vigilance, but tension was rarely observed. In contrast, encounters between one-male groups and extra-group males were tense and often aggressive.

The behavior of females and males during intergroup encounters provides additional support for the conclusion that intergroup encounters in *Presbytis pileata* involve mate defense rather than food defense. When females attempted to move in the direction of the other group during an encounter, the resident male rushed to the female and coercively moved her back towards the group. This behavior, coupled with the observations that females do move between groups and the apparent lack of successful male takeovers, suggests that the capped langur mating system is characterized by mate defense polygyny that is moderately unsuccessful on the part of the males, as the rate of female transfer appears to be high. Because social groups of most primate species to some extent defend the borders of an area in which both food and mates are located, hypotheses that can distinguish between resource defense and mate defense are difficult to test. Because of the absence of food source defense in capped langurs, the function of male and female behavior during intergroup encounters was clearly related to mating tactics.

If capped langurs are considered to be female-bonded, then several assumptions can be tested with regard to their ecology and mating system:

1) Females should lead groups during the group's daily range path, as the relatedness of adult females is expected to contribute to each female's inclusive fitness benefit in enhanced foraging efficiency and food-getting.

2) If high quality but widely dispersed food patches are preferred, they should be contested for by different groups sharing the home range. If they are not overtly competed for, then a clear intergroup dominance relationship should be discernable that mediates the frequency and intensity of such encounters over food sources.

3) Females should cooperate in aggression during such intergroup encounters, as they have a mutual inclusive fitness stake in defending food sources from neighboring groups.

4) Females should in general show affiliative behavior towards one another, in the form of alliances, grooming relationships and higher frequencies of spatial association among themselves than between themselves and the group male.

Only the first of these assumptions was found to be true for capped langurs (Stanford 1989); females determined the timing and direction of virtually all group travel during ranging. Even though during the rainy season ripe fruits were the most preferred food source, neither the frequency nor the intensity of intergroup encounters increased significantly in spite of the longer distances travelled to reach fruit trees. Affiliative levels among females were relatively low; females spent little time in close proximity (≤ 1 meter) to one another or to the group male (on average less than 4% of the active time of each female).

Because capped langur groups have broadly overlapping home ranges and do not contest food sources aggressively, it is likely that intergroup encounters in this species are related primarily to mate defense and female transfer. It would be unwise to speculate on the cognitive processes or motivation that prompt female emigration, but the protective/coercive behavior shown towards females by their group males during encounters with other males suggests that females use intergroup encounters to evaluate conditions in other one-male groups, or to assess the quality of a lone male or the males of an all-male band, as reported for mountain gorillas (Harcourt *et al.* 1976).

INTERGROUP COMPETITION

The absence of resource defense by *P. pilata* may be related to at least two measurable economic factors: the degree of defensibility of

food sources and the level of food abundance. Mitani and Rodman (1979) attempted to predict when a primate group should defend food sources according to the overall home range size in relation to the group's daily range length. If day range is insufficiently long to effectively monitor the perimeter of the group's range, then food sources are considered economically indefensible. Following this prediction, capped langurs at Madhupur should be expected to defend fruit trees during the rainy season, when their day range increases substantially and all groups feed heavily on ripe fruit within their overlapping 20 hectare home ranges. During the dry winter months, when mature leaves are the staple, day range is shorter and the economics of food source defense different; no defense is expected in this season. In fact, the animals never defended food sources, even when they were feeding on high quality clumps of fruit.

The other variable, the abundance of food in the habitat, is more difficult to measure. Vegetation analysis showed that few of the monkeys' food trees were clumped in distribution, and overall tree species diversity was quite low -- 28 species comprised nearly all of the animals' feeding records. During the dry season, approximately 70% of all Madhupur trees were more or less bare of foliage (Stanford 1989). Patch size of the most commonly eaten food, the young and mature leaves of *Wrightia tomentosa* (Apocynaceae), was uniformly small (average trunk diameter at-breast-height of individuals in sample transect = 6 cm). The monkeys fed on the mature and often desiccated leaves of whatever trees were in leaf and also fed on herbaceous ground cover and tree pith. These food items were available more or less evenly throughout the habitat. When fruit was eaten heavily, the preferred species of trees were widely scattered and the monkeys travelled further each day and spent more total time moving to reach them. The trees were not, however, competed for in an aggressive sense; even when two or three groups attempted to feed at the same tree, they either occupied opposite edges of the tree crown (for large *Ficus* trees) or waited for one group to finish before entering the tree. There was no consistent dominance relationship among the five main study groups.

If females in female-bonded groups should be expected to enhance their reproductive success by competing successfully for patches of high-quality foods, then the food must conform to two patterns: it must be defensible and there must be enough of it to feed all or most of the group. This raises the question of how to define a high-quality food patch. The concept of "patch" tends

to be defined by ecological primatologists in whatever way is best suited to the model at hand, rather than according to energy maximizing principles drawn from foraging theory (Stephens and Krebs 1986). Its use by primatologists varies and the concept is often used incorrectly to support assertions about the influence of ecology on social structure. Is a species that feeds extensively on leaves limited in the same way as is a frugivorous species? In foraging theory, the crucial difference is that leaves tend to be eaten only partially while fruits are more often consumed entirely. While some would argue that the problem is simply one of properly identifying the patch and measuring the energetic costs and benefits of exploiting it, it is important to note that there are important qualitative differences between different types of food patches. White and Wrangham (1988) point out that although it is tempting to relate chimpanzee grouping patterns and social structure directly to patch size, the size of food patches undoubtedly differs widely across the range of chimp habitats and there is no evidence that chimp social organization varies with it.

The implication of capped langur socioecology is that this species and other leaf-monkeys belie the utility of female- or non-female-bonded taxonomies. This may be true for nonhuman primates in general (Stanford in preparation). The question then is how to explain complex social systems in which there are different and variable rates of both male and female dispersal. Female lions, for instance, emigrate at varying rates in different populations but the result is the same: females that transfer breed later and suffer higher mortality than those who do not (Pusey and Packer 1987). Specific levels of emigration by females in a male-dispersal social system may be selected for, but the ecological or demographic factors that would mediate dispersal by only some rather than by all females are unknown. Possibly a small proportion of females can obtain benefits in the form of enhanced mating success or nutritional advantages in the form of reduced intra-sexual competition by emigrating, but selection against inbreeding may prevent large scale migration by females in species characterized by male dispersal. Small numbers of females might benefit by ending up as "novel" females in other, smaller groups while a large influx of females would not be favored. Models of purported intragroup cooperation in resource defense are also not readily operationalized. This sort of frequency dependence could produce the variation in dispersal patterns seen without invoking unwieldy inclusive fitness arguments that rely on such models of intragroup cooperation. Why there are only a few "female-transfer" species

among nonhuman primates is a puzzle.

The data on nonhuman primate patterns of dispersal and intergroup relations, therefore, suggest that: 1) the dichotomy drawn by Wrangham and others between "female-bonded" and "non-female-bonded" species is falsified by the range of mating systems and dispersal patterns found among the colobines; and 2) regardless of the mating system taxonomy used, levels of intergroup food competition vary widely between species and do not necessarily follow the axiom that high quality food sources produce intense intergroup competition which would favor individuals tolerating group life for the sake of access to better food.

Female-bonded models are ultimately extensions of resource-defense polygyny models of avian social systems. Among many bird species, males compete for territories rich in food and nest-site resources and females choose males on this basis (Emlen and Oring 1977). Variation in territory quality leads to differences in the reproductive potential of both males and females. In the avian model, males distribute themselves in space and influence the distribution of females on the basis of the females' choice of male territories. In the primate model, females choose the spatial distribution according to resources and males attach themselves to single or multiple females in order to enhance their chances of successful mating. Control of females is the key to mating success in both models. For species that are not female-bonded, males do not defend a fixed spatial area (e.g., mountain gorillas). Mate defense polygyny is then inferred from the nature of intergroup encounters. The capped langur data show that mate defense polygyny and resource defense can be easily conflated in a territorial species. Capped langurs also teach us that assumptions about the costs and benefits of intergroup resource competition must take into account seasonal differences in the values of different resources. Thus, the colobines in general illustrate the problems of applying unitary explanations to an exceedingly diverse set of primate social adaptations.

CONCLUSIONS

Vehrencamp and Bradbury (1984) point out that creating a taxonomy of mating systems according to any hierarchical ranking of the relative importance of different behavioral options is faulty in that by focusing on one component, attention is drawn away from other potentially important influences. Although it might be argued that this is unavoidable in hypothesis

formation, the problem can be minimized by allowing for a mixture of behavioral strategies rather than the hierarchy of evolutionary pressures proposed by female-bonded taxonomies. Examples drawn here from the colobine monkeys should be sufficient to show that such a typology of female-bonded versus female-transfer primate societies is simplistic and, in portraying social systems as largely built around the single independent variable of female food competition, it fails to explain the range of social behavior seen in just one primate taxon.

The preliminary alternative scenario presented here for colobine social system evolution can be no more accurate than the female-bonded model without more field data on the relationships between dispersal patterns and mating strategies and between ecology and intergroup relations. Future field studies of Old World monkeys will continue to reveal the complexity of social relationships within and among groups that confounds attempts to construct predictive models of observed behavior patterns.

I have previously suggested (Stanford 1989) a "frequency-dependent" interpretation of the primate field data on sex-biased dispersal and polygyny. The variety of mating systems in the colobines suggests a spectrum of rates of sex-biased dispersal and perhaps also a range of levels of aggression faced by immigrating males and females. Females should be expected to transfer because of the benefits they can receive in other groups (better access to food and mates), but increased transfer would not be favored as later arrivals find themselves in groups already occupied by previous immigrants. Although some strongly female philopatric primate species may fit the female-bonded and non-female-bonded taxonomy, most groups and even some species exhibit a continuum of dispersal, intergroup interactions and mating systems that have so far been given little attention and have defied genuine explanation. Ultimately the evolution of sex-biased dispersal in primates will have to be explained as it has been in other mammals. An evolutionary model of the behavioral options influencing the formation of female-bonded versus non-female-bonded species is needed to stimulate testable hypotheses in this area. These effects would have profound influences on the way in which we currently view the evolution of primate reproductive strategies.

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