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Vigilance Behavior During the Birth and Lactation Season in Naturally Occurring Ring-tailed Lemurs (*Lemur catta*) at the Beza-Mahafaly Reserve, Madagascar

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*I examined the vigilance behavior of adult males and females in two groups of ring-tailed lemurs (*Lemur catta*) during the birth and lactation season at the Beza-Mahafaly Reserve, southwestern Madagascar. I found no sex difference with respect to the rates of overall vigilance, rates of vigilance toward a potential predator or unfamiliar sound, or rates of vigilance toward conspecifics from other social groups, nor were there sex differences in the percentage of time spent vigilant in any of the above categories. Higher-ranking females were vigilant significantly more often toward predators or potential predators than lower-ranking females were. I detected no relationship between vigilance behavior and dominance rank among adult males. The alpha female in each group exhibited significantly more vigilance behavior than all other members of her group. It was predicted that males should exhibit more vigilance behavior than females do, particularly during the birth and lactation season, when predator pressure is high, if they are benefiting females in this respect. I discuss the results in the context of this prediction and in terms of how ring-tailed lemur males benefit females, and why they may be tolerated in social groups.*

KEY WORDS: vigilance behavior; ring-tailed lemurs; Madagascar; birth and lactation season.

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INTRODUCTION

van Schaik and van Noordwijk (1989), Baldellou and Henzi (1992), and Rose (1994) have examined the costs and benefits to females of resident males in multimale, multifemale primate social groups. Baldellou and Henzi (1992) argue that although female primates in such social groups incur costs in the areas of resource diversion and resource competition, they may benefit from permanent male association if males offer enhanced predator protection through vigilance behavior: scanning of the environment for predators. Male vervets and white-faced capuchins display vigilance behavior toward male conspecifics from other social groups in vervets and white-faced capuchins (Baldellou and Henzi, 1992; Rose and Fedigan, 1995). Vigilance of this type likely reflects mate or resource defense. Adult males may benefit by maximizing their vigilance behavior in return for female tolerance in a social group, as well as the potential for enhanced mating opportunities. Males of several primate species spend more time engaged in vigilance behavior than females do [three species of Cercopithecinae: (Gautier-Hion, 1980); vervets (Cheney and Seyfarth, 1981; Baldellou and Henzi, 1992); squirrel monkeys (Boinski, 1988); and three species of capuchins (van Schaik and van Noordwijk, 1989; Rose and Fedigan, 1995)]. Furthermore, in vervet monkeys, and in white-faced and brown capuchin groups, the highest-ranking male is most vigilant (Baldellou and Henzi, 1992; Rose and Fedigan, 1995; Janson, 1990).

All primate species in which sex differences in vigilance have been studied thus far are male dominant. Here I focus on whether sex differences in vigilance behavior exist in the ring-tailed lemur (*Lemur catta*), a prosimian species characterized by female dominance, multimale, multifemale social organization, and female philopatry. I also examine vigilance behavior comparatively in terms of dominance rank.

Vigilance behavior in ring-tailed lemurs may be expected to differ in some respects from that found in male-dominant primates due to certain aspects of the female dominance factor: females are the primary resource defenders (Jolly, 1966; Sussman, 1977; Sauther, 1992). Accordingly, they may be expected to exhibit more vigilance behavior toward conspecifics from other groups then males do. Furthermore, ring-tailed lemurs experience strict reproductive seasonality (Jolly, 1966), and predation pressure, particularly by avian predators, peaks between October and January, the birth and infant rearing season (Sauther, 1989). Various researchers have observed predation or predatory attempts on infants or young ring-tailed lemurs during this period (Ratsirarson, 1985; Koyama, 1992, in Goodman *et al.,* 1993; Durrell, unpublished data cited in Goodman *et al.,* 1993; Harcourt, unpublished data cited in Goodman *et al.,* 1993). In terms of sex

differences, if male ring-tailed lemurs benefit females with respect to vigilance behavior, I predict that they should exhibit more vigilance behavior than females in both frequency and duration during the birth and infant rearing season, when predation pressure is high.

Questions to be addressed in this paper include the following.

1) Do adult male ring-tailed lemurs exhibit vigilance behavior more often than adult females do?
2) Do adult male ring-tailed lemurs spend more time engaged in vigilance behavior than adult females do?
3) Are there sex differences with respect to the type of vigilance behavior displayed: scanning for potential predators vs. scanning for neighboring *Lemur catta* groups?
4) Is there a relationship between dominance rank and vigilance?

METHODS

Study Site and Focal Animals

Ring-tailed lemurs inhabit riverine and xerophytic forests in southern and southwestern Madagascar (Jolly, 1966; Sussman, 1977). Ring-tailed lemur social groups range from 5 to 27 individuals, with a sex ratio of approximately 1:1 (Jolly, 1966, 1972; Budnitz and Dainis, 1975; Sussman, 1977, 1991, 1992; Mertl-Milhollen *et al.*, 1979; Sauther and Sussman, 1993). Ring-tailed Lemurs experience marked behavioral seasonality in both the female reproductive cycle—mating, gestation, birth and lactation—and male migration (Jolly, 1966; Sussman, 1977, 1991, 1992; Jones, 1983; Sauther, 1991). The male migratory season in the Beza-Mahafaly region occurs between November/December and April/May annually (Sussman, 1992; Gould, 1994).

I conducted a study during the months of October, November, and December 1994 at the Beza-Mahafaly Special Reserve, in southwestern Madagascar (birth and lactation season). The parcel of the reserve in which I worked consists of an 80 ha area of riverine forest, changing to drier xerophytic forest in the western part of the reserve. Nine groups of ring-tailed lemurs live in the reserve, and several of them are well habituated to the presence of human observers, as they have been the subjects of numerous studies since 1985 (Ratsirarson, 1985; Sussman, 1991; Sauther, 1989, 1991, 1992; Sauther and Sussman, 1993). Beza-Mahafaly is also the site of a long-term demographic project on ring-tailed lemurs begun in 1987 (Sussman, 1991), and demographic, behavioral, and ecological data have been collected on the animals each year between 1987 and 1994 (Sussman,

1991, 1992; Sauther, 1991, 1992; Gould, 1994; Nash, unpublished data). Thus, age-class, tenure in group, and migratory status (of males) is known for lemurs in the focal groups at the onset of the study. If focal animals did not have identifying collars and tags, I identified them by facial features, pelage color, and idiosyncratic markings.

I chose all adult males and females in two groups—Red and Green—for the study (N = 15) (Table I). Two of the Green-group females (ET and SL) had been members of a very small group (Blue) in 1993. Upon my return to Beza-Mahafaly in 1994, Blue group no longer existed, and the two remaining females were peripheral members of Green group.

Data Collection and Analysis

Via continuous-time focal animal sampling (Altmann, 1974), I sampled a total of 424 15-min focal sessions on the 15 focal subjects between 0700 and 1130 and betwen 1400 and 1800. I rotated the order of focal-animal sampling so that lemurs were sampled equally during both morning and afternoon observation periods. The number of 15-min continuous-time samples collected on each focal animal ranges between 27 and 30 sessions.

Determination of Vigilance Behavior and Rank of Focal Animals

I considered subjects to exhibit vigilance behavior when they ceased the activity in which they were engaged, sat or stood upright with ears facing forward, and visually scanned the environment. A vigilance bout finished when the lemur resumed its prior activity. I scored two types of vigilance behavior: vigilance toward a potential predator or unknown source and vigilance toward conspecifics from another social group (all groups of ring-tailed lemurs within the reserve have home ranges overlapping at least that of one other group). Vigilance toward conspecifics was evident when animals from other groups could be seen or heard approaching the area that the focal group was occupying, and focal subjects responded in the manner described above. Vigilance behavior of this type was often followed by animals from the focal group moving toward the approaching group, and occasionally intergroup encounters followed. I scored vigilance behavior toward potential predators when sightings or vocalizations of predators occurred, and focal animals directed their vigilance behavior to that source. I also categorized a response to an unknown sound (not made by conspecifics) as vigilance in the potential predator category.

Jolly (1966), Budnitz and Dainis (1975), and Sussman, (1977) reported separate dominance hierarchies for females and males in *Lemur catta*. I

Table I. Group Composition, Ages or Age-Classes, and Dominance Ranks of Focal Animals During the Study Period[a]

		Known age-class or estimated age-class
Red group		
Adult females		
SC[b]	(1)	6 years
HL	(2)	Old
RB	(3)	4 years
RO	(4)	3 years
Adult males		
BT	(1)	6 years
OR	(2)	Probably prime/old prime
Adolescent male (2 years), 2 juveniles (1 year), 4 infants		
Green group		
Adult females		
YY[b]	(1)	Old prime
BB	(2)	9 years
GI	(3)	4 years
ET	(4)	Prime
SL	(5)	Young adult
Adult males		
CH	(1)	Probably prime
NO	(2)	Probably young prime
RU	(3)	Probably young adult/young prime
WM	(4)	4 years
No adolescents or juveniles 4 infants		

[a]Ages and age-class estimates are taken from previous census and demographic data (Sussman, 1992; Gould, unpublished data). True ages are known for subjects that had been captured previously or those that were juveniles (1 year olds) and adolescents (2 year olds) in a previous year-long study (Gould, 1994). I estimated age-classes of four of the focal males that had immigrated to the reserve in 1993 by pelage condition and scrotal size. Age-class estimates are as follows: young adult, 3–4 years; prime-aged adult, 5–9 years; and old adult, 10 years or older. The number in parentheses beside each focal animal identifier indicates its intrasexual rank in the group. All females in the sample except ET (Green group) had infants during the study period.

[b]Alpha female in that group.

determined the dominance hierarchy of the females and of the males in each group by observing the direction of approach/retreat interactions and the direction of agonistic and submissive signals (displacements, winners/losers in agonistic interactions) exhibited by the subjects. Females were

in higher- and lower-ranking groups based on the above criteria, as well as their dominance rank over a 3-year period (I knew the ranks of all females from my study in 1992/1993). Because four of the six males in the sample had immigrated into the focal groups in 1993, I divided males into higher- and lower-ranking groups based on the direction of agonistic/submissive signals and approach/retreat interactions. Age-classes of all focal females and two focal males are known from previous census records.

I determined rates of vigilance behavior per 15-min focal session for each focal animal by taking the total frequency of vigilance behaviors exhibited by subject and dividing it by the number of focal animal sessions collected on it.

I used the nonparametric Mann–Whitney *U*-test to determine whether significant sex and rank differences existed for each type of vigilance behavior. To determine if the alpha female in each group was significantly more vigilant than other adult group members, I employed the single-sample against the mean test (Sokal and Rohlf, 1981). This test can be used for small sample sizes such as those in this study (Sokal and Rohlf, 1981, pp. 230-231).

RESULTS

Sex Differences and Vigilance Behavior

Overall Vigilance

When both types of vigilance behavior are considered together—scanning for potential predators or an unknown source as well as scanning for conspecifics from other social groups—there is no significant difference in the rates of vigilance behavior exhibited by adult males (U_s; $N = 6$) or adult females (U_l, $N = 9$) (Mann–Whitney U test: $U_s = 34$, $U_l = 20$, tabular value = 10 at $P < 0.05$). (Fig. 1).

Furthermore, there is no sex difference with respect to the percentage of observed time spent in overall vigilance (Mann–Whitney U test: $U_s = 39$, $U_l = 15$, tabular value = 10 at $P < 0.05$) (Fig. 2).

Predator Vigilance and Vigilance Towards Conspecifics from Other Groups

I also considered each type of vigilance behavior separately: There is no significant difference between males and females in the rates of vigilance toward a predator, a potential predator, or an unknown source such as an unfamiliar sound (Mann–Whitney U test: $U_s = 36$, $U_l = 15$, tabular value

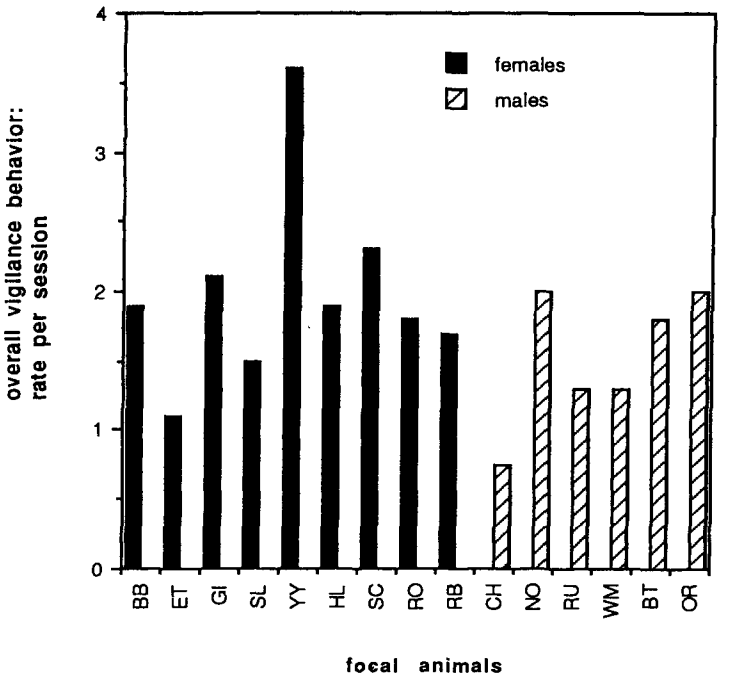

Fig. 1. Rates of overall vigilance (toward a potential predator or unknown source *and* toward conspecifics from other groups) exhibited by adult females and males.

= 10 at $P < 0.05$, n.s.) or differences in the rates of vigilance behavior toward conspecifics from another social group (Mann–Whitney U test: $U_s = 21$, $U_l = 33$, tabular value = 10 at $P < 0.05$, n.s.) (Fig. 3). All subjects exhibited higher rates of vigilance toward potential predators than toward conspecifics from other groups.

Based on the gross percentage of observed time spent in each type of vigilance behavior, females seemed to spend more time vigilant toward a predator, potential predator, or unknown source than male subjects did, although this empirical trend is not statistically significant (Mann-Whitney U test, $N1 = 9$, $N2 = 6$, $U_s = 43$, $U_l = 11$, tabular value = 10 at $P < 0.05$). There is no apparent difference between males and females in time spent vigilant toward conspecifics from other groups (Mann–Whitney U test, $N1 = 9$, $N2 = 6$, $U_s = 19$, $U_l = 35$, tabular value = 10 at $P < 0.05$). (Fig. 4).

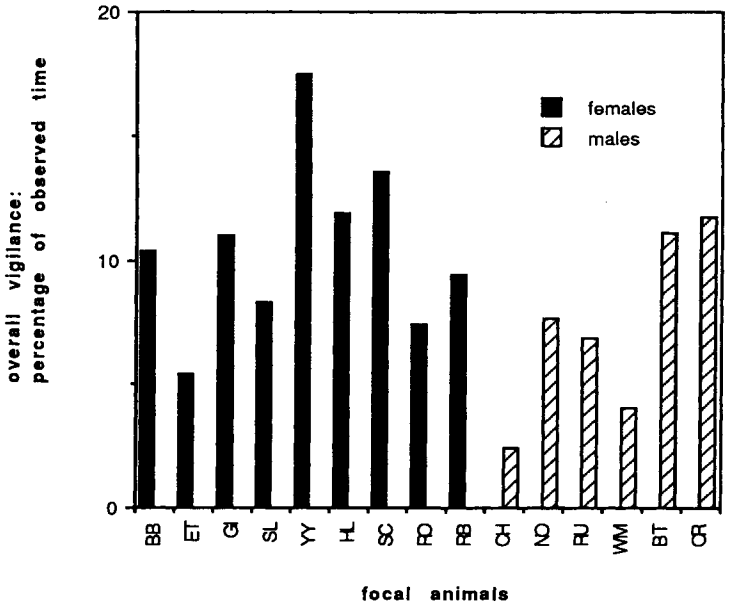

Fig. 2. Percentage of observed time adult females and males spent engaged in overall vigilance.

Vigilance and Dominance Rank

I compared the rates of overall vigilance exhibited by higher-ranking females versus lower-ranking females in both groups and found no significant difference [Mann–Whitney U test, method for very small samples (Siegal, 1956) ($n1$ or $n2 < 8$): $n1 = 4$, $n2 = 5$, $U = 7$, $P = 0.278$]. There is no difference between higher-ranking vs lower-ranking males [Mann–Whitney U test, method for very small samples (Siegal, 1956) ($n1$ or $n2 < 8$): $n1 = 2$, $n2 = 4$, $U = 2$, $P = 0.267$].

Considering dominance rank in relation to the two separate types of vigilance behavior, I found that higher-ranking females were vigilant significantly more often toward predators, potential predators, or unknown sounds than lower-ranking females were (Mann–Whitney U test, method for very small samples: $U = 2$, $P = 0.032$) (Fig. 5), but there is no difference in the rates of vigilance toward conspecifics from other groups ($P = 0.548$). Dominance rank did not affect rates of either type of vigilance among the

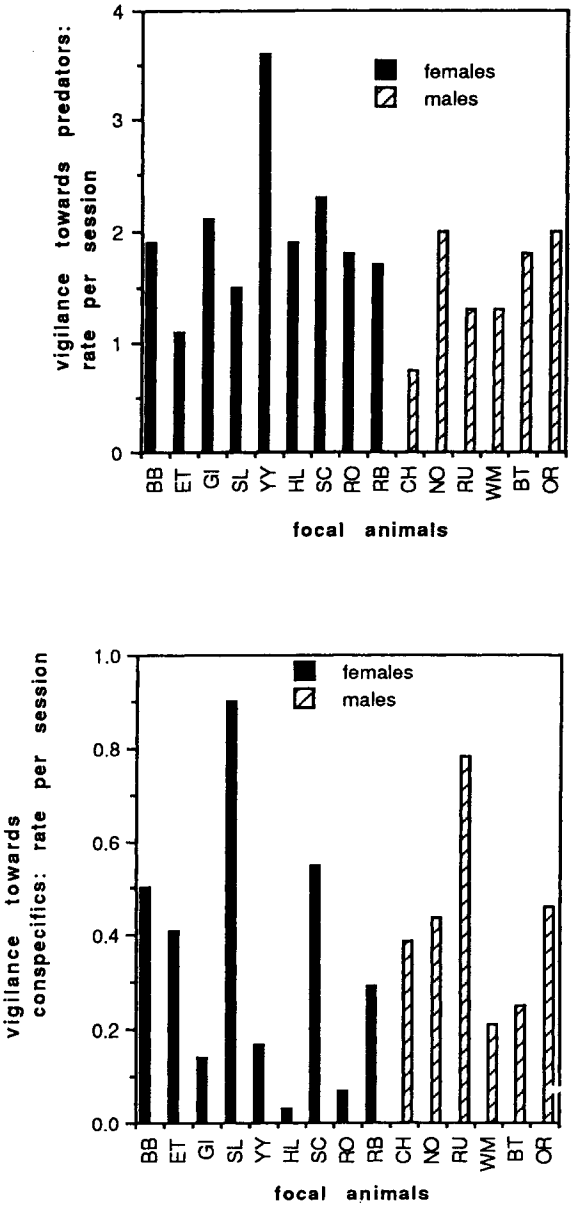

Fig. 3. Rates of vigilance exhibited by adult females and males toward a potential predator or unknown source. Rates of vigilance exhibited by adult females and males toward conspecifics from other groups.

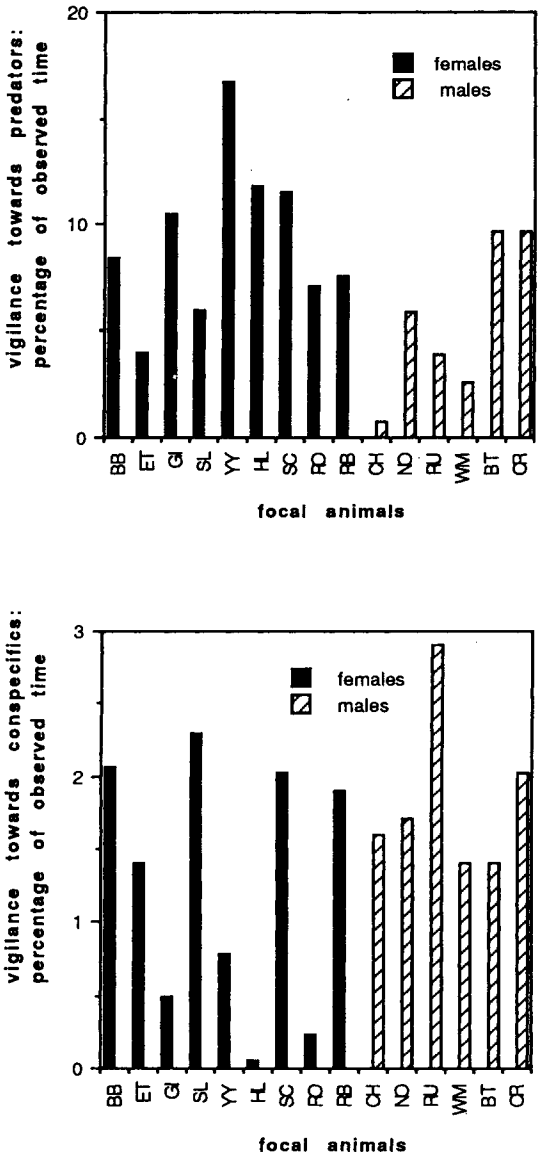

Fig. 4. Top: Percentage of observed time that adult females and males were vigilant toward a potential predator or unknown source. Bottom: Percentage of observed time that adult females and males were vigilant toward conspecifics from other groups.

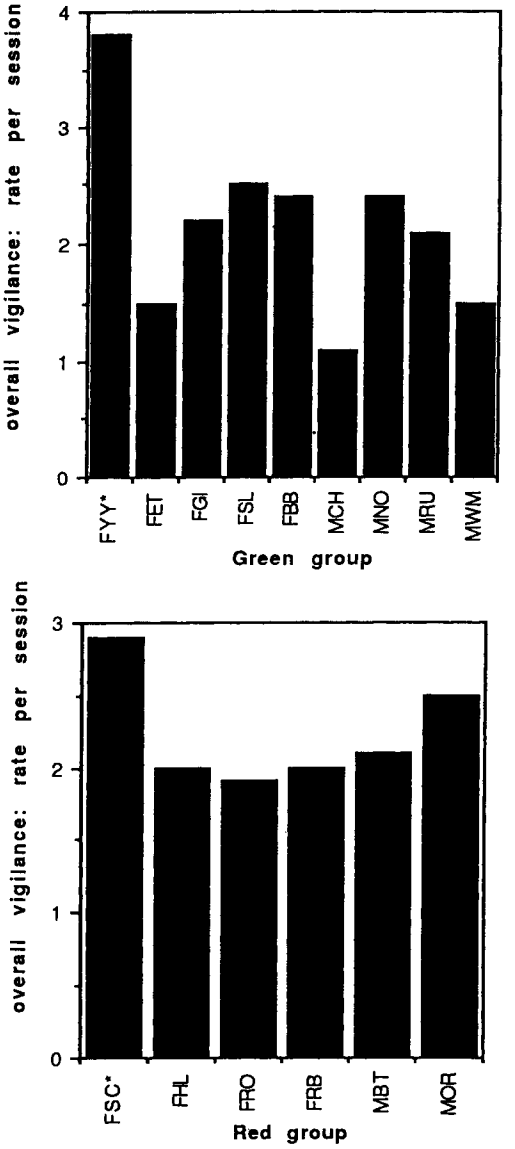

Fig. 5. Rates of overall vigilance exhibited by the alpha female in each group (indicated by an asterisk beside her identification letters) compared with all other animals in her group. Top: Green group. Bottom: Red group. Because females and males are not separated by color in the bars of the graph, I have indicated the sex of the animal by "F" or "M" beside the identification letters of each focal animal.

adult males in the sample ($U = 2$, $P = 0.267$ for both types of vigilance behavior).

Considering overall vigilance exhibited by the alpha female in each group compared with all other adults in her group, alpha females were vigilant significantly more often than the other adult group members were [single sample against the mean (Sokal and Rohlf, 1981): Green group: $t_s = 3.54$, df = 7, $P < 0.01$; Red group: $t_s = 3.49$, df = 4, $P < 0.05$).

DISCUSSION

Males, Females and Vigilance Behavior

Contrary to my prediction, the ring-tailed lemurs in the two study groups exhibited no sex difference in their rates of overall vigilance, vigilance toward conspecifics, or vigilance toward potential predators. Further, there is no significant sex difference in relation to the percentage of time spent vigilant in each of the categories of vigilance behavior, though females tended to spend somewhat more time vigilant toward predators than the males did. This finding contrasts with conditions in several male-dominant group-living primate species, in which males are more vigilant (see the Introduction). Furthermore, Artiss and Martin (1995) and van Schaik and van Noordwijk (1989) suggested that increased male vigilance benefits females by allowing them more time to forage and by removing from them the burden of predator detection. This should be especially important in a seasonal breeder like the ring-tailed lemur, since females undergo extreme stress during the lactation season because they are all lactating simultaneously (Sauther, 1993). Nevertheless, the Beza-Mahafaly females still spent as much or more time vigilant than the males did.

It appears that the Beza-Mahafaly males were not markedly benefitting females with respect to vigilance behavior. Why were males not more vigilant? Two possible explanations come to mind. First, females are the primary defenders of territory and resources in *Lemur catta* (Jolly, 1966; Sussman, 1977; Sauther, 1992), and during intergroup encounters, females are most active and aggressive (Sauther, 1992; Jolly *et al.*, 1993, personal observation). Females from opposing groups engage in moderate to extreme physical aggression during such encounters (Gould, 1989; Sauther, 1992; Jolly *et al.*, 1993), while males tend to engage in chasing and ritualized stink-fighting (Jolly *et al.*, 1993, personal observation). As the primary defenders of the home range and its resources, females may not have the option to "let their guard down," particularly during the lactation season

when they are under high nutritional stress, and in marked competition for food resources with other groups with overlapping home ranges.

Second, Caine and Marra (1988) suggested that in social organizations in which animals must pay more attention to conspecifics in order to avoid aggression, the rates of individual vigilance might be reduced vis-à-vis those in social organizations that are less hierarchical. Jolly *et al.*, (1993) have referred to ring-tailed lemurs as representing the extreme example of female dominance among primates. Females win 97–100% of disputes with males in all feeding and social contexts (Kappeler, 1990; Pereira *et al.*, 1990; Sauther, 1993). Furthermore, males are subject to increased agonism from females during the lactation season (Sauther, 1993). Sauther also found that feeding agonism between males and females peaked during the lactation and weaning period. Following Caine and Marra's (1988) argument, adult males may be directing more of their attention to female conspecifics and avoidance of agonism rather than to the environment and vigilance behavior during this period. Data on glance rates in this context are needed to test this suggestion.

Rank and Vigilance

Janson (1990) notes that in brown capuchins, the alpha male is the most aggressive individual in the group toward predators. In vervet monkeys and white-faced capuchins, the alpha male is more vigilant than other males in the group are (Baldellou and Henzi, 1992; Rose and Fedigan, 1995). The reverse trend is evident among female-dominant ring-tailed lemurs at Beza-Mahafaly. Baldellou and Henzi (1992) suggest that in vervets, the alpha male is most vigilant against predators, while Rose and Fedigan (1995) argue that in white-faced capuchins, the alpha male's increased vigilance is a result of male–male competition and the fact that the alpha male takes the most active role during intergroup encounters. At Beza-Mahafaly the alpha female lemur in each study group (YY and SC) was more vigilant overall than the other members of their respective groups were.

On two occasions when Red group members had left the reserve and were drinking from holes in the ground on the road bordering the reserve, the alpha female, SC, exhibited "sentry"-like behavior: sitting upright or standing bipedally and monitoring the environment, while the other group members drank. She did not drink until all other group members had finished. By drinking from holes in the road, they placed themselves in a vulnerable position with respect to feral and village dogs, and to humans passing in ox-carts, even though lemurs are not hunted or harassed by humans in this area. Although defense of resources is important during the

lactation season, vigilance towards potential predators may be even more important then because infants are extremely vulnerable to predation (Goodman *et al.*, 1993).

Intrasexual Rank and Vigilance

Baldellou and Henzi (1992) suggest that since vigilance and antipredator behavior are time-consuming and dangerous, higher-ranking animals should shift the burden of vigilance to lower-ranking subordinates. This was not the case for either the males or females at Beza-Mahafaly. No relationship was apparent between rank and vigilance in the males. The four higher-ranking females in the sample were older than four of the five lower-ranking females. All females except the one older lower-ranking female had infants during the study period. The higher-ranking females were vigilant significantly more often toward predators or potential predators than the lower-ranking females were. The marked difference between these two groups may relate to maternal experience. Three of the four younger mothers had been sexually immature two birth seasons before the study period (Gould, unpublished data), thus they either were primiparous or, at most, had given birth to their second infant during this study period. The older, multiparous mothers, having experienced multiple birth seasons, may have had an increased awareness of the need to be highly vigilant during the infant-rearing season, when predation pressure is high and infants are especially vulnerable.

Why Are Males Tolerated in Ring-tailed Lemur groups?

Rose and Fedigan (1994) and Rose (1994) suggest that in white-faced capuchins, a major benefit of group living—antipredator behavior—may derive primarily from males. The results from my study indicate that this is not the case in ring-tailed lemurs, at least not during the lactation season. However, even though the Beza-Mahafaly males did not exhibit more vigilance behavior than the females did, one can argue that they share responsibility for vigilance behavior. Sauther (1993) suggests that males may be tolerated in a group because they serve as low-cost sentinels, since females have priority of access to all resources. Furthermore, group-living reduces the likelihood of individual predation, (Hamilton, 1971). Thus, in ring-tailed lemurs, low-cost sentinels provide more eyes and ears with which to detect predators without incurring great cost to females. Therefore, in addition to the social benefits that resident males can provide females, for example, serving as affiliative and familiar mating partners and, occasion-

ally, providing alloparental care (Gould, 1992, 1994, 1996), males can enhance protection through vigilance behavior, even though they are not markedly more vigilant than females.

Among ring-tailed lemur males, seasonal variation probably exists in vigilance behavior, and one could predict that vigilance by males toward male conspecifics from other groups would be especially high during the brief mating season, when males from all neighboring social groups compete for access to estrous females (Koyama, 1988; Sauther, 1991; Gould, 1994).

The Need for Future Research on Vigilance in Lemurs

Not all group-living lemurs are female dominant (Sussman, 1974; Pereira *et al.*, 1990), but almost all species are strict seasonal breeders (Richard and Dewar, 1991; Sterling, 1993). Research on whether sex differences exist with respect to vigilance behavior in social, non-female-dominant lemur species affected by similar environmental stresses and predation pressure is needed to understand further vigilance patterns in prosimians and to provide a basis upon which to make further comparisons with anthropoid primates.

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