

## **Why Be Vigilant? The Case of the Alpha Animal**

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*We compared patterns of vigilance behavior in a male- and a female-dominant species—white-faced capuchins and ring-tailed lemurs—and used the results to test four hypotheses to explain vigilance behavior in primates. Adult male white-faced capuchins spent significantly more time vigilant than females did, and much male vigilance appeared to be directed toward males from other social groups. This finding supports the protection of paternity hypothesis. No sex difference existed in vigilance behavior among the ring-tailed lemurs, and subjects of both sexes exhibited more vigilance toward predators/potential predators than toward extragroup conspecifics, which supports the predator detection hypothesis. A trade-off argument, suggesting that females tolerate males in a group in return for greater male vigilance, does not apply to ring-tailed lemurs in our study. In both the male-dominant capuchins and the female-dominant ring-tailed lemurs, the alpha subject in the majority of the study groups was significantly more vigilant than other group members were. In white-faced capuchins, the alpha male mates more often than subordinate males do; therefore, the greater degree of vigilance exhibited by the alpha male may correspond to the protection of his reproductive investment. In ring-tailed lemurs, there can be more than one matriline in a group. Thus, the greater amount of vigilance behavior exhibited by the alpha female may be related to protection of her matriline, which could ultimately lead to greater inclusive fitness. Alpha subjects in our study groups exhibited certain behaviors more frequently or exclusively. Accordingly, there may be a constellation of behaviors characteristic of alpha animals.*

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**KEY WORDS:** vigilance behavior; white-faced capuchins; ring-tailed lemurs; alpha individual.

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## INTRODUCTION

Dominance patterns influence vigilance behavior in many species. For example, in some male-dominant primates such as cercopithecines and cebines, males engage in more vigilance than females, in terms of higher frequencies and greater amounts of time spent vigilant (Gautier-Hion, 1980; Cheney and Seyfarth, 1981; Boinski, 1988; van Schaik and van Noordwijk, 1989; Baldellou and Henzi, 1992; Rose and Fedigan, 1995). In vervet monkeys and capuchins, the highest-ranking male is most vigilant (de Ruiter, 1986; Baldellou and Henzi, 1992; Rose and Fedigan, 1995). Gould (1996) found no significant sex difference in vigilance behavior in the female dominant ring-tailed lemur, when all females were compared with all males, but the most dominant female in each study group was significantly more vigilant than other group members.

There are four major hypotheses that address reasons for vigilance behavior in vertebrates. The primary explanation for vigilance as well as for group living is the predator-detection hypothesis (Alexander, 1974; Diamond and Lazarus, 1974; van Schaik *et al.*, 1983; Terborgh and Janson, 1986; Biben *et al.*, 1989; Cords, 1990; Lima, 1990; Burger and Gochfeld, 1992; Catterall *et al.*, 1992), which suggests that individuals that scan the environment for nonfeeding purposes are attempting to protect themselves and their relatives from surprise attacks by predators. Two trade-off arguments have been made about antipredator vigilance: females may tolerate males in their social groups in return for male detection of, and protection from, predators; and dominant males may tolerate additional, subordinate males in their groups in return for assistance with predator detection and defense. The former argument leads to the prediction that males will be more vigilant than females. The latter argument leads to the prediction that alpha males will be less vigilant than subordinates, because subordinates have assumed the costly task of vigilance. The predator detection hypothesis also leads to the prediction that vigilance is directed toward predators instead of conspecifics.

A second explanation, specifically addressing vigilance by adult males, is related to protection of both mates and paternity. Baldellou and Henzi (1992) and Rose and Fedigan (1995) used circumstantial evidence to argue that while male primates are often the first to detect predators, they may actually be directing much of their vigilance toward male competitors from other groups. This explanation for vigilance has also been presented for some bird species (Artiss and Martin, 1995), wherein it is referred to as the mate guarding or protection of paternity hypothesis. Accordingly, vigilant males attempt to keep other males away from their mates and thus minimize the chances of cuckoldry. This explanation leads to the prediction

that alpha males will be more vigilant than subordinates, because they are protecting their reproductive advantage, and that males will direct most of their vigilance to same-sex conspecifics rather than predators. Heretofore there was no hypothesis or prediction concerning the relationship between female dominance and vigilance patterns.

A third explanation for vigilance behavior is that animals of both sexes may be vigilant against competitors from outside their groups in order to protect their resources and their home ranges or territories from encroachment by members of other groups (Baldellou and Henzi, 1992; Rose and Fedigan, 1995). This resource-defense hypothesis suggests that most vigilance is directed to conspecifics of both sexes rather than to predators.

Finally, a few researchers have argued that primates are vigilant against other members of their own groups (Keverne *et al.*, 1978; Caine, 1984; Caine and Marra, 1988; Maestripietri, 1993), which is labeled social monitoring. Although it is difficult to distinguish various targets outside the group—vigilance against predators from vigilance against conspecifics—it is usually possible in the field to distinguish watchfulness directed at close range to members of one's own group from scanning of the environment outside of the group. Researchers studying social monitoring within the group (Caine and Marra, 1988; Baldellou and Henzi, 1992) postulate that subordinate individuals will be more vigilant than dominant ones, because the former have a greater need to monitor and to avoid dominant individuals.

We compare sex-related patterns of vigilance and antipredator behavior in a male-dominant species—the white-faced capuchin (*Cebus capucinus*)—and a female-dominant species—the ring-tailed lemur (*Lemur catta*). The two species are similar in overall body size, ecological niche, social system, and female philopatry, but different in terms of sexual dimorphism, reproductive seasonality, and dominance relations between the sexes. Both species are primarily arboreal, but spend some time feeding terrestrially. Ring-tailed lemurs are somewhat more terrestrial than white-faced capuchins are, spending up to 20–30% of their time on the ground (Sussman, 1977). We have applied our findings from the two studies to the first three hypotheses listed above, in order to explain the kinds of vigilance patterns. We also address hypotheses as to why, in both species, the top-ranking (alpha) individuals of the groups exhibit more vigilance behavior than other group members. Since, in both studies, we focused on vigilance directed outside rather than within the group, we do not consider the social monitoring explanation of vigilance.

## METHODS

### Study Species

Ring-tailed lemurs (*Lemur catta*) live in riverine and xerophytic forests in southern and southwestern Madagascar (Jolly, 1966; Sussman, 1977). Social organization is multimale, multifemale, and social groups range from approximately 5 to 27 individuals, with a sex ratio of approximately 1:1 (Jolly, 1966, 1972; Budnitz and Dainis, 1975; Sussman, 1977, 1991, 1992; Sauther and Sussman, 1993). Females remain in their natal groups and males migrate approximately every 2.5 years (Sussman, 1991, 1992). This species exhibits marked reproductive seasonality (Jolly, 1966), the time of which varies somewhat according to location. At Beza-Mahafaly, the birth season occurs over 3 weeks, beginning at the end of September. Potential predators include several species of raptors, the endemic fossa, and feral cats and dogs (Sauther, 1989; Goodman *et al.*, 1993).

White-faced capuchins (*Cebus capucinus*) are Central American monkeys, distributed from southern Belize through Panama. They live in multimale, multifemale groups in which females usually remain and breed in the natal groups, while males disperse to other groups (Fedigan, 1993). Males are 25–30% larger than females and are typically dominant over them (Fedigan, 1990; Glander *et al.*, 1991). White-faced capuchins are omnivorous, and though they travel and forage mainly in the canopy, they come to the ground to feed and to cross open areas. They are not, strictly speaking, seasonal breeders, but at our study site in Santa Rosa National Park, Costa Rica, significantly more infants are born in the dry season (December–May) than the wet season (June–November), indicating a birth peak in the dry season, at which time small infants may be particularly vulnerable to predation (Fedigan and Rose 1995). Potential and observed predators of monkeys in the park include boa constrictors, felids, coyotes, tayras, and raptors (Freese, 1983; Chapman, 1986).

### Data Collection

L. G. collected data on ring-tailed lemurs at the Beza-Mahafaly Reserve, Madagascar, between October and December 1994, during the birth and lactation season. She recorded a total of 429 15-min continuous-time focal-animal sessions (107.25 hr) on all adults in two study groups ( $N=15$ ). L. M. F. and L. M. R. collected the white-faced capuchin data at Santa Rosa National Park, Costa Rica, between January and June 1986 and between January and July 1991. We recorded 10-min continuous-time focal

animal sessions, totaling 743 hr, on adult and subadult animals in four study groups ( $N = 36$ ). For both capuchins and lemurs, vigilance behavior is defined as intently staring beyond immediate vegetation with a stationary, alert posture. In both species, individuals were considered to exhibit vigilance behavior when they ceased an activity and sat or stood upright, facing forward, and visually scanned the environment. We collected data on rates of vigilance and time spent engaged in vigilance behavior for both species.

We used the Mann-Whitney  $U$  test (Siegal, 1956) to compare vigilance between the sexes and the single sample against the mean test (Sokal and Rohlf, 1981) to compare alpha individuals against other group members.

### Establishment of Dominance Hierarchies

In both studies, we documented intrasexual dominance hierarchies for each focal group at the onset of the vigilance study. We determined them by observing the direction of approach/retreat of agonistic and submissive signals—displacements, winner/losers in agonistic interactions—exhibited by the adult members of each focal group.

## RESULTS

### Sex Differences in Vigilance Behavior

The adult male capuchins ( $U_1$ ,  $N = 20$ ) spent significantly more time engaged in vigilance behavior than the females did ( $U_s$ ;  $N = 16$ ), based on the percentage of the total observed time spent vigilant, (Mann-Whitney  $U$  test,  $U_s = 229$ ,  $U_1 = 91$ , tabular value = 98 at  $p < 0.05$ ). Males spent on average 6% of their time engaged in scanning the environment, while females spent on average only 2% of their time exhibiting vigilance.

Males also had higher hourly rates of vigilance behavior. However, this difference is not statistically significant (Mann-Whitney  $U$ -test,  $U_s = 218$ ,  $U_1 = 104$ , tabular value = 98 at  $p < 0.05$ ). These findings indicate that female capuchins scan their environment almost as often as males, but do so for much shorter periods of time.

Among ring-tailed lemurs there is no significant sexual difference either in the percentage of observed time spent in vigilance behavior (Mann-Whitney  $U$ -test;  $U_s = 39$ ,  $U_1 = 15$ , tabular value = 10 at  $p < 0.05$ ) or in the rates of vigilance behavior exhibited by adult males ( $U_s$ ;  $N = 6$ ) or adult females ( $U_1$ ;  $N = 10$ ) (Mann-Whitney  $U$  test,  $U_s = 34$ ,  $U_1 = 20$ , tabular value = 10 at  $p < 0.05$ ). On average, females spent 10.5% of their

time vigilant, and males spent an average of 7.3%. These figures represent vigilance directed toward both predators and conspecifics from other groups.

### Differences Between Alpha Animals and Other Group Members

In three of the four capuchin groups, the alpha males exhibited significantly higher rates of vigilance than other group members did (Fig. 1) (single sample against the mean: Group 1  $t = 2.43$ ,  $df = 6$ ,  $p = 0.05$ ; Group 2  $t = 3.46$ ,  $df = 5$ ,  $p = 0.018$ ; Group 3  $t = 13.46$ ,  $df = 5$ ,  $p = 0.000$ ; Group 4  $t = .01$ ,  $df = 12$ ,  $p = 0.99$ ). In a later study at the same site, Hall (1995) found two other alpha males to be the most vigilant in their groups (single sample against the mean; Group 1  $t = 4.47$ ,  $df = 5$ ,  $p = 0.018$ ; Group 2  $t = 7.73$ ,  $df = 6$ ,  $p < 0.001$ ).

The alpha female in both ring-tailed lemur groups was vigilant significantly more often than all other group members (single sample against the mean: green group  $t = 3.54$ ,  $df = 7$ ,  $p < 0.01$ ; red group  $t = 3.49$ ,  $df = 4$ ,  $p < 0.05$ ).

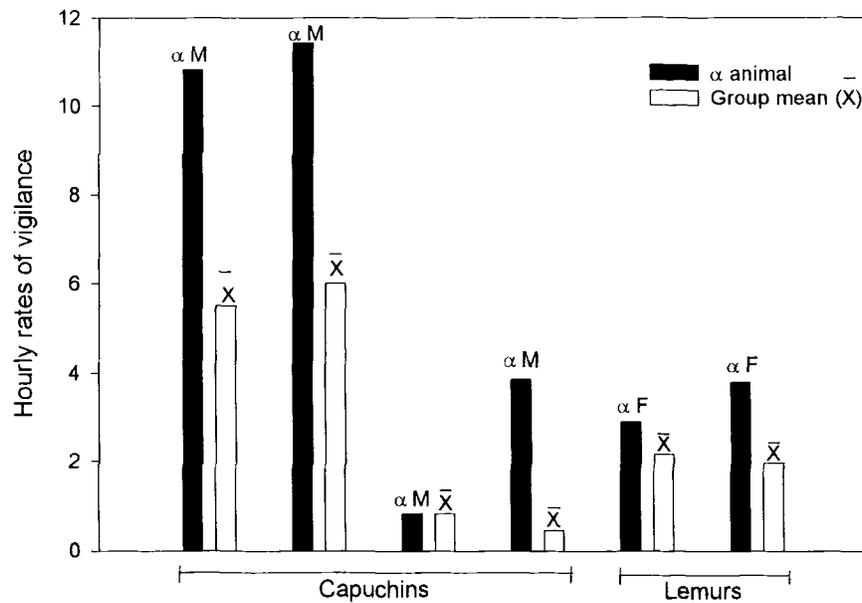


Fig. 1. Hourly rates of vigilance: comparisons of alpha individuals in each study group versus group means.

## DISCUSSION

Among white-faced capuchins, monkeys of both sexes are vigilant against both predators and other groups, but males spend more time than females scanning the environment, and they appear to direct much of their vigilance toward males outside the group (Rose and Fedigan, 1995). If vigilance is directed primarily toward predators, then one should expect more vigilance behavior in areas where primates are most vulnerable, for example at water sources. If vigilance is being directed primarily toward males from other groups, vigilance should occur more frequently by males in areas of home range overlap. The latter was the case with the capuchins.

In the ring-tailed lemur study, we could accurately distinguish vigilance directed at conspecifics in other groups from vigilance directed toward predators. No significant sex difference existed in either type of vigilance behavior (Gould, 1996). Both females and males were more vigilant toward predators or potential predators than toward conspecifics from other groups, which supports the predator detection hypothesis as the primary explanation of vigilance in this species. However, all animals in the ring-tailed lemur groups were also vigilant toward conspecifics from neighboring groups, and conspecific vigilance at times resulted in agonistic intergroup encounters when a neighboring group came within close proximity.

### Why Are There Sex Differences in Vigilance?

Many analyses of vigilance are attempts to explain why males are more vigilant than females. If the primary function of vigilance is predator detection, then males are believed to be more vigilant than females as a trade-off for female tolerance of male presence in groups and, also, as a way of freeing females for more effective foraging with greater safety. Males are able to offer this service in part because they are better suited physically for defense against predators and intruders. In species in which males are larger than females or have larger canines or both, they are better equipped to defend themselves and their mates and offspring against predator attacks. Predator detection on the part of adult males is also believed to be a crucial aspect of paternal investment in offspring.

If the primary function of vigilance is protection of paternity, then males should exhibit more vigilance than females as part of the overall sex difference in mating strategy that follows from sexual selection theory. If females are a limiting resource for males, then males will compete for access to them and will attempt to keep other males from mating. As for

female-female competition, it is generally assumed that female mammals do not compete for males.

If the main function of vigilance is believed to be defense of resources, then two mutually exclusive predictions may be made about sex differences. The first is that the philopatric sex—usually females in primates—will have the greater interest in protecting home-range resources and, thus, will be more vigilant in order to detect and to exclude others (Wrangham, 1987). Contrarily, the dispersing sex—usually males—may provide a benefit via vigilance behavior to the philopatric sex in return for the advantages of group membership (Wrangham, 1987; van Schaik and van Noordwijk, 1989; Baldellou and Henzi, 1992).

Each of the three main explanatory models for vigilance directed outside the group can lead to the prediction that males will be more vigilant than females, albeit by different logic. But only the protection-of-paternity hypothesis predicts that males will be more vigilant and that they will direct their vigilance primarily to male competitors, as we found among capuchins. Thus, although vigilance by both sexes probably provides benefits in the form of predator detection, the protection-of-paternity hypothesis seems to offer the best explanation of sex differences in vigilance in white-faced capuchins.

How might we best explain the lack of sex differences in vigilance that we found in ring-tailed lemurs? The simplest explanation is that vigilance in this species is directed primarily toward potential predators. As ring-tailed lemurs are monomorphic, males are no larger or better equipped to deal with predators than females are, and there is no reason to predict that males would be more vigilant toward predators than females would be. In fact, equal investment in vigilance by both sexes would be consistent with the predator-detection-hypothesis in a monomorphic species. However, the trade-off argument suggests that females tolerate males in return for vigilance behavior, hence males should be more vigilant. We might expect this to be particularly applicable in the case of a female dominant species, such as the ring-tailed lemur; however, males were not more vigilant during the birth and infant rearing season when predation pressure on infants is high (Sauther, 1989; Gould, 1996). Thus, for ring-tailed lemurs, there are two possibilities: male ring-tailed lemurs are tolerated by females for reasons other than vigilance behavior or there are additional factors promoting female vigilance in this species which effectively cancel out differences between the sexes. There is no evidence that male ring-tailed lemurs provide alternate benefits for females. What factors might lead to increased vigilance on the part of female primates?

Of the three main explanatory models of vigilance presented here, only the resource-defense hypothesis emphasizes female vigilance as a conse-

quence of female philopatry. Female ring-tailed lemurs are the primary resource defenders and take the more active role in intergroup encounters (Jolly, 1966; Sussman, 1977; Sauther, 1992; Jolly *et al.*, 1993), which may promote vigilance toward conspecific groups. A second possibility is that female ring-tailed lemurs are particularly vigilant during the birth and lactation season, when the study at Beza-Mahafaly was conducted, because of the predation risk to dependent infants. We lack the data to address the question of seasonal differences in vigilance behavior, but our findings suggest that predation risk is the primary explanation for vigilance in ring-tailed lemurs.

While the higher rates of vigilance in male capuchins would easily fit each of the models that have been developed to explain vigilance in primarily male-dominant, sexually dimorphic primate species, ring-tailed lemurs present us with a conundrum. In any case, it is clear that female-dominant systems are not just mirror images of the patterns found in male-dominant societies.

#### **Why Are Alpha Animals More Vigilant than Other Group Members?**

Having set the explanatory stage for vigilance studies, it is now possible to address our central question of why the top-ranking members of our study groups were more vigilant than other group members. Because most theories have been developed to explain behavior in male-dominant, sexually dimorphic species, it is again easier to interpret our capuchin results than our ring-tailed lemur findings. We first outline why alpha male capuchins might be predicted to be more vigilant than other group members, and then see how well these explanations would hold for alpha female ring-tailed lemurs.

For alpha males, the most obvious explanation for higher rates of vigilance is that they are protecting their greater reproductive investment. Although studies of the relationship between male dominance and reproductive success have a long and contradictory history in primatology, most researchers assume that the top-ranking male in a group has greater reproductive success than those of other males (Smuts, 1987). In two species of South American capuchin (*Cebus olivaceus* and *C. apella*), Janson (1984) and Robinson (1988) reported that the top-ranking male in each group was the only reproductively successful male, as he was the only actively mating male in the group. In the Central American white-faced capuchin, males other than the alpha male mate with estrous females, sometimes discreetly, but at other times in full view of the alpha male. The latter may ignore quite obvious mating activity or he may harass subordinate males

trying to mate (Fedigan, 1993; Perry, 1995). Nonetheless, alpha male white-faced capuchins engage in more mating than subordinates, and if we assume that the alpha males in our study groups have sired more of the offspring than other males have, then explanations for their higher rates of vigilance follow easily. It could be argued that the alpha male is more vigilant because (1) he is protecting a greater number of offspring and mates from predators, (2) he is more vigilant for male intruders that might encroach on his mating opportunities or injure his offspring, (3) he is vigilant for other groups that would trespass on the resources available to his offspring and his mates, and (4) he is vigilant within the group because he is detecting and deterring other group males from mating.

Note, however, that the trade-off argument that alpha males tolerate subordinate males in the group in order to shift the burden of vigilance onto subordinates, does not hold true in our capuchin study groups.

Would a reproductive investment argument work for alpha female ring-tailed lemurs? Since females probably do not compete for mates and mating opportunities in the same way as males do, the arguments are more difficult to apply. However, females compete for resources that affect reproductive success (Sauther, 1992,1993), and if high-ranking females are, in general, more reproductively successful than lower-ranking ones are, then alpha female ring-tailed lemurs could have more relatives in the group and thus more to protect. To date, however, we have no evidence to support this argument. There can be more than one matriline in a ring-tailed lemur group (Taylor, 1986; Vick and Pereira, 1989), and the alpha female may be more vigilant because she is protecting her matriline with respect to both predation and enhanced protection of scarce resources, which could ultimately lead to greater inclusive fitness.

The fact that alpha females direct most of their vigilance toward possible predators rather than conspecifics suggests that the primary function of their watchfulness is to protect themselves and their offspring from predators, not to fight off competitors.

Bernstein (1964, 1966; Bernstein and Sharpe, 1966; Bernstein *et al.*, 1979) conducted a series of studies and experiments on the alpha male role in capuchins and macaques. He described a constellation of behaviors that made up the alpha male role, including the tendency to be more watchful against intruders and other primate groups, or any outside disturbances, to be more active in group defense and group movement patterns, to intervene in agonistic interactions, usually on the side of the victim, and to be sought more for coalitions and proximity. He argued that the function of the alpha male is to control intragroup disturbances and the responses of the group to external challenges. Accordingly, he referred to this constellation of behaviors as the control role. He described the behavior of

the alpha male as not only quantitatively but also qualitatively different from that of other group members, and he documented that removal or death of the alpha male will cause another individual to begin to exhibit the same behaviors almost immediately.

Fedigan (1976) and Gouzoules (1980a,b) documented that the top-ranking females in macaque groups behave in distinctive ways that support the concept of an alpha female role. Top-ranking female macaques tend to be confident aggressive individuals that frequently exhibit behaviors thought to be more characteristic of males—e.g., courtship behaviors, agonistic interventions, displays—and that exhibit fewer affiliative and submissive behaviors than other females do. Stambach (1978) demonstrated that female hamadryas baboons will take over the alpha male role in the absence of a male, and will exhibit male protective and herding behaviors. Gouzoules (1980a,b) argued that the alpha female acts as the center of attention and influences group activity, and he documented that females will compete for the alpha position.

In ring-tailed lemur groups at Beza-Mahafaly, the alpha female was always active in intergroup agonistic encounters, whereas lower-ranking females often participated, but not all in every encounter (Sauther, unpublished data; Gould, unpublished data). One of the alpha females in the study behaved as a sentry on two occasions when the group was outside of the reserve and drinking from a hole in the ground, which made them extremely vulnerable to predation. The alpha female stood bipedally and watched the surrounding area while all other group members drank. No other group member behaved in this sentry-like fashion. Thus, there seem to be certain behaviors in which alpha females engage either more often or uniquely.

Today the concept of social roles is considered group selectionist and mentalistic, and explanations of behaviors are much more likely to be phrased in terms of selection for individual reproductive strategies. However, what can be utilized from the earlier role studies is the notion of a package of related behaviors that is characteristic of any individual occupying the top-ranking position in a social group, with no implication of rights, obligations, expectations, or conscious behaviors. We suggest that the alpha animal in primate groups may not be simply one rank higher than the beta animal. Instead, the alpha animal may behave in a distinctive pattern made up of a variety of related behaviors pertaining to control of the interactions within the group and management of the relationship between the group and external factors. Perhaps the most complete explanation for the higher rates of vigilance that we found to be exhibited by top-ranking males and females in our study groups will come from a

reconsideration of the entire constellation of behaviors characteristic of alpha individuals, of which vigilance is only a part.

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