

The Function of Howling in the Ring-Tailed Lemur (*Lemur catta*)

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Abstract Long calls are sex-specific vocalizations used for mate attraction or mate defense in many animal species. Ring-tailed lemurs (*Lemur catta*), female-dominant strepsirrhines, have a male-specific long call termed a howl, with proposed functions that have never been empirically tested. I aimed to investigate why ring-tailed lemur males howl and to test whether the mate defense and mate attraction hypotheses for long-calling were applicable to this species. From March to July 2010, I collected 600 h of focal data on 25 males aged ≥ 3 year at Beza Mahafaly Special Reserve, Madagascar. I observed each male continuously for 30 min at a time and noted all agonism using one-zero sampling at 2.5-min intervals. I calculated male dominance rank from these data. I recorded days when female estrus occurred and noted howling and intergroup encounters using all-occurrences sampling. Howling rate was not significantly related to female estrus or male dominance rank, providing no support for the mate attraction hypothesis or the intragroup mate defense hypothesis. In contrast, the intergroup mate defense hypothesis was strongly supported. During intergroup encounters, male howling rate significantly increased compared to howling rate at times without other groups present, and a greater number of males participated in multimale howling choruses when compared to times without nongroup members present. My results suggest that male ring-tailed lemurs howl to advertise their presence and location to other groups, but not to male or female members of their own group. Howling could discourage male immigration by advertising the number of males already present in a group. Long calls are used for similar mate defense purposes during intergroup encounters by other primates, including Thomas langurs (*Presbytis thomasi*) and chacma baboons (*Papio ursinus*).

Keywords Long call · Loud call · Mate attraction hypothesis · Mate defense hypothesis

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Introduction

A variety of vocalizations are used to mediate social relationships in group-living animals. One of the best-researched types of vocalization is the long call or loud call. Birds, amphibians, and mammals including nonhuman primates make male-specific long calls, and such calls carry for spans of >1 km in some species, such as Sumatran orangutans (*Pongo abelii*; Delgado 2006). Across species, long calls advertise a male's presence at long distance and may also attract females or repel rival males (Bradbury and Vehrencamp 1998; Delgado 2006). The leading hypothesis for male long calling in primates is the mate defense hypothesis, which states that males long call to mediate intrasexual competition for female mates (Wich and Nunn 2002). According to this hypothesis, males make long calls to deter the approach of other males, both from within their group and from other groups, and to prevent these other males from mating with estrous females. The mate defense hypothesis has support from several species of primates. Male Thomas langurs (*Presbytis thomasi*) advertised their presence in a group through long calling during intergroup encounters, and a high level of male–male agonism in intergroup encounters reflected mate defense rather than territoriality (van Schaik *et al.* 1992). Male chacma baboons (*Papio ursinus*) were more likely to long call and engage in aggression during intertroop encounters when estrous females were present, and dominant males called more frequently than low-ranking males (Cheney and Seyfarth 1977; Cowlshaw 1995; Kitchen *et al.* 2004a).

An alternative hypothesis for male long calling is the mate attraction hypothesis, which suggests that males make long calls as a courtship display to entice estrous females to mate with them (Delgado 2006; Wich and Nunn 2002). This hypothesis has support from primates. In gibbons (*Hylobates* spp.), which are pair-bonded, unpaired males consistently long called whereas paired males did not, and unpaired males also produced the longest song bouts, suggesting a mate attraction function (Cowlshaw 1992; Mitani 1988; Raemaekers *et al.* 1984). Gray mouse lemur males (*Microcebus murinus*) produced trill calls at much higher rates when in the presence of an estrous female, and males that called at higher rates had greater reproductive success (Zimmermann 1995; Zimmermann and Lerch 1993).

Ring-tailed lemurs (*Lemur catta*) are female-dominant strepsirrhine primates endemic to southern Madagascar (Jolly 1966). They are gregarious and live in multimale–multifemale groups of up to 27 individuals (Gould *et al.* 2003; Pride 2005; Sussman 1991). Males disperse from their natal group at 3–4 year of age and move to new groups *ca.* every 3 years, whereas females usually remain in their natal groups for their entire lives (Budnitz and Dainis 1975; Jones 1983; Sussman 1992). Ring-tailed lemur groups are territorial, with females taking the primary role in group defense during intertroop encounters (Jolly 1966; Mertl-Millhollen 2006).

Although females are dominant, males have their own dominance hierarchy, which is often linear (Budnitz and Dainis 1975; Gould 1994; Taylor 1986). Dominance confers social advantages for high-ranking males, typically including first sexual access to group females when they are in estrus (Koyama 1988; Sauther 1991). Ring-tailed lemurs have an annual breeding season that begins in April/May in Madagascar, with females in asynchronous estrus (Jolly 1966). Each female stays in estrus for 3.25–24 h, and during this time females mate with multiple males (Jolly

1966; Parga 2006; Sauther 1991; Van Horn and Resko 1977). Although resident males typically have mating priority, nongroup males also mate with females (Koyama 1988; Sauther 1991; Sussman 1992). Mating opportunities are usually restricted to nonnatal males, which are sexually mature and unrelated to group females (Parga 2010; Sauther 1991; Taylor and Sussman 1985). The competition between nonnatal males for mates leads to a high degree of male–male aggression during the breeding season and can lead to severe injuries and even death (Gould and Zeigler 2007; Jolly 1966; Sauther 1991).

As highly social strepsirrhines, ring-tailed lemurs have a large vocal repertoire comprising 22 distinct vocalizations for adults (Macedonia 1993). These consist of eight calls used in affiliative interactions, six calls used in agonistic behavior, and eight antipredator vocalizations (Macedonia 1993). Of these 22 calls, several are long-range and two are male specific (Jolly 1966; Macedonia 1986, 1990, 1993). The howl is a male-specific vocalization that carries for up to 1 km through riverine forest (Jolly 1966). The howl is tonal, song-like, and repetitive, with single howls lasting seconds combining into bouts of 10 or more (Andrew 1963; Jolly 1966). A single male may howl alone, or some or all of the males in his troop may join him in a howling bout (Andrew 1963; Jolly 1966; Macedonia 1990). When multiple males howl at the same time to create a howling chorus, each male howls at his own rate without entrainment (Macedonia 1990). All ring-tailed lemur males that are past infancy howl (Macedonia 1990), but females do not typically howl and have been observed howling only on rare occasions (Jolly 1966; Sauther 1991).

Ring-tailed lemur males howl in a number of different social situations. Males howl throughout the year at dusk when settling in night sleeping trees (Jolly 1966; Koyama 1988; Macedonia 1990), and in response to other howls or recurring loud sounds (Andrew 1963). Howling rate also seems to increase both during the breeding season, when many males howl throughout the day and night (Jolly 1966; Mertl-Milhollen *et al.* 1979), and at the end of the birthing season (Budnitz and Dainis 1975). Past researchers proposed that howling functions as an intertroop signal, broadcasting the presence and location of the troop (Jolly 1966; Macedonia 1990; Petter and Charles-Dominique 1979), which supports the intergroup mate defense hypothesis.

This study evaluates whether the mate defense and the mate attraction hypotheses for long-calling are applicable to ring-tailed lemur howls. Male–male competition in this species occurs both inside and outside social groups (Jolly 1966; Sussman 1992). For this reason, I address the mate defense hypothesis for male long calling separately within and between groups.

Hypothesis 1: Intergroup Mate Defense

Resident males may howl to advertise their presence and to discourage extragroup males from approaching females, as has been hypothesized for other primate species (Wich and Nunn 2002). If this is the case, then I predict that the howling rate of male ring-tailed lemur group members will be higher during intertroop encounters as opposed to contexts without nongroup members present. Further, a greater number of ring-tailed lemur resident males will join in howling bouts given during intergroup encounters than when nongroup members are not present.

Hypothesis 2: Intragroup Mate Defense

Males may howl to indicate their presence and high rank and to discourage other males from their group from mating with females. If this is the case, I predict that higher ranking ring-tailed lemur males will have higher howling rates than lower ranking males.

Further, high ranking ring-tailed lemur males will produce howling bouts containing a greater number of howls than low ranking males, and males will howl during male–male agonistic contexts, including immediately before or after agonistic interactions.

Hypothesis 3: Mate Attraction

Males may howl as a mate attraction signal to estrous females. If this is the case, I predict that male ring-tailed lemur howling rate will be higher on days of known estrus as opposed to days without estrus. Further, estrous females will seek out or move toward males immediately after they are heard howling.

Methods

I collected all data for this study between March 1 and July 1, 2010 at Beza Mahafaly Special Reserve, a protected governmental reserve in southwest Madagascar (23°30'S lat., 44°40'E long.; Sussman and Ratsirarson 2006; Sussman *et al.* 2012). This reserve was established in 1978 and has been protected since 1986 (Gould *et al.* 2003; Sussman *et al.* 2012). It consists of two noncontiguous forest types: dry forest in the western area of the reserve (Parcel II, 500 ha) and riverine forest on the eastern side (Parcel I, 80 ha) (Sussman and Ratsirarson 2006). A system of labeled trails roughly divided Parcel I into 100-m² squares, making this forest easy to navigate.

Approximately 225 free-ranging ring-tailed lemurs lived in 11 groups in Parcel I, and almost all adult lemurs were individually known (Gould and Zeigler 2007; Sauther and Cuzzo 2008). Most individuals were collared and labeled with visible numbers, an identification system dating to the late 1980s (Cuzzo *et al.* 2010; Cuzzo and Sauther 2006; Sauther and Cuzzo 2009; Sauther *et al.* 2002; Sussman 1991). I could easily identify any uncollared individuals by patches of black dye in different body areas, applied by another researcher in February, 2010. Five groups from Parcel I were the focus of this study.

Focal Individuals

I performed behavioral focal follows 6 days/week from dawn until dusk on 25 males aged ≥ 3 year (Table I) and collected 600 h of data. I followed one group per day and studied each group 1–2 days/week. I sampled resident males on a randomized, rotational basis (Altmann 1974). Ages for all collared lemurs ≥ 2 year were known from the decade-long work by Sauther and Cuzzo, who identify lemurs first as subadults (second year of age) when first captured, and determine age from a series of variables including dental development, sexual maturity (or lack thereof), body mass,

Table 1 Ring-tailed lemur males studied at Beza Mahafaly Special Reserve, March–July 2010

Troop	Individual name	Group membership status	Dominance index score in %
Green	Umm1g	Nonnatal	91.9
Green	Umm2g	Nonnatal	85
Green	175	Nonnatal	71.9
Green	Umm3g	Nonnatal	38.9
Green	203	Nonnatal	36.4
Orange	263	Nonnatal	98.2
Orange	259	Nonnatal	83
Orange	Umm1o	Nonnatal	49.1
Orange	291	Nonnatal	45.7
Orange	318	Natal	37.8
Orange	226	Nonnatal	12.6
Purple	Umm2p	Nonnatal	100
Purple	Umm1p	Nonnatal	76.5
Purple	Umm4p	Nonnatal	69.9
Purple	323	Natal	46.4
Purple	322	Natal	41.7
Purple	Umm3p	Nonnatal	36.1
Red	280	Nonnatal	85
Red	273	Nonnatal	72.7
Red	308	Natal	28.6
Red	307	Natal	13.7
Yellow	208	Nonnatal	79.2
Yellow	Umm2y	Nonnatal	75.2
Yellow	230	Nonnatal	74.4
Yellow	Umm1y	Nonnatal	46.2

and somatic development (Cuozzo and Sauther 2006; Cuozzo *et al.* 2010; Sauther and Cuozzo 2008, 2009). I estimated age for all individuals with names beginning with UMM (unmarked male) as ≥ 3 . All UMM individuals were sexually mature males and new, nonnatal members to collared study groups in Parcel I within the last year (Beza Mahafaly Special Reserve *unpubl. data*). I included both natal and nonnatal male group members in all analyses because I observed some natal males mating with female group members (Bolt *unpubl. data*). The study groups included 9–20 individuals, with 4–8 males, 4–10 females, and 0–3 infants present per group.

Data Collection

I collected male howl vocalizations via all-occurrences sampling (Altmann 1974) at all times of contact with the troop, noting the time, identity of the caller, number of howls in the bout, and number of males participating in the bout. This sampling method was appropriate because male howling vocalizations occurred infrequently throughout the day and howls by any member of the focal group were easily audible.

I noted days of observed female estrus opportunistically during the mating season and used ad libitum sampling to note them (Altmann 1974). I identified female estrus as a period of time when a female copulated and made proceptive sexual presentations toward males (Beach 1976).

I defined intertroop interactions as another troop being in visible distance and within 20 m of the focal troop. I noted all intertroop interactions using all-occurrences sampling (Altmann 1974).

During focal sampling, I followed each subject continuously for 30 min at a time, recording data every 2.5 min on a programmed palm pilot (Palm Z-22) using one-zero sampling (Martin and Bateson 2007) to document agonistic interactions. I noted the names of the actors and details of the agonistic encounter. I defined an agonistic interaction as any behavior involving contest competition between two individuals, including one or more acts of avoidance, aggression, or defense (see ethograms by Gould 1994; Jolly 1966; Pereira and Kappeler 1997). This could consist of low-arousal behavior, e.g., a displacement or lunge-withdraw, or higher-arousal behavior, e.g., cuff, bite, or jump fight.

I determined dominance rank from all focal data using all decided agonistic interactions to assign each male a dominance percentage within its group (Zumpe and Michael 1986). This method of calculation takes the number of interacting males within each group into consideration, thus accounting for differences in group size and allowing for comparisons of rank between groups (Zumpe and Michael 1986). I treated all agonistic behaviors, e.g., chase, lunge-withdraw, cuff, equally in calculating dominance indices (Gould 1994), and calculated dominance indices separately for each group.

Data Analysis

Data were not normally distributed, and the sample size was small ($N=25$ males), making nonparametric tests appropriate.

For hypothesis 1, I used a Wilcoxon test to test the prediction that howling rate will be higher during intertroop encounters. Because howling was an infrequent behavior that I noted using all-occurrences sampling, I calculated howling rates for each male using total focal time for each ring-tailed lemur troop, rather than the focal time of individual males. I also used a Wilcoxon test to evaluate whether a greater number of ring-tailed lemur males participated in a howling bout when nongroup members were present. To test further whether a greater number of males participated in a howling bout when nongroup members were present compared with times when only group members were present, I used a one-sample binomial test to determine whether howling bouts involving two or more group members were given during intertroop encounters more often than expected from chance.

For hypothesis 2, I used a Spearman rank correlation test to test whether high-ranking males have higher howling rates. I also used a Spearman test to evaluate whether high-ranking males have howling bouts containing a greater number of howls. I excluded males from analysis if they were never heard howling ($N=12$ males excluded) or if the number of howls within their bout was not accurately recorded ($N=1$ male excluded). I used a one-sample binomial test to determine whether howling occurred immediately before or after times of male-male agonism more often than expected by chance.

For hypothesis 3, I used a Wilcoxon test to evaluate whether male howling rate was higher on days of known estrus. I excluded males from analysis if estrus was not observed in their group ($N=6$ males excluded, from 1 group). I used the binomial test to evaluate whether howling was associated with females moving toward howling males within 1 min more often than expected by chance.

All tests were two-tailed. I report means and standard deviations. I set the α level at 0.05 for all tests, and performed all statistical tests using SPSS version 20 (IBM SPSS Statistics, IBM Corporation, Armonk, NY). SPSS identified outliers as data points with a distance from the nearest quartile of >1.5 times the interquartile range, and I removed these values when doing recalculations.

Results

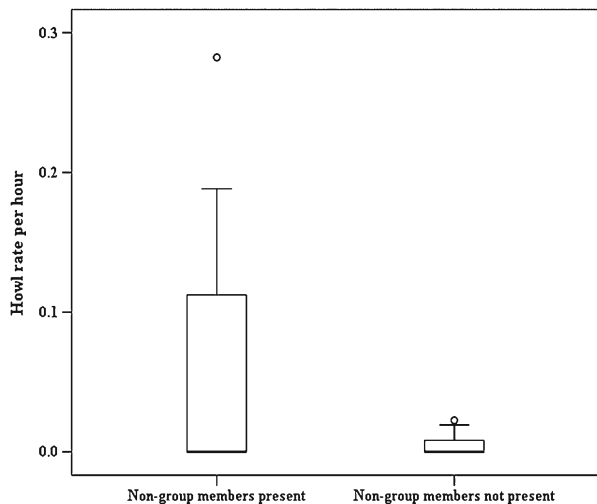
Males Howl More During Intergroup Encounters

There was a significant difference in male howling rate during intergroup encounters compared to periods without nongroup members present (Wilcoxon signed rank test: $Z=-2.77$, $N=25$ males, $P=0.006$; Fig. 1). This result remained significant when I excluded outliers ($Z=-2.32$, $N=21$ males, $P=0.02$).

A greater mean number of resident males participated in howling bouts when nongroup members were present ($0.81 \pm \text{SD } 1.24$, $N=25$ males) than when they were not present ($0.24 \pm \text{SD } 0.44$, $N=25$ males, Wilcoxon test: $Z=-2.17$, $P=0.03$). This result remained significant when I excluded outliers ($Z=-2$, $N=16$ males, $P=0.046$).

All 11 howling bouts involving two or more males occurred in the presence of nongroup members, and the participation of multiple group members in a howling bout was significantly related to the presence of non-group members (binomial test: $Z=5.2$, $P=0.001$).

Fig. 1 Male howling rate per hour during periods when nongroup members were, and were not, present, in ring-tailed lemurs. Boxes represent interquartile ranges, lines represent median values, whiskers represent maximum and minimum values, and dots represent outliers.



Howling Rate was not Significantly Associated with Dominance Status

Male howling rate did not correlate with male dominance index (Spearman rank correlation: $r_s = -0.04$, $N = 25$ males, $P = 0.842$, Fig. 2) and the mean number of howls in a male howling bout did not correlate with male dominance index ($r_s = -0.16$, $N = 12$ males, $P = 0.614$; Fig. 3). Further, howling was less likely to occur immediately before or after male–male agonism than at other times: Of 30 howls by identified males heard during the study period, 3 (10 %) were given by males after they lost an agonistic interaction with another male, whereas 27 (90 %) were given in non-agonistic contexts (binomial test: $Z = -4.38$, $P < 0.0001$).

Howling Rate was not Significantly Associated with Female Estrus

There was no significant difference in mean male howling rate on estrus days than on nonestrus days (Wilcoxon test: $Z = -0.86$, $N = 19$ males, $P = 0.388$; Fig. 4). These results remained nonsignificant when I removed outliers ($Z = -1.28$, $N = 17$ males, $P = 0.202$). Finally, male howling did not appear to attract estrous females. Of five howls by identified focal males heard on estrus days, only one was associated with females moving toward howling males within 1 min (binomial test: $Z = -1.34$, $P = 0.375$).

Discussion

My results support the intergroup function of the mate defense hypothesis and suggest that males howl to advertise their presence to ring-tailed lemurs from other groups. Male howling rate increased during intertroop encounters, with significantly more males participating in howling bouts when nongroup ring-tailed lemurs were within 20 m and in visual range. In contrast, I found no support for the predictions of the intragroup mate defense hypothesis, nor for the mate attraction hypothesis.

Fig. 2 Mean howling rate vs. dominance index score in male ring-tailed lemurs.

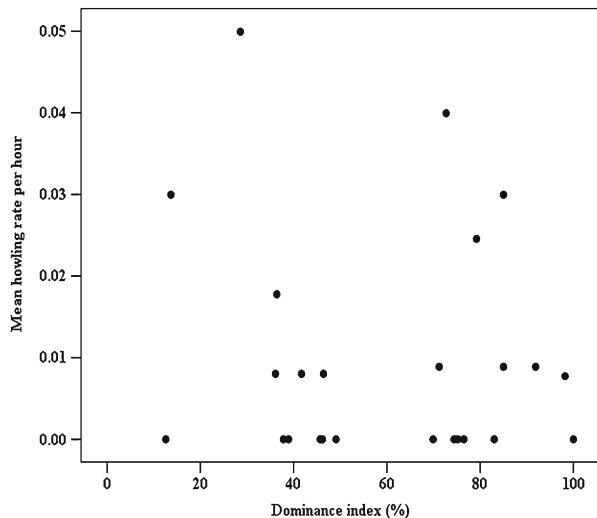
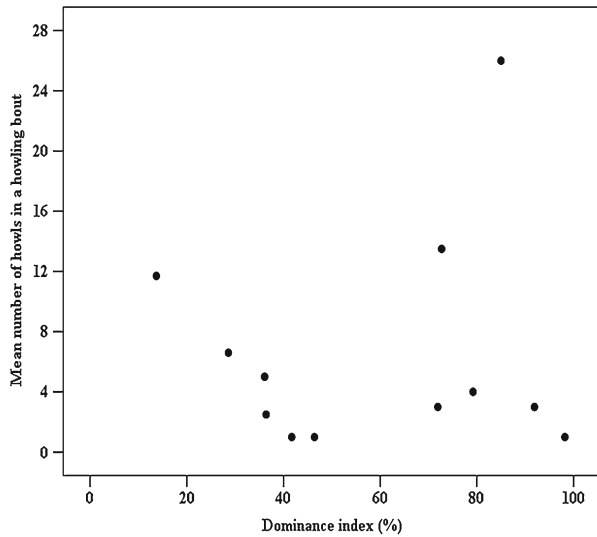
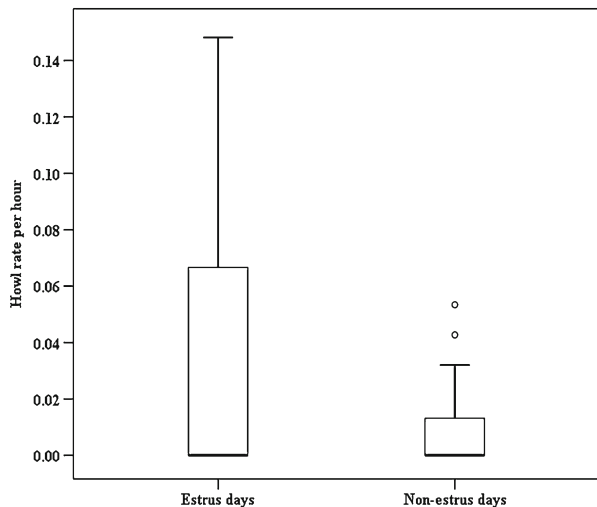


Fig. 3 Mean number of howls in a howling bout vs. dominance index score in male ring-tailed lemurs.



Contrary to reports that high-ranking ring-tailed lemur males howl more often than low-ranking males (Jolly 1966; Koyama 1988; Macedonia 1990), male dominance did not significantly correlate with howling rate or bout length, nor was howling significantly associated with male–male agonism. Further, howling did not appear to attract estrous females. Howling rate did not significantly increase during female estrus. However, males did show a nonsignificant tendency to howl more frequently when females in the same troop were in estrus. A future study should examine whether females from adjacent troops are in estrus during intergroup encounters as males may howl more during intergroup encounters in response to the proximity of estrous females from other groups.

Fig. 4 Mean howling rate on estrus and nonestrus days in male ring-tailed lemurs. *Boxes* represent interquartile ranges, *lines* represent median values, *whiskers* represent maximum and minimum values, and *dots* represent outliers.



My study supports suggestions by Jolly (1966) and Macedonia (1993) that the male howl indicates a group's presence and location. Howling also indicates a minimum number of males resident in a troop, with more focal males joining in howling bouts during intertroop encounters. Because individual voices are staggered within a ring-tailed lemur howling chorus (Macedonia 1990), this may signal the number of howlers participating in a bout, and thus the number of males already present in a ring-tailed lemur group to neighboring troops. This notion has also been proposed for other species with offset long calls comprising group-wide choruses: lions (*Leo* spp.: McComb *et al.* 1994); red howlers (*Alouatta seniculus*: Sekulic 1982); and black howlers (*Alouatta caraya*: Kitchen 2004; Kitchen *et al.* 2004b). However, it is unknown how nongroup male ring-tailed lemurs respond to howling choruses. In other primate species such as gray-cheeked mangabeys (*Lophocebus albigena*), social groups use long calls as a means of spacing themselves by avoiding other calling groups (Waser 1975). Ring-tailed lemur males may use howls similarly to space themselves.

Kitchen (2004, 2006) observed that primate group-level fighting ability likely depends on the number of participants in the fight, and groups with more competitors have a greater chance of winning in an agonistic interaction. Group members assess the relative number of competitors in two different groups, or their "numeric odds," through assessing long calls in several mammal species (Kitchen 2006, p. 74): lions (Grinnell *et al.* 1995), chimpanzees (*Pan troglodytes*: Wilson *et al.* 2001); and black howlers (Kitchen 2004). According to the predictions of game theory, which suggest that individuals and groups should avoid fights that they will likely lose (Maynard Smith 1982), in black howlers, relative combat ability can be gauged at group level through howling displays, allowing groups to withdraw from fights they would be unlikely to win (Kitchen *et al.* 2004b). Ring-tailed lemur howling choruses may play a similar role in intergroup interactions. Because females typically take the primary role in resource and group defense in this species (Gould *et al.* 2003), male howling would be unlikely to dissuade nongroup females from taking resources, or from attacking resident males. Instead, howling is likely to function to advertise male presence to males from other groups and to discourage nongroup males from approaching and gaining sexual access to group females, as the mate defense hypothesis predicts (Wich and Nunn 2002).

Ring-tailed lemur howling choruses also have the potential to mediate male migration. Dispersing ring-tailed lemur males are more likely to choose a group with fewer mature males (Parga and Lessnau 2008) and so may choose a group with few or no howling males. In sympatric lemur species, such as Verreaux's sifaka (*Propithecus verreauxi*), resident males form coalitions to forcibly keep extragroup males out of a social group to prevent them from mating with estrous females (Lewis and van Schaik 2007). The group-wide howling bouts of ring-tailed lemurs may be a form of acoustic coalition that accomplishes the same mate-defense purpose.

Within the polygynandrous mating system of ring-tailed lemurs, most nonnatal males in a social group have the opportunity to mate with at least some estrous females, regardless of their rank (Gould 1994; Parga 2006; Sauther 1991; Sussman 1992). I observed sexually mature natal males mating with a resident female (Bolt *unpubl. data*) and nongroup males also mating with estrous females (Koyama 1988; Sauther 1991; Sussman 1992). There are, therefore, potential fitness consequences for

resident males if extragroup males are allowed to remain in the area when resident females are in estrus. Accordingly, repelling nongroup male competitors is beneficial for all resident males, as Kitchen *et al.* (2003) suggest for chacma baboons. Howling may be the means by which this is accomplished in ring-tailed lemurs.

Conclusions

Male howling rate increased during intergroup encounters in ring-tailed lemurs, but was not significantly related to female attraction or male dominance rank. Howling advertised male presence and was a signal directed toward nongroup conspecifics, as opposed to males or females within a social group. Multimale howling choruses were strongly associated with intertroop encounters and honestly indicated the minimum number of resident males in a ring-tailed lemur group. My results support the intergroup function of the mate defense hypothesis.

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