

Antipredator Vocalization Usage in the Male Ring-Tailed Lemur (*Lemur catta*)

Laura M. Bolt^a Michelle L. Sauter^b Frank P. Cuzzo^c
Ibrahim Antho Youssouf Jacky^d

^aDepartment of Anthropology, University of Toronto, Toronto, Ont., Canada;

^bDepartment of Anthropology, University of Colorado, Boulder, Colo., and

^cDepartment of Anthropology, University of North Dakota, Grand Forks, N.Dak., USA;

^dDepartment of Animal Biology, University of Toliara, Toliara, Madagascar

Key Words

Male vocalization · Antipredator behavior · Alarm call · Vocalization rate · Male dominance · Predator abundance · Predator confusion hypothesis · Group maintenance hypothesis · Predation risk allocation hypothesis · *Lemur catta*

Abstract

The ring-tailed lemur (*Lemur catta*) is a group-living strepsirrhine primate endemic to Madagascar that faces considerable predation pressure from aerial and terrestrial predators. This species engages in mobbing and vigilance behavior in response to predators, and has referential alarm vocalizations. Because *L. catta* is female dominant, less is known about the alarm calls of males. We tested 3 hypotheses for male antipredator vocalization behavior on *L. catta* at the Bezà Mahafaly Special Reserve in Madagascar: the predator confusion, group maintenance, and predation risk allocation hypotheses. We found support for 2 hypotheses. When a male *L. catta* made an antipredator call, other group members vocalized in response. Dominant males did not make alarm calls at higher rates than subordinate males. Predators were more abundant on the western side of Parcel 1, but an even greater number of antipredator vocalizations occurred in this area than predator abundance warranted. We show that male *L. catta* consistently participated in group-level antipredator vocalization usage in high-risk locations. Although female *L. catta* are known to hold the primary role in group defense, male *L. catta* are also key participants in group-wide behaviors that may confuse or drive away predators.

© 2015 S. Karger AG, Basel

Introduction

Group-living diurnal primates have evolved a number of different strategies to avoid predation, including vigilance, predator mobbing and alarm vocalizations [reviewed in Fichtel, 2007]. Although antipredator behavior is well studied in primates [Cheney and Seyfarth, 1985; Rose and Fedigan, 1995; Lewis, 2005], the specific contributions of individual group members, such as males, to group-wide antipredator strategies is still poorly understood for many species. Baldellou and Henzi [1992] predicted that in exchange for being tolerated in social groups, immigrant and low-ranking males should offer females increased predator vigilance. Gould and Sauther [2006] suggest that males may be less vigilant than females in female-dominant species, which by extension implies that males may also be less likely to alarm-call. Primate alarm calls are thought to alert other group members to predator presence as well as to discourage predator attack [Zuberbühler et al., 1999], so may be selfish and/or altruistic signals [Fichtel, 2007]. We elucidate male contributions to group-wide antipredator behaviors in a female-dominant, female-philopatric primate species, the ring-tailed lemur (*Lemur catta*).

L. catta is a group-living strepsirrhine primate species endemic to Madagascar that faces considerable predation pressure from aerial and terrestrial predators [Jolly, 1966; Sauther, 1989; Macedonia, 1990, 1993; Gould and Sauther, 2006]. This species engages in mobbing behavior in response to predators and has referential alarm calls based on predator class (table 1) [Sauther, 1989; Macedonia, 1990, 1993; Macedonia and Evans, 1993]. While previous studies have found that both males and females engage in predator vigilance [Gould, 1996], the level of participation of male *L. catta* in group-wide alarm-calling behaviors is unknown. In this study, we test 3 hypotheses for male antipredator vocalization behavior on *L. catta* at the Bezà Mahafaly Special Reserve in Madagascar.

Hypothesis 1: Predator Confusion

The predator confusion hypothesis [Wheeler, 2008] predicts that when a group member makes an antipredator vocalization, other group members will also make alarm calls, in an attempt to confuse the predator and drive it away. We predicted that when a focal male makes an antipredator alarm call, one or more group members will also vocalize using the same antipredator call.

Hypothesis 2: Group Maintenance

The group maintenance hypothesis [Wheeler, 2008] predicts that higher-ranking individuals are more likely to make antipredator calls than lower-ranking individuals. Dominant males may alarm-call at higher rates in order to gain increased sexual access to females from their social group and thus increase their likelihood of paternity [van Schaik and van Noordwijk, 1989], and/or because their individual predation risks are lower due to the dilution effect combined with their superior fitness [Bertram, 1978; Alatalo and Helle, 1990]. We predicted that males with higher dominance ranks would make antipredator vocalizations at higher rates than males with lower dominance ranks.

Hypothesis 3: Predation Risk Allocation

The predation risk allocation hypothesis [Lima and Bednekoff, 1999] predicts that animals are more likely to respond strongly to potential predators if they are in

Table 1. *L. catta* antipredator vocal repertoire

Call name	Predator type	Arousal level
Click ¹	Terrestrial	Low
Click series	Terrestrial	Medium
Yap	Terrestrial	High
Gulp	Aerial	Low
Rasp ¹	Aerial	Medium
Shriek	Aerial	High

All terms from Macedonia [1993].

¹ Excluded from analysis in this study.

Table 2. *L. catta* study group composition at the Bezà Mahafaly Special Reserve

Group name	Total group membership	Number of males aged ≥1 year	Number of females aged ≥1 year	Number of infants (born 2009)
Green	13	6	6	1
Orange	20	7	10	3
Purple	15	8	5	2
Red	9	4	5	0
Yellow	12	6	4	2

an area with an increased predation risk. We predicted that males are more likely to use high-arousal antipredator vocalizations (i.e. shriek or yap; table 1) when in an area of greater predator abundance than when in an area of lower predator abundance.

Methods

We collected all data in the Parcel 1 riverine gallery forest at Bezà Mahafaly Special Reserve, Madagascar (23°30' S, 44°40' E) [Sussman and Ratsirarson, 2006]. Thirty males aged older than 1 year from 5 groups of *L. catta* comprised the study animals (table 2). All focal animals (table 3) were collared with visible numbered tags [Sauther et al., 2002; Cuzzo and Sauther, 2006; Sauther and Cuzzo, 2008; Cuzzo et al., 2010] or could be identified by spots of black dye on different body areas placed by a previous researcher [Bolt, 2013b].

Potential known predators of lemurs at Bezà Mahafaly Special Reserve include the harrier hawk (*Polyboroides radiatus*), domestic dogs (*Canis lupus familiaris*), felids (*Felis* sp. *Incertae sedis*), which weigh an average of 3.24 kg at the reserve [Sauther and Cuzzo, unpubl. data], the fosa (*Cryptoprocta fosa*) and the small Indian civet (*Viverricula indica*) [Gould and Sauther, 2006]. The last can weigh as much as 2.46 kg at the reserve [Sauther and Cuzzo, unpubl. data].

To assess predator frequency, we situated 9 camera traps (Moultrie M-80XT Game Spy 4.0 Digital Camera, Alabama, USA) near trails throughout the parcel from June 2008 to July 2009 to assess the relative frequency of terrestrial predators within the reserve (fig. 1). We set these traps on a 24-hour cycle to assess both diurnal and nocturnal predator presence. Camera traps posi-

Table 3. *L. catta* male study individuals at the Bezà Mahafaly Special Reserve

Group	Individual name	Group membership status	Dominance index score, %
Green	Umm1g	Nonnatal	91.9
Green	Umm2g	Nonnatal	85
Green	175	Nonnatal	71.9
Green	Umm3g	Nonnatal	38.9
Green	203	Nonnatal	36.4
Green	335	Natal	0
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
Orange	331	Natal	0
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
Purple	337	Natal	22.6
Purple	340	Natal	3.6
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
Yellow	313	Natal	20

tioned west of the center trail (5/9 traps) were considered to be on the west side of the reserve, while traps situated on or east of the center trail (4/9 traps) were considered on the east side of the reserve. In addition, from June 2008 to July 2009 we collected terrestrial predator fecal samples ($n = 32$) during weekly surveys along all marked trails within Parcel 1. We identified fecal samples by predator type (felid, canid or viverrid) and recorded GPS locations for each fecal sample. It should be noted that the physical features of the terrain throughout the reserve are similar in that the whole area is very flat, so this helped limit variation in predator detection in the different areas. In addition, all known predators commonly use the trails to move throughout the reserve.

To assess the antipredator vocalization rate, we collected 480 h of focal data on 30 male *L. catta* in 2010. During 30-min samples, we recorded antipredator vocalizations (table 1) using one-zero sampling [Altmann, 1974] at 2.5-min intervals on a programmed palm pilot (Palm Z-22). We also recorded vocalization types made by one or more other group members during each sample. We noted all-occurrences of group-wide high-arousal antipredator vocalizations (shriek or yap), along with group GPS location.

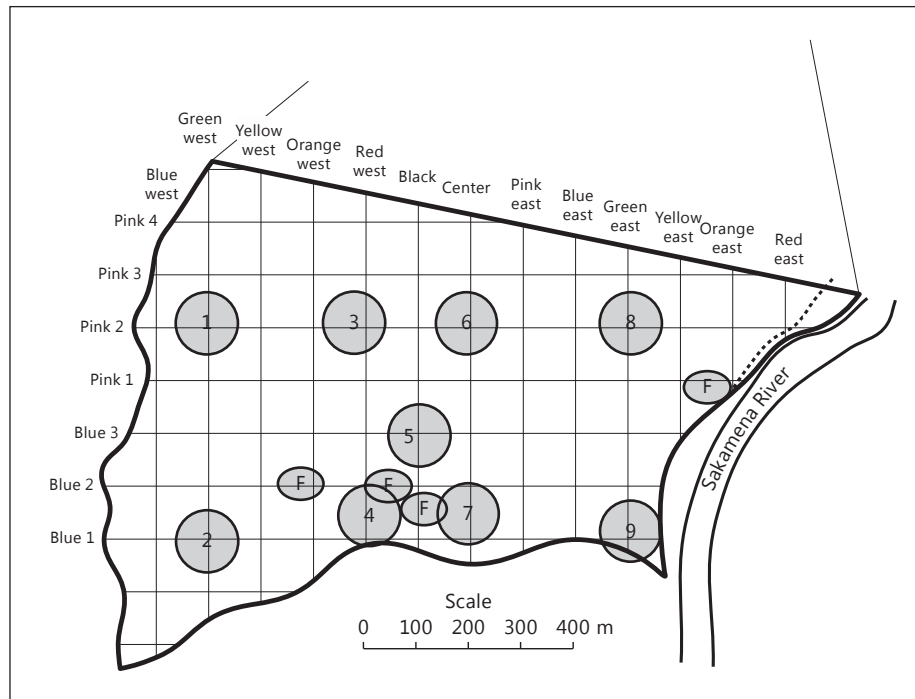


Fig. 1. Camera trap placement (1–9) and location of felid predator fecal samples containing lemur remains (F) in Parcel 1 at Bezà Mahafaly Special Reserve.

During focal samples, we noted all agonistic interactions involving focal males, along with the names of other individuals, and the outcomes of decided interactions. An agonistic interaction is defined as any behavior involving contest competition between two individuals, which may be of low arousal (e.g. a lunge-withdraw or displacement) or higher arousal (e.g. cuff or bite) [Gould, 1994]. We determined male dominance ranks from these data following the methodology explained in detail by Bolt [2013a, c, 2014], using dominance index calculations [Zumpe and Michael, 1986], which take all aggressive and submissive interactions in each troop into account and assign an individual dominance percentage to each group member based on the relative number of agonistic wins.

For each data set used in our study, data were not normally distributed, and the sample size was small, requiring the use of nonparametric tests. Click calls (table 1) were excluded from all analyses due to wide use across social contexts [Bolt, unpubl. data], while rasp calls were excluded from analysis due to lack of data. We used the binomial test to assess if, when antipredator vocalizations were made by focal males, one or more group members were likely to make the same antipredator vocalization more often than expected by chance. We used the Spearman rank correlation test to evaluate whether high-ranking males had higher rates of antipredator vocalizations than lower-ranking males. We determined predator abundance on the east and west sides of Parcel 1 by dividing the number of predators noted in fecal surveys and camera traps by the number of study days. We determined predator perception by dividing the number of high-arousal antipredator vocalizations heard during the study period by the number of focal days spent mostly or entirely on the east or west side of Parcel 1. All tests were 2-tailed and performed using SPSS version 22 (IBM SPSS Statistics, IBM Corporation, Armonk, N.Y., USA, 2013). The alpha level was set to 0.05.

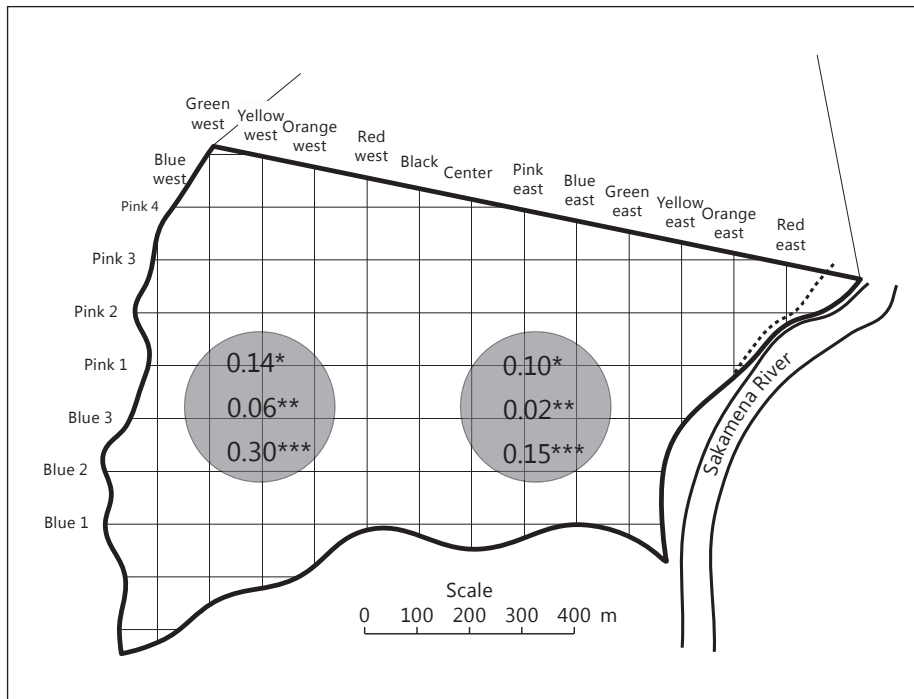


Fig. 2. West versus east predator abundance in Parcel 1 at Bezà Mahafaly Special Reserve. * Based on camera trap data divided by number of camera trap days. ** Based on predator fecal samples divided by number of sample days. *** *L. catta* antipredator vocalizations from focal data divided by number of study days.

Results

Hypothesis 1: Predator Confusion

Antipredator vocalizations were made by focal males as well as other group members during the study period. When a focal male made an antipredator vocalization, one or more group members made the same vocalization more often than expected by chance (binomial tests, click series: $p < 0.0001$, $n = 3,147$; yap: $p < 0.001$, $n = 21$; gulp: $p < 0.001$, $n = 301$; shriek: $p = 0.004$, $n = 9$).

Hypothesis 2: Group Maintenance

Males of all dominance ranks made antipredator vocalizations of all arousal levels during the study period. No significant correlation occurred between male dominance rank and vocalization rate for any antipredator vocalization (Spearman tests, click series: $n = 30$ males, $r_s = 0.22$, $p = 0.234$; yap: $n = 30$ males, $r_s = 0.16$, $p = 0.407$; gulp: $n = 30$ males, $r_s = -0.02$, $p = 0.913$; shriek: $n = 30$ males, $r_s = -0.08$, $p = 0.694$). Higher-ranking males did not utter any antipredator call at a higher rate than lower-ranking males.

Hypothesis 3: Predation Risk Allocation

All group-wide shriek and yap calling bouts involved male participants, and male behaviors were consistent with group-wide vocal responses. Camera trap data and predator fecal samples showed greater terrestrial predator density on the west side of Parcel 1 when compared to the east side (camera trap data: 0.14 or 200 photos/1,459 camera trap days on the west vs. 0.10 or 109 photos/1,129 camera trap days on the east; fecal samples: 0.06 or 23 samples/365 days on the west vs. 0.02 or 9 samples/365 days on the east). Canids, felids and viverrids were represented in fecal and camera trap data (camera trap data: 142 photos of canids, 140 photos of felids, 27 photos of viverrids; fecal samples that could be identified to genus: 6 canid samples, 22 felid samples, 4 viverrid samples). Of the samples collected in June–July 2008 within the reserve, only felid fecal samples showed evidence of lemur predation (*L. catta*, *Propithecus verreauxi* or *Lepilemur petteri*), with 4/14 (29%) containing lemur remains that included *L. catta* bone fragments as well as a microchip associated with a known collared *L. catta*. Of note, the majority of these were found in the western part of the reserve (fig. 1). Focal data showed that predator perception, as indicated by high-arousal antipredator vocalizations, was also greater on the west side of Parcel 1 when compared to the east side (0.30 or 6 calls/20 focal days on the west vs. 0.15 or 9 calls/62 focal days on the east; fig. 2). Antipredator vocal response in the western area of the reserve was stronger than estimated predator presence by our measures and also higher than the response in the eastern reserve area. One study group (purple) with a range entirely in the western Parcel 1 and areas south of the parcel made more antipredator vocalizations (6/15 or 40% of total shriek/yap calls) than the other 4 focal groups, which had ranges primarily in the eastern side of Parcel 1.

Discussion

Within the limitations of our experimental design, we found support for 2 of our hypotheses. We show that *L. catta* males participated in group-level antipredator vocalization usage. Males both initiated and consistently joined in with group antipredator vocalization behaviors, contributing to alarm call bouts of low, medium and high arousal. This male participation in collective alarm calling is consistent with the predator confusion hypothesis, although direct evidence of predator confusion is not available. Support for the predator confusion hypothesis has also been found in rodents [Sherman, 1985] and birds [Cresswell, 1994].

Although male *L. catta* participated in group-wide antipredator vocalization bouts, dominant males did not participate at higher rates. Therefore, our results did not support the group maintenance hypothesis [Wheeler, 2008] and showed no significant relationship between individual male dominance rank and alarm-calling rate. Previous support for this hypothesis had been found in vervet monkeys (*Chlorocebus pygerythrus*) and tufted capuchin monkeys (*Cebus apella*) [Cheney and Seyfarth, 1985; van Schaik and van Noordwijk, 1989]. For some *L. catta* vocalizations, the vocalization rate is known to be correlated with individual male dominance rank [Bolt, 2013c, 2014], but alarm calls do not fit this trend. In contrast to primate species such as *C. pygerythrus* and *C. apella*, in which dominant males are thought to derive fitness benefits from calling at increased rates [Cheney and Seyfarth, 1985; van Schaik

and van Noordwijk, 1989], dominant male *L. catta* may not alarm-call at higher rates because they may not receive any benefits from doing so. Further research is needed to test this speculation. *L. catta* males of all dominance ranks thus contribute to group-wide alarm calling behavior.

Based on our results, we suggest that predator abundance may be higher on the western side of Parcel 1, but the male *L. catta* antipredator vocalization response was even stronger than estimated predator abundance. The predation risk allocation hypothesis predicts that during high-risk periods (i.e. during a predator sighting) in high-risk predation environments (i.e. areas with greater predator concentration), prey animals should increase their antipredator response [Ferrari et al., 2009]. Given that the west side of Parcel 1 was a higher-risk environment compared to the east side, the stronger alarm response of male *L. catta* to potential predators in the west is consistent with the prediction of this hypothesis. This stronger response to perceived threats in high-risk areas is consistent with findings on antipredator behaviors in fish [Giles and Huntingford, 1984; Mirza et al., 2006] and amphibians [Woodward, 1983].

We show that male *L. catta* consistently participated in alarm calling in high-risk locations, thus incurring personal threat in order to engage in antipredator behaviors. Both male and female *L. catta* participate in antipredator vigilance [Gould, 1996], so it follows that males as well as females should participate in group-wide alarm calling. When our results are viewed in light of the prediction that immigrant and low-ranking males should offer females increased predator protection in exchange for social tolerance [Baldellou and Henzi, 1992], we find limited support. Individual male dominance rank had no significant relationship with the alarm-calling rate, suggesting that males with lower dominance ranks did not engage in more antipredator behaviors than other group members. Further, *L. catta* males are typically low-ranking immigrants in this female-dominant, female-philopatric species [Jolly, 1966; Gould, 1994], yet alpha females are known to be the most vigilant group members [Gould and Sauther, 2006], and females hold the primary role in group defense [Gould et al., 2003]. Notwithstanding the major role of females in collective antipredator actions, our study shows that male *L. catta* are also key participants in group-wide vocalization behaviors that may confuse or drive away predators.

Acknowledgments

Research funding was provided by the Natural Sciences and Engineering Research Council of Canada, the American Museum of Natural History, the St. Catherines Island Foundation, the Edward J. Noble Foundation, the International Primatological Society, Primate Conservation Inc., the Margot Marsh Biodiversity Foundation, the Explorer's Club, Sigma Xi, the University of Toronto, the University of Colorado-Boulder, the University of North Dakota, ND EPSCoR, and the US National Science Foundation BCS 0922465. We thank the ecological monitoring staff at the Bezà Mahafaly Special Reserve for their assistance with data collection, and Jenifer Ness for her assistance with predator scat collection and scat sample processing at Bezà Mahafaly in 2008. We also thank Madagascar National Parks (formerly ANGAP) and the Département des Eaux et Forêts, Ecole Supérieure des Sciences Agronomiques, Université de Antananarivo, for permission to work at Bezà Mahafaly. Finally, we thank Anna Nekaris, Robin Crompton and 2 anonymous reviewers for their helpful comments.

References

- Alatalo R, Helle P (1990). Alarm calling by individual willow tits, *Parus montanus*. *Animal Behaviour* 40: 437–442.
- Altmann J (1974). Observational study of behavior: sampling methods. *Behaviour* 49: 227–265.
- Baldellou M, Henzi S (1992). Vigilance, predator detection and the presence of supernumerary males in vervet monkey troops. *Animal Behavior* 43: 451–461.
- Bertram B (1978). Living in groups: predators and prey. In *Behavioural Ecology: An Evolutionary Approach* (Krebs J, Davies N, eds.), pp 64–96. Oxford, Blackwell Scientific.
- Bolt L (2013a). The function of howling in the ring-tailed lemur (*Lemur catta*). *International Journal of Primatology* 34: 157–169.
- Bolt L (2013b). *The Relationship between Dominance and Vocal Communication in the Male Ring-Tailed Lemur* (*Lemur catta*). PhD dissertation, University of Toronto.
- Bolt L (2013c). Squealing rate indicates dominance rank in the male ring-tailed lemur (*Lemur catta*). *American Journal of Primatology* 75: 1174–1184.
- Bolt L (2014). Male-specific use of the purr in the ring-tailed lemur (*Lemur catta*). *Folia Primatologica* 85: 201–214.
- Cheney D, Seyfarth R (1985). Vervet monkey alarm calls: manipulation through shared information? *Behaviour* 94: 150–166.
- Cresswell W (1994). The function of alarm calls in redshanks, *Tringa tetanus*. *Animal Behaviour* 47: 736–738.
- Cuozzo F, Sauther M (2006). Severe wear and tooth loss in wild ring-tailed lemurs (*Lemur catta*): a function of feeding ecology, dental structure, and individual life history. *Journal of Human Evolution* 51: 490–505.
- Cuozzo F, Sauther M, Gould L, Sussman R, Villers L, Lent C (2010). Variation in dental wear and tooth loss in known-aged, older ring-tailed lemurs (*Lemur catta*): a comparison between wild and captive individuals. *American Journal of Primatology* 72: 1026–1037.
- Ferrari M, Sih A, Chivers D (2009). The paradox of risk allocation: a review and prospectus. *Animal Behavior* 78: 579–585.
- Fichtel C (2007). Avoiding predators at night: antipredator strategies in red-tailed sportive lemurs (*Lepilemur ruficaudatus*). *American Journal of Primatology* 69: 611–624.
- Giles N, Huntingford F (1984). Predation risk and inter-population variation in anti-predator behavior in the three-spined stickleback, *Gasterosteus aculeatus*. *Animal Behaviour* 32: 264–275.
- Gould L (1994). *Patterns of Affiliative Behavior in Adult Male Ringtailed Lemurs* (*Lemur catta*) at the Beza-Mahafaly Reserve, Madagascar. PhD dissertation, Washington University, St Louis.
- Gould L (1996). Vigilance behavior in naturally occurring ringtailed lemurs (*Lemur catta*) during birth and lactation season. *International Journal of Primatology* 17: 331–347.
- Gould L, Sauther M (2006). Anti-predator strategies in a diurnal prosimian, the ring-tailed lemur (*Lemur catta*), at the Beza Mahafaly Special Reserve, Madagascar. In *Primate Anti-Predator Strategies* (Gursky S, Nekaris K, eds.), pp 275–288. New York, Springer.
- Gould L, Sussman R, Sauther M (2003). Demographic and life-history patterns in a population of ring-tailed lemurs (*Lemur catta*) at Beza Mahafaly Reserve, Madagascar: a 15-year perspective. *American Journal of Physical Anthropology* 120: 182–194.
- Jolly A (1966). *Lemur Behavior: A Madagascar Field Study*. Chicago, University of Chicago Press.
- Lewis R (2005). Sex differences in vigilance in Verreaux's sifaka: are males providing a predator detection service? *American Journal of Physical Anthropology* 40: 138.
- Lima S, Bednekoff P (1999). Temporal variation in danger drives antipredator behavior: the predation risk allocation hypothesis. *The American Naturalist* 153: 649–659.
- Macedonia J (1990). What is communicated in the anti-predator calls of lemurs: evidence from playback experiments with ring-tailed and ruffed lemurs. *Ethology* 86: 177–190.
- Macedonia J (1993). The vocal repertoire of the ringtailed lemur (*Lemur catta*). *Folia Primatologica* 61: 186–217.
- Macedonia J, Evans C (1993). Variation among mammalian alarm call systems and the problem of meaning in animal signals. *Ethology* 93: 177–197.
- Mirza R, Mathis A, Chivers D (2006). Does temporal variation in predation risk influence the intensity of antipredator responses? A test of the risk allocation hypothesis. *Ethology* 112: 44–51.
- Rose L, Fedigan L (1995). Vigilance in white-faced capuchins, *Cebus capucinus*, in Costa Rica. *Animal Behavior* 49: 63–70.
- Sauther M (1989). Antipredator behavior in troops of free-ranging *Lemur catta* at Beza Mahafaly Special Reserve, Madagascar. *International Journal of Primatology* 10: 595–606.
- Sauther M, Cuozzo F (2008). Somatic variation in living, wild ring-tailed lemurs (*Lemur catta*). *Folia Primatologica* 79: 55–78.

- Sauther M, Sussman R, Cuzzo F (2002). Dental and general health in a population of wild ring-tailed lemurs: a life history approach. *American Journal of Physical Anthropology* 117: 122–132.
- Sherman P (1985). Alarm calls of Belding's ground squirrels to aerial predators: nepotism or self-preservation? *Behavioral Ecology and Sociobiology* 17: 313–323.
- Sussman R, Ratsirarson J (2006). Beza Mahafaly Special Reserve: a research site in southwestern Madagascar. In *Ringtailed Lemur Biology: Lemur catta in Madagascar* (Jolly A, Sussman R, Koyama N, Rasamimanana H, eds.), pp 43–51. New York, Springer.
- Van Schaik C, van Noordwijk M (1989). The special role of male *Cebus* monkeys in predation avoidance and its effect on group composition. *Behavioral Ecology and Sociobiology* 24: 265–276.
- Wheeler B (2008). Selfish or altruistic? An analysis of alarm call function in wild capuchin monkeys, *Cebus apella nigrinus*. *Animal Behaviour* 76: 1465–1475.
- Woodward B (1983). Predator-prey interactions and breeding-pond use of temporary-pond species in a desert anuran community. *Ecology* 64: 1549–1555.
- Zuberbühler K, Jenny D, Bshary R (1999). The predator deterrence function of primate alarm calls. *Ethology* 105: 477–490.
- Zumpe D, Michael R (1986). Dominance index: a simple measure of relative dominance status in primates. *American Journal of Primatology* 10: 291–300.