

RESEARCH ARTICLE

Squealing Rate Indicates Dominance Rank in the Male Ring-Tailed Lemur (*Lemur catta*)

Laura M. Bolt*

Department of Anthropology, University of Toronto, Toronto, Ontario, Canada

Squeals are sharp and forceful short-range vocalizations used as aggressive and submissive agonistic signals by many mammalian species. The ring-tailed lemur (*Lemur catta*), a female-dominant strepsirhine primate, has a male-specific squeal call with proposed male–male agonistic functions and male–female courtship functions that have never been empirically tested. The goal of my study is to clarify why ring-tailed lemur males squeal at other males and females by applying the handicap hypothesis to this male-specific vocalization. This hypothesis has rarely been tested in primates, and this study elucidates how the rate of a male-specific call relates to male–male and male–female behavior in a Malagasy strepsirhine. To test whether males squeal towards other males to assert dominance, I predict that male squealing rate is positively correlated with dominance rank. I further predict that male ring-tailed lemurs squeal at other males while engaged in agonistic interactions, and that squealing during an interaction is positively correlated with winning that encounter. To test whether males squeal towards females as a mate attraction signal, I predict that male squealing rate is higher on estrus days, and that estrous females indicate attraction by approaching squealing males. From March to July 2010, 480 hr of focal data were collected on 25 males aged three and older at Beza Mahafaly Special Reserve, Madagascar. I continuously observed each male for 30 min at a time and recorded all agonistic interactions and squeal vocalizations using 1–0 sampling at 2.5-min intervals. Squealing rate was higher during times of male–male agonism when compared to times without male–male agonism, and males with higher dominance ranks had higher squealing rates. In contrast, the mate attraction hypothesis was not supported. My results suggest that the male squeal is an agonistic signal when used in male–male interaction in ring-tailed lemurs, but does not specifically indicate aggression or submission. *Am. J. Primatol.* 75:1174–1184, 2013. © 2013 Wiley Periodicals, Inc.

Key words: *Lemur catta*; squeal; vocalization rate; handicap hypothesis; mate attraction hypothesis

INTRODUCTION

Male-specific vocalizations are found in a variety of animal species, and are primarily used in courtship and threat situations [Bradbury & Vehrencamp, 1998; Snowdon, 2004]. Males direct sex-specific calls toward females in order to gain sexual access, and toward other males during competition for resources such as food, mates, and dominance status [Andersson, 1994; Snowdon, 2004]. Males are known to repeat sex-specific calls at high rates [Andersson, 1982]. In species where such repeated vocalization displays occur, there is also evidence that vocalization rate is related to quality, such that males with high call repetition rates have higher dominance rank and better fighting ability [common toad (*Bufo bufo*): Davies & Halliday, 1978; red deer (*Cervus elaphus*): Clutton-Brock & Albon, 1979; chacma baboon (*Papio ursinus*): Kitchen et al., 2003], as well as greater reproductive success

[reviewed in Ryan & Keddy-Hector, 1992; red deer: McComb, 1991; fallow deer (*Dama dama*): McElligott & Hayden, 1999; gray mouse lemur (*Microcebus murinus*): Zimmermann & Lerch, 1993]. Males of these animal species repeat the same sex-specific

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*Correspondence to: Laura M. Bolt, Department of Anthropology, University of Toronto, 19 Russell Street, Toronto, ON, Canada M5S 2S2. E-mail: laurabolt@gmail.com

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vocalization at times of female estrus and male–male agonism, and this advertises their fitness, as a rival and mate [Bradbury & Vehrencamp, 1998]. Repeated vocalizations are considered energetically expensive because increasing repetition rate increases the cost of signaling [Andersson, 1994; Vehrencamp, 2000]. Repeated vocalizations can therefore be considered quality handicap signals [Zahavi, 1975; Zahavi & Zahavi, 1997].

Handicap signals, as male-specific utterances used in both courtship and intra-sexual agonism, are likely to be honest as well as costly [Zahavi, 1975]. Repeated vocalizations cause a male to incur costs (thus “handicapping” him), and the sum of the costs that he is able to bear honestly indicates his quality. Over generations, high-quality signalers will have higher fitness since they will be better able to bear the costs associated with the honest signal [Grafen, 1990, 1991; Zahavi, 1975; Zahavi & Zahavi, 1997]. Females are thought to preferentially select such males as mates so that their high-quality genes will be inherited by their offspring [Andersson, 1982, 1994; Snowdon, 2004].

In a variety of animal species, including anuran amphibians, red deer, chacma baboons, and oscine songbirds, the repetition rate of a male-specific vocalization is known to relate to male quality, such that males with high call repetition rates are more likely to win in fights with other males, and/or to be preferred as mates by females [reviewed in Ryan & Keddy-Hector, 1992; red deer: Clutton-Brock & Albon, 1979; amphibians: Davies & Halliday, 1978; baboons: Kitchen et al., 2003]. Red deer males who utter their sex-specific roar call at higher rates are known to have greater mating and reproductive success, and are more likely to win in male–male fights [McComb, 1991]. Similarly, in fallow deer, the rate of the male-specific groan is positively linked to both male mating success and intra-sexual agonism [McElligott & Hayden, 1999]. Such correlations have also been found in primate species. In the chacma baboon, males with high sex-specific vocalization rates are likely to have high dominance ranks [Kitchen et al., 2003]. In the gray mouse lemur, males with high rates of the sex-specific trill vocalization have greater mating and reproductive success than males with lower trilling rates [Zimmermann, 1995; Zimmermann & Lerch, 1993]. However, male calling rate has not been examined with reference to the intra- and inter-sexual predictions of the handicap hypothesis in other primates. Despite strong evidence for male-specific calling rate being linked to courtship and male–male agonism in other animal species, the handicap hypothesis with respect to vocalization rate has rarely been tested in primates. With few exceptions besides the chacma baboon and mouse lemur, it is largely unknown how the rate of male-specific calls relates to male–male agonistic behavior and

male–female sexual behavior in primates. Further study of how sex-specific calling rate relates to these variables is important, both as a means of better understanding how communicatory signals relate to dominance and mating behavior in individual species, and as a means of better understanding the evolution of vocal communication in the primate order.

The ring-tailed lemur is a social primate indigenous to the southern regions of Madagascar [Jolly, 1966]. This female-dominant strepsirhine lives in mixed-sex groups of between 5 and 27 animals [Gould et al., 2003; Pride, 2005; Sussman, 1991]. Ring-tailed lemurs are female philopatric, with males leaving their natal group at three to four years old and usually joining a new group every three years [Budnitz & Dainis, 1975; Jones, 1983; Sussman, 1992]. During April or May in Madagascar, an annual mating season begins, with asynchronous estrus for females in the same group [Jolly, 1966]. Each female enters an estrus period that lasts for less than 24 hr [Jolly, 1966; Parga, 2006a; Sauther, 1991; Van Horn & Resko, 1977]. While a female is in estrus, she mates with multiple males, giving non-natal resident males mating priority and also mating with non-group males, but less frequently copulating with natal males from her social group [Bolt, 2013; Jolly, 1966; Koyama, 1988; Parga, 2010; Sauther, 1991; Sussman, 1992; Taylor & Sussman, 1985]. There is fierce competition between non-natal males for sexual access to females, which results in a high level of male–male agonism throughout the mating season, and sometimes leads to serious wounds or death for males [Gould & Zeigler, 2007; Jolly, 1966; Sauther, 1991].

Male ring-tailed lemurs are subordinate to sexually mature females, but compete with one other for status in a separate male dominance hierarchy in each group [Budnitz & Dainis, 1975; Gould, 1994; Taylor, 1986]. Within each group, male dominance rank is often linear, but can also be non-linear [Budnitz & Dainis, 1975; Gould, 1994; Jolly, 1966; Nakamichi & Koyama, 1997]. In both linear and non-linear hierarchies, between one and three males are usually markedly more dominant than the rest of the males in the group [Jolly, 1966; Sauther & Sussman, 1993]. These dominant males are usually between 6 and 9 years old and in their physical prime [Gould, 2006]. Male dominance rank can remain relatively stable for much of the year [Jolly, 1966], but can also vary between seasons and years as new males enter a group, and as resident males reach and pass their prime [Gould, 1994, 1997, 2006; Gould & Zeigler, 2007; Jolly, 1967; Parga, 2006b; Pereira & Kappeler, 1997]. Male rank becomes highly unstable during the breeding season, when lower-ranking males often temporarily outcompete higher-ranking males in agonistic encounters [Budnitz & Dainis, 1975; Gould, 1994,

1997; Gould & Zeigler, 2007; Koyama, 1988; Parga, 2009; Sauther, 1991].

High rank is important because dominance holds many advantages for male ring-tailed lemurs. Agonistically dominant males usually hold spatial positions of privilege within a group, commanding a place in the group's center while resting, feeding, or foraging [Sauther, 1991]. High-ranking males feed more, are allowed a greater amount of high-quality foods, and have greater drinking site access [Sauther, 1993; White et al., 2007]. They are also known to interact with females at greater rates and to receive the majority of mating opportunities [Ichino & Koyama, 2006; Sauther, 1991; Sauther & Sussman, 1993; but see Gould, 1994]. Dominant males also typically receive first-mating privileges with estrous females from their group, with mating order often corresponding to male dominance order [Koyama, 1988; Parga, 2006a; Sauther, 1991; but see Gould, 1994], and early mating possibly providing a paternity advantage for ring-tailed lemur males [Pereira & Weiss, 1991]. In other polygynandrous strepsirhines [Jolly, 1966; Sauther, 1991], dominant males are known to be preferred by females as mates [Verreaux's sifaka (*Propithecus verreauxi*): Brockman, 1999] and/or to sire the majority of offspring [red-fronted lemur (*Eulemur rufifrons*): Kappeler & Port, 2008; Verreaux's sifaka: Kappeler & Schaffler, 2008]. This trend also holds for a number of other animal species, in which there is a well-documented relationship between male dominance rank and mating and reproductive success [reviewed in Dewsbury, 1982]. Data relating male dominance to reproductive success in the ring-tailed lemur are lacking [White et al., 2007], but are likely to be similar to other polygynandrous strepsirhines. With likely reproductive success, feeding priority, and spatial comfort as the privileges of male dominance in the ring-tailed lemur, it is apparent why dominance is a desirable characteristic for males.

Ring-tailed lemur males maintain their dominance hierarchy through physical combat as well as through ritualized scent marking and tail-waving displays [Gould, 1994; Gould & Zeigler, 2007; Palagi et al., 2003; Scordato & Drea, 2007]. In addition to these displays, vocalizations play an important role in male ring-tailed lemur social behavior [Andrew, 1963; Bolt, 2013; Jolly, 1966; Macedonia, 1990, 1993; Oda, 1996; Petter & Charles-Dominique, 1979; Sauther, 1989]. With strepsirhine vocal repertoires ranging in size from 5 to 22 vocalizations [McComb & Semple, 2005], the ring-tailed lemur has one of the largest, with 22 disparate call types for adults [Macedonia, 1993]. Eight of these vocalizations signal affiliation, six are used in agonistic interactions, and eight are used in response to predators [Macedonia, 1993]. Two of these vocalizations are male-specific, including the squeal [Jolly, 1966; Macedonia, 1990, 1993].

The ring-tailed lemur squeal is a male-specific sharp call used in both agonistic and sexual contexts [Andrew, 1963; Macedonia, 1990, 1993; Petter & Charles-Dominique, 1979]. Males are thought to squeal towards females to determine if they are in estrus, and toward other males to indicate low-intensity agonism in competitive situations [Gould, 1994; Jolly, 1966; Macedonia, 1990; Sbeglia et al., 2010]. Only sexually mature and sometimes juvenile males are known to squeal, and they usually do so while tail waving [Andrew, 1963; Gould, 1994, 2006; Jolly, 1966; Macedonia, 1990, 1993; Petter & Charles-Dominique, 1979]. Males also squeal when chasing other males who are subordinate in rank [Andrew, 1963], and when aggressively staring at other males [Jolly, 1966]. Jolly [1966] noted an increase in squealing rate during the mating season, which paralleled an increase of other forms of male-male aggression. Last, Petter and Charles-Dominique [1979] and Macedonia [1990, 1993] thought that males squealed towards other males to manifest their dominance, and towards females as a courtship ritual. However, these proposed functions for ring-tailed lemur squealing have never been empirically tested. Although these observations by other researchers suggest that the squeal is widely used in intra- and inter-sexual contexts, it is unknown what role the squeal vocalization may play in male ring-tailed lemur mate attraction and intra-sexual agonism. The squeal, as a male-specific vocalization known to be used in situations of male-male agonism and male-female courtship, is an ideal vocalization on which to test the predictions of the handicap hypothesis for vocalization rate. This study aims to elucidate why ring-tailed lemur males squeal towards other males and females, and to determine how squealing rate relates to dominance rank and mate attraction in a Malagasy strepsirhine.

Hypothesis 1: Males Squeal to Display Dominance to Other Males

Squealing rate may honestly indicate male dominance rank in the ring-tailed lemur, as has been found for male-specific agonistic vocalization rates in chacma baboons [Kitchen et al., 2003]. If this is the case, then I predict that males with higher dominance ranks will squeal at higher rates than males with lower dominance ranks, and that squealing rate will increase during male-male agonistic contexts.

Given the transience of male dominance in the ring-tailed lemur during the breeding season [Parga, 2009], I also investigate whether the squeal is associated with winning in male-male agonistic interactions, independently from dominance rank. I predict that males who squeal at higher rates during agonistic interactions will be more likely to win that encounter.

Hypothesis 2: Males Squeal to Attract Estrous Females

Male-specific handicap signals are also known to attract females in courtship situations. In the male ring-tailed lemur, squealing may function as a mate attraction signal which entices females to mate with calling males, as predicted by the handicap hypothesis, and as found for the male-specific trill call in the gray mouse lemur [Zimmermann & Lerch, 1993]. If the ring-tailed lemur squeal attracts females, then I predict that males will squeal at higher rates on days of known estrus when compared to days without estrus. Since copulation only occurs during estrus in the ring-tailed lemur [Van Horn & Resko, 1977], it stands to reason that if the squeal is a mate attraction signal, males should squeal at higher rates at times when they have some chance of mating. I also predict that if the squeal does attract estrous females, then estrous females will indicate their attraction by moving toward males immediately after they are heard squealing.

METHODS

Field Site

I collected focal data from March 1 to July 1, 2010 at Beza Mahafaly Special Reserve, a protected reserve in the southwest of Madagascar (23°30'S latitude, 44°40'E longitude) [Sussman & Ratsirarson, 2006; Sussman et al., 2012]. Beza Mahafaly was established in 1978 and has been a government-protected area since 1986 [Gould et al., 2003; Sussman et al., 2012]. This reserve is comprised of two non-contiguous forest types, riverine forest in the eastern area of the reserve (Parcel I, 80 ha) and dry forest in the western area (Parcel II, 500 ha) [Sussman & Ratsirarson, 2006]. Parcel I is divided into 100 m² squares by a system of labeled trails. Beza Mahafaly is an ideal field site for gathering high-quality data on vocalization use due to its isolated location away from major roads, which limited environmental noise.

Study Animals

Approximately 225 ring-tailed lemurs from 11 troops lived in Parcel I, and within these groups nearly all adults were individually known [Gould & Zeigler, 2007; Sauther & Cuzzo, 2008]. Most lemurs were collared and had visible numbers, a system of identification dating to the earliest ring-tailed lemur research at the reserve in the late 1980s [Cuzzo & Sauther, 2006; Cuzzo et al., 2010; Sauther & Cuzzo, 2009; Sauther et al., 2002; Sussman, 1991]. Any individuals lacking collars could be identified by spots of black dye on different body areas for each lemur.

I performed behavioral focal follows 6 days a week on all males aged 3 and older, with only one

group followed per day. This study focused on five groups from Parcel I. Each group was studied 1–2 days per week. Resident males were focal sampled on a randomized, rotational basis from dawn until dusk [Altmann, 1974]. These data were collected as part of a large-scale study on ring-tailed lemur vocalization behavior. I collected 480 hr of focal data from 25 sexually mature males in total (Table I). The amount of focal data collected from individual males ranged from 14.7 to 24.6 hr, with mean observation time being 19.2 hr per male. Ages for most individuals were known from the decade-long work by Sauther and Cuzzo, who identify lemurs as subadults (2nd year of age) when first captured, with age determined from a series of variables including dental development, sexual maturity (or lack thereof), body mass, and somatic development [Cuzzo & Sauther, 2006; Cuzzo et al., 2010; Sauther & Cuzzo, 2008, 2009]. Thus collared lemurs aged two or greater were of known age. Age for all individuals with names beginning with “UMM” (unmarked male) was estimated by Bolt as three or more. All “UMM” individuals were sexually mature males who were known to have joined study groups in Parcel I within the last year (Beza Mahafaly Special Reserve unpublished data). Following the methodology of Bolt [2013], both natal and non-natal males were included in statistical analyses because several natal males were seen mating with females from their social group. At Beza Mahafaly Special Reserve, the five groups that were the focus of this study ranged from 9 to 20 individuals, with 4–8 males, 4–10 females, and 0–3 infants present per group (see Table II).

Field Methods

During focal sampling, each randomly sampled male subject was followed for 30 min at a time, with data recorded every 2.5 min on a programmed palm pilot (Palm Z-22). I used instantaneous sampling [Altmann, 1974] to record the focal individual's general behavior (resting, vigilant, allogrooming, autogrooming, feeding, foraging, sunning, scent marking, tail waving, traveling, urinating/defecating, other, out of sight). I used 1–0 sampling [Martin & Bateson, 2007] recorded at 2.5 min intervals to note whether or not the animal vocalized during the preceding 2.5-min time period, which vocalization types the focal animal uttered (moan, wail, howl, hmm, huh, purr, chirp, yip, cackle, squeal, twitter, plosive bark, chatter, gulp, rasp, shriek, click, click series, yap) [following Macedonia, 1990], whether or not the focal individual squealed, and the targets of squeal vocalizations. Only squeals emitted by the focal animal were noted. I also used 1–0 sampling recorded at 2.5 min intervals to note agonistic interactions involving the focal animal, the names of the individuals involved, and the winner and loser

TABLE I. Ring-Tailed Lemur Male Study Individuals at Beza Mahafaly Special Reserve, March–July 2010

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

of decided interactions. Animals were watched continuously during the focal period, and all focal data were gathered solely by the principal investigator.

I determined the recipients of male squeals by noting the identity of the individual the focal male approached and tail-waved at while squealing. In each case where a squeal recipient was noted, focal males looked at, moved towards, and appeared to direct their squeal towards an individual within 2 m.

Rates of squealing were determined in two ways. Firstly, squealing rates were determined using the total number of squeals for individual males divided by total focal time for that male (Fig. 1). Secondly,

squealing rates were determined using only squeals given during male–male agonism for individual males divided by total focal time for each male (Fig. 2). Both intra- and inter-group squealing were used in calculating squealing rates.

Estrus days were noted opportunistically during the study period, and recorded using ad libitum sampling [Altmann, 1974]. Female estrus was defined as a period of time when a female copulated with and made proceptive gestures toward males [Beach, 1976].

An agonistic interaction was defined as any behavior involving contest competition between two individuals, characterized by one or more acts of defense, avoidance, or aggression. Agonistic interactions included aggressive and/or submissive behaviors. The ethogram for agonistic behavior used in this study was based on those used by Gould [1994], Jolly [1966], Parga [2006b], and Pereira and Kappeler [1997]. Agonistic interactions included aggressive behaviors (bite, cuff, grab, push, nose poke, lunge, displace, chase, aggressive stare, attack, take food), submissive behaviors (cower, be displaced, withdraw, jump away, flee), low-arousal behaviors (e.g., aggressive stare-displacement), and high-arousal behaviors (e.g., bite or chase) [Gould, 1994; Jolly, 1966; Parga, 2006b; Pereira & Kappeler, 1997]. I defined an agonistic win as an individual displaying only aggressive or non-agonistic behavior toward another individual and receiving only submissive behavior from that individual [Pereira & Kappeler, 1997]. Only decided agonistic interactions, where a clear winner and loser were apparent, were used in determining male dominance ranks.

Calculating Male Rank

Dominance was determined from focal data using dominance index calculations. Dominance indices were calculated independently for males within each group. Agonistic interactions between males from different groups were not included in these calculations. A dominance index calculation accounts for all definite aggressive and submissive interactions in each troop and assigns an individual dominance percentage to each male group member [Zumpe &

TABLE II. Composition of Ring-Tailed Lemur Study Groups at Beza Mahafaly Special Reserve, March–July 2010

Group name	Number of females aged >1	Number of natal males aged 1–3	Number of natal males aged ≥3	Number of non-natal males	Number of infants (b. 2009)	Total number in group	Total number of males aged ≥3
Green	6	1	0	5	1	13	5
Orange	10	1	1	5	3	20	6
Purple	5	2	2	4	2	15	6
Red	5	0	2	2	0	9	4
Yellow	4	2	0	4	2	12	4
Total	30	6	5	20	8	69	25

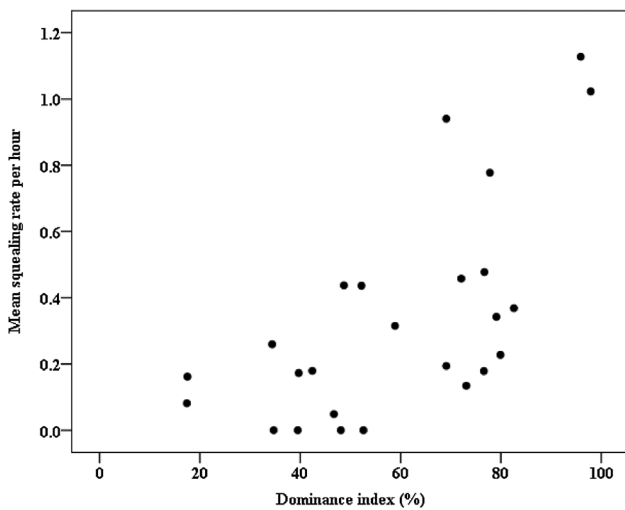


Fig. 1. Correlation between male ring-tailed lemur dominance index score and mean male squealing rate.

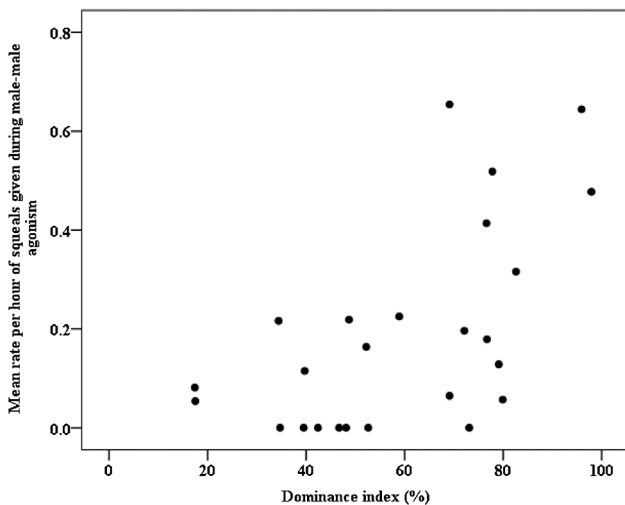


Fig. 2. Correlation between male ring-tailed lemur dominance index score and mean rate for squeals given during male-male agonism.

Michael, 1986]. All agonistic behaviors (e.g., jump away, cuff, displace) were treated equally in male rank determinations [Gould, 1994]. Dominance index was calculated using the following equation [Zumpe & Michael, 1986]:

$$\text{Dominance index per male} = \frac{1}{n} \sum_{i=1}^n (\%A + \%S)_i$$

In this equation, n represents the total number of males in the group with whom the male had agonistic interactions, $\%A$ represents the percent aggression given within each male-male dyad, $\%S$ represents submission received within each male-male dyad, and i represents the index of summation. Successive values of i are determined by adding 1 to the previous

value of i , stopping when i is equal to the total number of males in the group with whom the male in question had agonistic interactions (i.e., when $i = n$). Output values approaching 100% indicated high dominance rank, while those approaching 0% indicated comparatively low dominance rank. Within each male-male dyad in each group, $\%A$ was calculated from the number of aggressive actions expressed by each male and calculated as a percentage of the total number of aggressive behaviors given by both males to one another [Zumpe & Michael, 1986]. For each male-male dyad, $\%S$ was calculated in the same way as $\%A$. For each male, the $\%A$ and $\%S$ scores were added, then divided by the total number of males in the group with whom the male had agonistic interactions to produce a dominance index [Zumpe & Michael, 1986]. Males with higher dominance percentages won more fights and had a higher ranking within their troops.

Data Analysis

For each dataset used in my study, my sample size was small ($N = 25$ males) and data were not normally distributed, requiring the use of non-parametric tests.

For hypothesis 1, I used the Spearman rank correlation test to evaluate the prediction that higher-ranking males would have higher squealing rates than lower-ranking males. I also used a Spearman rank correlation to test whether higher-ranking males have higher squealing rates than lower-ranking males when only squeals used in male-male agonism were considered. I used the Wilcoxon signed-rank test to evaluate the prediction that squealing rate would be higher during times of male-male agonism when compared to times without male-male agonism. Finally, I used the Wilcoxon signed-rank test to examine whether squealing rate would be higher during winning agonistic interactions when compared to squealing rate during losing agonistic interactions.

For hypothesis 2, I used the Wilcoxon signed-rank test to assess the prediction that squealing rate would be higher on known estrus days, as opposed to days without known estrus. Males were not included in analysis if less than 1 hr of focal data was collected from them on known estrus days ($N = 9$ males from three groups removed), or if estrus was not observed in their group ($N = 6$ males from one group removed). I used the binomial test to examine whether estrous females moved towards males immediately after squealing more often than expected by chance.

In this study, the alpha level for all tests was set to 0.05. Means were reported with standard deviations (SD), and all tests were 2-tailed. SPSS version 20 (IBM SPSS Statistics, IBM Corporation, Armonk, NY, USA, 2011) was used to perform all statistical tests. SPSS identified outliers as data points with a

distance from the nearest quartile of more than 1.5 times the inter-quartile range, and I removed these values when doing re-calculations.

This study adhered to the ethical guidelines for the treatment of non-human primates advised by the American Society of Primatologists. My research protocol was approved by the University of Toronto Animal Care Committee, and conducted with the approval of Madagascar National Parks (MNP), and the Département des Eaux et Forêts de l'École Supérieure des Sciences Agronomiques (ESSA).

RESULTS

A total of 1,270 intra-group agonistic interactions between focal males were included in dominance index calculations, with a mean of 50.8 and range of 24–80 male–male agonistic interactions recorded per focal male. Dominance index calculations indicated transitive dominance hierarchies for the males in the orange, purple, and red groups, and non-linear hierarchies for the males in the green and yellow groups (Table I).

Of total recorded squeals by focal males, 97% of squeals appeared to be directed towards a single other individual (147/152), and squeal recipients were accurately identified 99% of the time (146/147). Of identified squeal recipients, squeals were directed towards other males 66% (97/146) of the time and towards females 34% (49/146) of the time.

There was a correlation between male dominance rank and squealing rate such that males with higher dominance index scores had higher mean squealing rates (152 squeals, Spearman's rank correlation: $r_s = 0.67$, $P = 0.0001$, $N = 25$ males; Fig. 1). In addition to male dominance rank being correlated with overall squealing rate, this correlation was significant when squealing rate using only squeals given during male–male agonism were considered (91 squeals, Spearman's rank correlation: $r_s = 0.56$, $P = 0.003$, $N = 25$ males; Fig. 2). Further, there was a significant difference in male squealing rate during times of male–male agonism when compared to times without male–male agonism (91 agonistic squeals, 6 male–male non-agonistic squeals, Wilcoxon test: $Z = -3.81$, $P = 0.0001$, $N = 25$ males; Fig. 3). Mean squealing rate was higher at times with male–male agonism (2.86 ± 3.25 SD squeals per hour, $N = 25$ males) when compared to times without male–male agonism (0.17 ± 0.16 SD squeals per hour, $N = 25$ males). When tests were re-done with the outlier removed (male 273 with a value of 12 removed from analysis), results remained statistically significant (Wilcoxon test: $Z = -3.7$, $P = 0.0001$, $N = 24$ males). In contrast, mean squealing rate was not significantly higher for males during intra-sexual agonistic wins when compared with squealing rate during agonistic losses (53 squeals during wins, 38 squeals during losses,

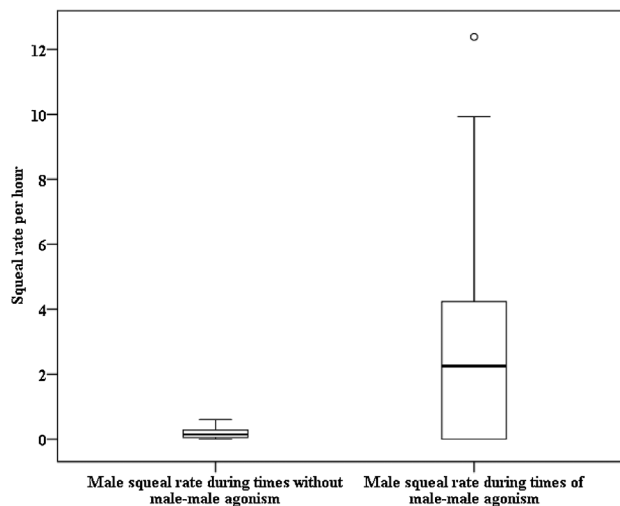


Fig. 3. Mean male ring-tailed lemur squealing rate per hour during periods of male–male agonism versus male squealing rate during times without agonism. Boxes represent inter-quartile ranges, lines represent median values, whiskers represent maximum and minimum values, and dots represent outliers.

Wilcoxon test: $Z = -0.93$, $P = 0.352$, $N = 25$ males, NS; Fig. 4; 0.11 ± 0.15 squeals per hour during wins, $N = 25$ males; 0.08 ± 0.12 squeals per hour during losses, $N = 25$ males). When the outliers were removed (three males removed from analysis: male 263 with values of 0.65 and 0, male Umm2p with values of 0.2 and 0.27, and male 273 with values of 0.16 and 0.57), results remained non-significant (Wilcoxon test: $Z = -1.29$, $P = 0.196$, $N = 22$ males, NS).

There was no significant difference in mean male squealing rate on estrus days when compared with

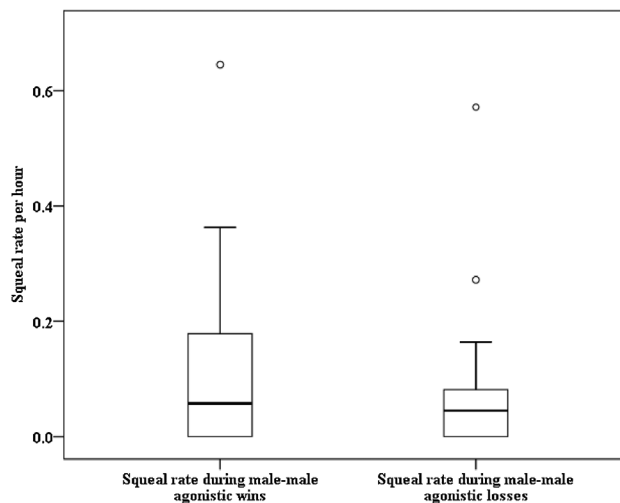


Fig. 4. Mean male squealing rate per hour during male–male agonistic wins versus squealing rate during male–male agonistic losses. Boxes represent inter-quartile ranges, lines represent median values, whiskers represent maximum and minimum values, and dots represent outliers.

non-estrus days (15 squeals on estrus days, 58 squeals on non-estrus days, Wilcoxon test: $Z = -0.77$, $P = 0.441$, $N = 10$ males, NS; Fig. 5; 1.0 ± 1.84 squeals per hour on estrus days, $N = 10$ males; 0.29 ± 0.27 squeals per hour on non-estrus days, $N = 10$ males). These results remained non-significant when I removed outliers ($Z = -0.676$, $P = 0.499$, $N = 8$ males, NS; two males removed from analysis: male 273 with values of 5.8 and 0.67, and male 230 with values of 0 and 0.82). When only squeals given on days of known female estrus were considered, estrous females moved towards squealing males immediately after 20% (3/15) of squeals. Males were significantly less likely to have estrous females approach them after squealing (binomial test: $Z = -2.32$, $P = 0.035$, $N = 15$ squeals on estrus days).

DISCUSSION

My results support the hypothesis that ring-tailed lemur males squeal to display dominance. Males squealed at higher rates during intra-sexual agonistic contexts when compared to contexts without agonism, and male dominance rank was positively correlated with squealing rate. In contrast, I found no support for the mate attraction hypothesis. Contrary to observations that males squeal towards females as a courtship signal [Macedonia, 1990, 1993; Petter & Charles-Dominique, 1979], male squealing rate did not significantly increase on estrus days, and estrous females were not significantly more likely to approach squealing males.

Males did show a non-significant tendency to squeal at higher rates on estrus days, but this result may be related to increased levels of intra-sexual

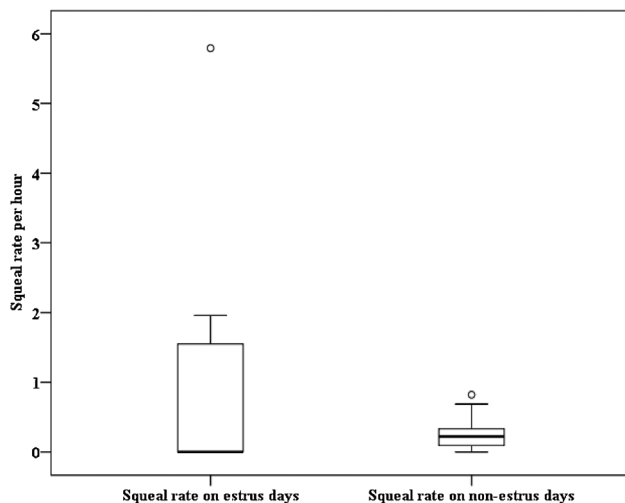


Fig. 5. Mean male ring-tailed lemur squealing rate per hour during known estrus days versus male squealing rate on days without known estrus. Boxes represent inter-quartile ranges, lines represent median values, whiskers represent maximum and minimum values, and dots represent outliers.

agonism on estrus days (Bolt, unpublished data) rather than due to male squealing to attract mates. My findings do not support the mate attraction hypothesis, and it seems probable that male squealing does not factor into female mate choice decisions.

My result that ring-tailed lemurs squeal as a sign of agonism in male–male interactions is consistent with squeal usage in this species as reported anecdotally by Jolly [1966] and Macedonia [1990, 1993]. Jolly [1966] reported that males squeal when aggressively staring at other males, while Macedonia [1990, 1993] noted the squeal as an assertion of status when directed at other males. These findings correspond with accounts of agonistic squeal usage throughout the primate order. Some primate species use squealing as a submissive vocalization in threatening agonistic situations [siamang (*Symphalangus syndactylus*): Andrew, 1963; red-fronted lemur: Pereira & Kappeler, 1997], and one species uses the squeal primarily as an aggressive threat during agonism [dwarf lemur (*Cheirogaleus* spp.): Andrew, 1963]. Many more primate species from a variety of suborders use the squeal as both an aggressive and submissive signal in agonistic interactions [gray mouse lemur: Andrew, 1963; guenon (*Cercopithecus* spp.): Andrew, 1963; greater bamboo lemur (*Prolemur simus*): Bergey & Patel, 2008; rhesus macaque (*Macaca mulatta*): Bernstein et al., 1993; common marmoset (*Callithrix jacchus*): Bezerra & Suoto, 2008; black-handed spider monkey (*Ateles geoffroyi*): Carpenter, 1935; Senegal bushbaby (*Galago senegalensis*): Charles-Dominique, 1977]. My results, indicating that the ring-tailed lemur squealed to show both aggression and submission in agonistic situations, are consistent with squeal usage reported for other primate species.

Although usage of the ring-tailed lemur squeal conformed to broadly observed taxonomic trends for primate squealing behavior, my results were also mixed. The ring-tailed lemur squeal was used during both wins and losses in male–male agonistic interaction, yet was also significantly correlated with male dominance. If squealing rate indicates dominance rank, I expected squealing to also be associated with winning in male–male agonistic interactions, given that agonistic interactions were the criterion used to determine dominance rank in this study. Males did squeal at higher rates while winning intra-sexual agonistic encounters, but this trend was non-significant. Analysis of a larger dataset may show a significant correlation between high squealing rate and winning, but other explanations are also possible. One possible reason for my mixed result for male–male squeal usage in the ring-tailed lemur may be the transience of male dominance during the mating season [Gould & Zeigler, 2007; Parga, 2009], which my data collection period encompassed. The ring-tailed lemur male dominance hierarchy is well-known to be unstable during the mating season

[Budnitz & Dainis, 1975; Gould, 1994, 1997; Gould & Zeigler, 2007; Koyama, 1988; Parga, 2009; Sauther, 1991], and in my study, males who were dominant before and after the mating season did not consistently win agonistic encounters throughout [Bolt, unpublished data]. My mixed results suggest that squealing rate may not vary with varying dominance status, but rather may be an individual characteristic of males, or could be bound to individual male qualities, like age and health, which often correlate with male dominance rank [Gould, 2006]. In the chacma baboon, male dominance rank is known to correlate with vocalization rate independently of physical qualities such as body size [Kitchen et al., 2003], but the reverse may be true for other primates [reviewed in Ey et al., 2007]. For example, larger rhesus macaques utter longer coo vocalizations than smaller rhesus macaques [Hammersmidt et al., 2000]. Similar links between vocalization behavior and physical traits may also be found in other primates, including the ring-tailed lemur. However, further research is needed to test this speculation.

A second possible explanation for my mixed result is consideration that male ring-tailed lemur males do not squeal during every intra-sexual agonistic encounter (91 squeals/1,270 male–male agonistic interactions were observed). In the red-fronted lemur, the squeal was produced during a similarly small proportion of agonistic encounters [Pereira & Kappeler, 1997]. In this study, male dominance rank was determined independently of vocalization behavior and was calculated from all observed male–male agonistic encounters, many of which did not involve squealing. It may be that squealing has no specific association with winning or losing in ring-tailed lemur male–male agonism, but that males who are dominant are simply more likely to produce this vocalization at higher rates in all social contexts, including while winning and while losing agonistic encounters.

Amongst the various primate species that squeal during agonism, there is no common social system or dominance system. Squealing primates may be largely solitary [dwarf lemur: Andrew, 1963] or live in groups of up to 200 individuals [rhesus macaque: Bernstein et al., 1993]; they may have no observable dominance hierarchy [red-fronted lemur: Pereira & Kappeler, 1997], a largely stable dominance hierarchy [common marmoset: Digby, 1995], or an unstable hierarchy [rhesus macaque: Bernstein et al., 1993]. These vast differences in dominance systems between squealing species suggest that the type and stability level of the dominance system in a species may have little to do with squealing behavior. In the ring-tailed lemur, the instability of the male dominance rank may be unrelated to the squeal's use as an assertive and submissive vocalization in male–male agonism. A replication of this study involving data collection on ring-tailed lemur males across multiple

seasons and years would help to further clarify whether squealing rate changes with changing dominance rank, or is simply a characteristic of individual males.

Since dominant males squealed more in this study, the squeal shows potential to honestly indicate fitness in the ring-tailed lemur, and future study should evaluate whether this vocalization is a handicap signal. It is also unknown whether squeals directed towards males in agonistic situations differ structurally from squeals directed towards females to elucidate sexual receptivity. Past research involving sound spectrograms [Macedonia, 1990, 1993] made no distinction between these two types of squeals, but future research involving sound spectrographic analysis should explore whether spectral differences exist between squeals directed toward males and squeals directed toward females.

Results from this study support the hypothesis that squealing rate indicates male dominance rank, but did not appear to support the mate attraction hypothesis. The squeal is a meaningful signal in intra-sexual agonism and is correlated with dominance status for the male ring-tailed lemur, although it functions as both an aggressive and a submissive signal when directed towards other males.

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REFERENCES

- Altmann J. 1974. Observational study of behavior: sampling methods. *Behavior* 49:227–269.

- Andersson M. 1982. Sexual selection, natural selection and quality advertisement. *Biol J Linn Soc* 17:375–393.
- Andersson M. 1994. Sexual selection. Princeton, NJ: Princeton University Press. 599 p.
- Andrew R. 1963. The origins and evolution of calls and facial expressions of the primates. *Behavior* 20:1–109.
- Beach F. 1976. Sexual attractivity, proceptivity, and receptivity in female mammals. *Horm Behav* 7:105–138.
- Bergey C, Patel E. 2008. A preliminary vocal repertoire of the greater bamboo lemur (*Prolemur simus*). *Nexus* 1:69–84.
- Bernstein I, Judge P, Ruehlmann T. 1993. Kinship, association, and social relationships in rhesus monkeys (*Macaca mulatta*). *Am J Primatol* 31:41–53.
- Bezerra BM, Suoto A. 2008. Structure and usage of the vocal repertoire of *Callithrix jacchus*. *Int J Primatol* 29:671–701.
- Bolt L. 2013. The function of howling in the ring-tailed lemur (*Lemur catta*). *Int J Primatol* 34:157–169.
- Bradbury J, Vehrencamp S. 1998. Principles of animal communication. Sunderland, MA: Sinauer Associates. 917 p.
- Brockman D. 1999. Reproductive behavior of female *Propithecus verreauxi* at Beza Mahafaly, Madagascar. *Int J Primatol* 20:375–398.
- Budnitz N, Dainis K. 1975. *Lemur catta*: ecology and behavior. In: Tattersall I, Sussman R, editors. *Lemur biology*. New York: Plenum Press. p 219–235.
- Carpenter C. 1935. Behavior of red spider monkeys in Panama. *J Mammol* 16:171–180.
- Charles-Dominique P. 1977. Ecology and behavior of nocturnal primates: prosimians of equatorial West Africa. London: Duckworth and Co. Ltd. 277 p.
- Clutton-Brock T, Albon S. 1979. The roaring of red deer and the evolution of honest advertisement. *Behavior* 69:145–169.
- 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. *J Hum Evol* 51:490–505.
- Cuozzo F, Sauther M, Gould L, et al. 2010. Variation in dental wear and tooth loss in known-aged, older ring-tailed lemurs (*Lemur catta*): a comparison between wild and captive individuals. *Am J Primatol* 72:1026–1037.
- Davies N, Halliday T. 1978. Deep croaks and fighting assessment in toads (*Bufo bufo*). *Nature* 274:683–685.
- Dewsbury D. 1982. Dominance rank, copulatory behavior, and differential reproduction. *Q Rev Biol* 57:135–159.
- Digby L. 1995. Social organization in a wild population of *Callithrix jacchus*: II. Intragroup 371 social behavior. *Primates* 36:361–375.
- Ey E, Pfefferle D, Fischer J. 2007. Do age- and sex-related variations reliably reflect body size in non-human primate vocalizations? *Primates* 48:253–267.
- Gould L. 1994. Patterns of affiliative behavior in adult male ringtailed lemurs (*Lemur catta*) at the Beza-Mahafaly reserve, Madagascar [dissertation]. St. Louis, MO: Washington University. 258 p. Available from University Microfilms, Ann Arbor, MI; AA D74-23.
- Gould L. 1997. Intermale affiliative behavior in ringtailed lemurs (*Lemur catta*) at the Beza-Mahafaly Reserve, Madagascar. *Primates* 38:15–30.
- Gould L. 2006. Male sociality and integration during the dispersal process in *L. catta*: a case study. In: Jolly A, Sussman R, Koyama N, Rasamimanana H, editors. *Ring-tailed lemur biology*. New York: Springer. p 296–310.
- Gould L, Zeigler T. 2007. Variation in fecal testosterone levels, inter-male aggression, dominance rank and age during mating and post-mating periods in wild adult male ring-tailed lemurs (*Lemur catta*). *Am J Primatol* 69:1325–1339.
- 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. *Am J Phys Anthropol* 120:182–194.
- Grafen A. 1990. Biological signals as handicaps. *J Theor Biol* 144:475–546.
- Grafen A. 1991. Modelling in behavioral ecology. In: Krebs J, Davies N, editors. *Behavioral ecology: an evolutionary approach*. 3rd edition. Oxford: Blackwell. p 5–31.
- Hammerschmidt K, Newman J, Champoux M, Suomi S. 2000. Changes in rhesus macaque 'coo' vocalizations during early development. *Ethology* 106:873–886.
- Ichino S, Koyama N. 2006. Social changes in a wild population of ringtailed lemurs (*Lemur catta*) at Berenty, Madagascar. In: Jolly A, Sussman R, Koyama N, Rasamimanana H, editors. *Ringtailed lemur biology*. New York: Springer. p 233–244.
- Jolly A. 1966. *Lemur behavior: a Madagascar field study*. London: University of Chicago Press. 187 p.
- Jolly A. 1967. Breeding synchrony in wild *Lemur catta*. In: Altmann S, editor. *Social communication among primates*. Chicago: University of Chicago. p 3–14.
- Jones K. 1983. Inter-troop transfer of *Lemur catta* males at Berenty, Madagascar. *Folia Primatol* 40:145–160.
- Kappeler P, Port M. 2008. Mutual tolerance or reproductive competition? Patterns of reproductive skew among male redfronted lemurs (*Eulemur ruffifrons*). *Behav Ecol Sociobiol* 62:1477–1488.
- Kappeler P, Schaffler L. 2008. The lemur syndrome unresolved: extreme male reproductive skew in sifakas (*Propithecus verreauxi*), a sexually monomorphic primate with female dominance. *Behav Ecol Sociobiol* 62:1007–1015.
- Kitchen D, Seyfarth R, Fischer J, Cheney D. 2003. Loud calls as indicators of dominance in male baboons (*Papio cynocephalus ursinus*). *Behav Ecol Sociobiol* 53:374–384.
- Koyama N. 1988. Mating behavior of ring-tailed lemurs (*Lemur catta*) at Berenty, Madagascar. *Primates* 29:163–175.
- Macedonia J. 1990. Vocal communication and antipredator behavior in the ringtailed lemur (*Lemur catta*) [dissertation]. Durham, NC: Duke University. 324 p. Available from University Microfilms, Ann Arbor, MI; AA D74-23.
- Macedonia J. 1993. The vocal repertoire of the ringtailed lemur (*Lemur catta*). *Folia Primatol* 61:186–217.
- Martin P, Bateson P. 2007. *Measuring behavior: an introductory guide*. 3rd edition. Cambridge, UK: Cambridge University Press.
- McComb K. 1991. Female choice for high roaring rates in red deer, *Cervus elaphus*. *Anim Behav* 41:79–88.
- McComb K, Semple S. 2005. Coevolution of vocal communication and sociality in primates. *Biol Lett* 1:381–385.
- McElligott AG, Hayden TJ. 1999. Context-related vocalization rates of fallow bucks, *Dama dama*. *Anim Behav* 58:1095–1104.
- Nakamichi M, Koyama N. 1997. Social relationships among ring-tailed lemurs (*Lemur catta*) in two free-ranging troops at Berenty Reserve, Madagascar. *Int J Primatol* 18:73–93.
- Oda R. 1996. Effects of contextual and social variables on contact call production in free-ranging ringtailed lemurs (*Lemur catta*). *Int J Primatol* 17:191–205.
- Palagi E, Telara S, Borgognini Tarli S. 2003. Sniffing behavior in *Lemur catta*: seasonality, sex, and rank. *Int J Primatol* 24:335–350.
- Parga J. 2006a. Male mate choice in *Lemur catta*. *Int J Primatol* 27:107–131.
- Parga J. 2006b. Sexual selection in the ringtailed lemur (*Lemur catta*): female choice, male mating strategies, and male mating success in a female dominant primate [dissertation]. Austin, TX: University of Texas at Austin. 297 p. Available from University Microfilms, Ann Arbor, MI; AA D74-23.
- Parga J. 2009. Dominance rank reversals and rank instability among male *Lemur catta*: the effects of female behavior and ejaculation. *Am J Phys Anthropol* 138:293–305.
- Parga J. 2010. Evaluation of male inter-troop transfer as a mating strategy in ring-tailed lemurs on St. Catherines Island, USA. *Folia Primatol* 81:146–162.

- Pereira M, Kappeler P. 1997. Divergent systems of agonistic behavior in lemurid primates. *Behavior* 134:225–274.
- Pereira M, Weiss M. 1991. Female mate choice, male migration, and the threat of infanticide in ringtailed lemurs. *Behav Ecol Sociobiol* 28:141–152.
- Petter J, Charles-Dominique P. 1979. Vocal communication in prosimians. In: Doyle G, Martin R, editors. *The study of prosimian behavior*. New York: Academic Press. p 247–305.
- Pride R. 2005. Optimal group size and seasonal stress in ring-tailed lemurs (*Lemur catta*). *Behav Ecol* 16:550–560.
- Ryan M, Keddy-Hector A. 1992. Directional patterns of female mate choice and the role of sensory biases. *Am Nat* 139:4–35.
- Sauther M. 1989. Antipredator behavior in troops of free-ranging *Lemur catta* at Beza Mahafaly Special Reserve, Madagascar. *Int J Primatol* 10:595–606.
- Sauther M. 1991. Reproductive behavior of free-ranging *Lemur catta* at Beza Mahafaly Special Reserve, Madagascar. *Am J Phys Anthropol* 84:463–477.
- Sauther M. 1993. Resource competition in wild populations of ringtailed lemurs (*Lemur catta*): implications for female dominance. In: Kappeler P, Ganzhorn J, editors. *Lemur social systems and their ecological basis*. London: Plenum Press. p 135–152.
- Sauther M, Cuzzo F. 2008. Somatic variation in living, wild ring-tailed lemurs (*Lemur catta*). *Folia Primatol* 79:55–78.
- Sauther M, Cuzzo F. 2009. The impact of fallback foods on wild ring-tailed lemur biology: a comparison of intact and anthropogenically disturbed habitat. *Am J Phys Anthropol* 140:671–686.
- Sauther M, Sussman R. 1993. A new interpretation of the social organization and mating system of the ringtailed lemur (*Lemur catta*). In: Kappeler P, Ganzhorn J, editors. *Lemur social systems and their ecological basis*. London: Plenum Press. p 111–121.
- Sauther M, Sussman R, Cuzzo F. 2002. Dental and general health in a population of wild ring-tailed lemurs: a life history approach. *Am J Phys Anthropol* 117:122–132.
- Sbeglia G, Tang-Martinez Z, Sussman R. 2010. Effects of food, proximity, and kinship on social behavior in ringtailed lemurs. *Am J Primatol* 72:981–991.
- Scordato E, Drea C. 2007. Scents and sensibility: information content of olfactory signals in the ringtailed lemur (*Lemur catta*). *Anim Behav* 73:301–314.
- Snowdon C. 2004. Sexual selection and communication. In: Kappeler P, van Schaik C, editors. *Sexual selection in primates: new and comparative perspectives*. Cambridge: Cambridge University Press. p 57–70.
- Sussman R. 1991. Demography and social organization of freeranging *Lemur catta* in the Beza Mahafaly Reserve, Madagascar. *Am J Phys Anthropol* 84:43–58.
- Sussman R. 1992. Male life history and intergroup mobility among ringtailed lemurs (*Lemur catta*). *Int J Primatol* 13:395–413.
- Sussman R, Ratsirarson J. 2006. Beza Mahafaly special reserve: a research site in southwestern Madagascar. In: Jolly A, Sussman R, Koyama N, Rasamimanana H, editors. *Ringtailed lemur biology: Lemur catta in Madagascar*. New York: Springer. p 43–51.
- Sussman R, Richard A, Ratsirarson J, et al. 2012. Beza Mahafaly special reserve: a research site in southwestern Madagascar. In: Kappeler P, Watts D, editors. *Long term field studies of primates*. New York: Springer. p 45–66.
- Taylor L. 1986. Kinship, dominance, and social organization in a semi-free ranging group of ringtailed lemurs (*Lemur catta*) [dissertation]. St. Louis, MO: Washington University. 218 p. Available from University Microfilms, Ann Arbor, MI; AA D74-23.
- Taylor L, Sussman R. 1985. A preliminary study of kinship and social organization in a semi-free-ranging group of *Lemur catta*. *Int J Primatol* 6:601–614.
- Van Horn R, Resko J. 1977. Reproductive cycle of the ringtailed lemur (*Lemur catta*): sex steroid levels and sexual receptivity under controlled photoperiods. *Endocrinology* 101:1579.
- Vehrencamp S. 2000. Handicap, index, and conventional signal elements of bird song. In: Espmark Y, Amundsen T, Rosenqvist G, editors. *Animal signals: signalling and signal design in animal communication*. Trondheim, Norway: Tapir Academic Press. p 277–300.
- White F, Overdorff D, Keith-Lucas T, et al. 2007. Female dominance and feeding priority in a prosimian primate: experimental manipulation of feeding competition. *Am J Primatol* 69:295–304.
- Zahavi A. 1975. Mate selection: a selection for a handicap. *J Theor Biol* 53:204–214.
- Zahavi A, Zahavi A. 1997. *The handicap principle: a missing piece of Darwin's puzzle*. Oxford: Oxford University Press. 287 p.
- Zimmermann E. 1995. Acoustic communication in nocturnal prosimians. In: Alterman L, Doyle G, Izard M, editors. *Creatures of the dark: Biology of nocturnal prosimians*. New York: Plenum Press. p 311–330.
- Zimmermann E, Lerch C. 1993. The complex acoustic design of an advertisement call in male mouse lemurs (*Microcebus murinus*, Prosimii, Primates) and sources of its variation. *Ethology* 93:211–224.
- Zumpe D, Michael R. 1986. Dominance index: a simple measure of relative dominance status in primates. *Am J Primatol* 10:291–300.