

Male-Specific Use of the Purr in the Ring-Tailed Lemur (*Lemur catta*)

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Key Words

Purr · Ring-tailed lemur · *Lemur catta* · Sex-specific behaviour · Information signal · Male vocalization · Dominance rank · Call rate · Male agonism · Epiphenomenon

Abstract

In mammals, purring has been described in mostly affiliative contexts. In the ring-tailed lemur (*Lemur catta*), both males and females purr, but only males were observed purring in agonistic contexts. In order to determine whether male ring-tailed lemurs purr as aggressive displays during intrasexual agonistic encounters, 480 h of focal data were collected on 25 adult males from Beza Mahafaly Special Reserve, Madagascar, from March to July 2010. The male purring rate increased during periods of male-male agonism when compared to times without intrasexual agonism, and the purring rate was positively correlated with male dominance rank. However, the purring rate was not significantly higher during winning agonistic interactions when compared with losing encounters. My results indicate that the male ring-tailed lemur purr is used most frequently as an agonistic vocalization in male-male encounters, in addition to being used less frequently in other social contexts, including during tail-waving at females, resting, scent-marking, feeding and copulation. Dominant males have higher purring rates across social situations, suggesting that the purring rate may be driven by intrinsic male qualities rather than functioning as a meaningful signal in each disparate social context. Male purring in intrasexual agonistic encounters can be added to previously described social contexts for ring-tailed lemur purring.

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Introduction

For many animal species, vocal signals that are loud and long-range tend to receive attention from researchers, while low-amplitude vocalizations have been understudied [Bradbury and Vehrencamp, 1998]. Male-specific long-range calls made

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by birds, amphibians and mammals can carry for distances of up to 2.5 km through indigenous environments, and they serve as long-distance advertisements of an animal's presence in a certain location (birds [Radesater et al., 1987; Alatalo et al., 1990]; amphibians [Prestwich, 1994]; mammals [Clutton-Brock and Albon, 1979; McComb, 1991; Delgado, 2006]). In contrast, short-range calls are generally only audible by individuals within the same social group and in close proximity to the caller, e.g. within 9 m for the pygmy marmoset (*Cebuella pygmaea*) [de la Torre and Snowdon, 2002], within 3 m for the domestic cat (*Felis catus*) [Frazer Sissom et al., 1991] and even less for other animals [Bradbury and Vehrencamp, 1998]. Although such low-amplitude vocalizations are typically thought to be affiliative, they are also used in agonistic social contexts. Birds such as song sparrows (*Melospiza melodia*), blackbirds (*Turdus merula*) and dark-eyed juncos (*Junco hyemalis*) have male-specific, low-amplitude vocalizations called 'soft songs', which are used as aggressive signals during intra-sexual agonism (song sparrows [Searcy et al., 2006; Anderson et al., 2008]; blackbirds [Dabelsteen and Pedersen, 1990; Dabelsteen et al., 1998]; dark-eyed juncos [Titus, 1998]). In primates, many species have low-amplitude contact calls, which function to maintain group cohesion [reviewed in Kondo and Watanabe, 2009]. Species including mountain gorillas (*Gorilla berengei*) also have low-amplitude 'close calls' which have agonistic as well as affiliative functions [Harcourt et al., 1993]. Like these low-amplitude calls in birds and primates, other short-range vocalizations such as the mammalian purr are also known to be used in non-affiliative contexts.

A purr is a uniquely mammalian broad-band vocalization characterized by very low amplitude [Bradbury and Vehrencamp, 1998; Peters, 2002]. A variety of mammals have purr vocalizations, including cats, rodents, bears, civets, peccaries, bats and primates [reviewed in Peters, 2002]. The most familiar example of the purr is that made by the domestic cat, and most purring research has focused on this species [Heffner and Heffner, 1985; Frazer Sissom et al., 1991; Peters, 2002]. Purring in mammals is typically associated with affiliative and consummatory behaviours, including nursing, feeding, copulation, cuddling, grooming, play, affiliative approach and courtship [Bradbury and Vehrencamp, 1998; Peters, 2002]. However, purring also occurs in some non-affiliative situations. The domestic cat purrs when giving birth and when severely wounded, and in these situations of extreme pain and stress, purring is thought to function as an appeasement signal, advertising helplessness towards a nearby individual [Leyhausen, 1979; Beaver, 1992], or as an 'autocommunicatory signal' which allows the animal to self-soothe [Peters, 2002, p. 264].

For close-range vocalizations including the purr, Morton's [1977] motivational-structural rules suggest that there is a strong relationship between the structure of sounds and their function because natural selection has resulted in the structural convergence of many animal vocalizations used for common functions. These motivation-structural rules predict that broad-band, low-frequency vocalizations should be associated with aggressive social contexts [Morton, 1977]. Despite its use in many affiliative contexts, the broad-band structure of the purr vocalization would suggest it as being more likely a threat call.

The range of usage and possible informational meaning of the purr vocalization in primates, and in mammals in general, is not well understood [Peters, 2002]. Factors influencing the rate and utterance of this vocalization are even less well understood. Purring may be an 'epiphenomenal sound without communicatory function' or a communicatory signal in primates [Peters, 2002, p. 265]. Despite the dearth of a

systematic study of purring in primates [Peters, 2002], anecdotal and preliminary reports suggest that purring is used most widely in affiliative contexts – e.g. Old World monkey: rhesus macaque (*Macaca mulatta*) [Jürgens, 1979]; New World monkey: red titi monkey (*Callicebus cupreus*) [Maestriperi and Call, 1996]; strepsirhine: eastern woolly lemur (*Avahi laniger*) [Petter and Charles-Dominique, 1979]. However, purring is also used in agonistic situations in some species. Male and female greater bamboo lemurs (*Prolemur simus*) purr in situations widely ranging from affiliation to aggression to submission, with 62% of purring bouts occurring in agonistic contexts [Bergey and Patel, 2008]. The common squirrel monkey (*Saimiri sciureus*) also purrs in a wide range of different contexts including agonistic situations [Jürgens, 1979, 1983], where purring is thought to reflect ‘preparedness for aggression’ [Baldwin and Baldwin, 1981, p. 316]. My study expands the investigation of purring in agonistic contexts. Although previous research has identified general patterns of species-wide purr vocalization usage in other primates [Jürgens, 1979; Bergey and Patel, 2008], my study is the first to examine the relationship between individual qualities and purring usage and rate in a primate species, the ring-tailed lemur (*Lemur catta*). Although this vocalization is used by ring-tailed lemurs of both sexes and all ages [Jolly, 1966; Macedonia, 1990, 1993], my study will concentrate on adult male use of purring, since anecdotal reports [Jolly, 1966] as well as my preliminary data collection on adult females provide evidence for male purring only in agonistic contexts. Additionally, a strong precedent exists for male-focused behavioural studies to be undertaken in this species [Gould, 1994, 1997, 2006; Gould and Overdorff, 2002; Gould et al., 2003, 2005; Parga, 2006a; Gould and Ziegler, 2007], and my study will add to this rich literature on male behaviours.

The ring-tailed lemur is a female-dominant, female-philopatric strepsirhine primate endemic to southern Madagascar [Jolly, 1966; Jones, 1983; Sussman, 1991, 1992; Gould et al., 2003]. It is a gregarious animal that lives in multi-male, multi-female groups of up to 27 animals [Sussman, 1991; Gould et al., 2003; Pride, 2005b]. The ring-tailed lemur is an ideal species in which to study purring due to their large group size and sociality, as well as their terrestriality and maintenance of close proximity to other group members [Jolly, 1966; Sauther, 1991; Gould, 1994; Nakamichi and Koyama, 1997]. In the ring-tailed lemur, the purr is part of a large vocal repertoire comprised of 22 vocalizations for adults, according to a captive study by Macedonia [1990, 1993].

Like purring in other mammals, ring-tailed lemur purrs are very short-range vocalizations produced during both inhalation and exhalation phases of breathing [Jolly, 1966; Macedonia, 1990; but see Peters, 2002], and can be seen spectrally as ‘a relatively continuous stream of broad-band vertical striations’, with ‘striations [representing] rapid, unvoiced glottal pulses that are emitted while breathing’ [Macedonia, 1990, p. 62]. Past studies have anecdotally noted that both sexes of adults purr while allogrooming and resting, and infants purr while being groomed or licked by their mother [Jolly, 1966; Petter and Charles-Dominique, 1979; Keith-Lucas et al., 1999]. Macedonia [1990] suggested that purring in the ring-tailed lemur ‘appears to express pleasure or satisfaction’, further elaborating that purring ‘may communicate non-aggressive intent of an adult [ring-tailed lemur] during close contact’ (p. 62).

Although reported female and infant purring contexts are affiliative, Jolly [1966] also noted that males often purred while rubbing their tails across their scent glands while tail-marking, prior to tail-waving. These sex-specific behaviours are known to

mediate the male dominance hierarchy [Gould, 1994; Palagi et al., 2003; Gould and Ziegler, 2007; Scordato and Drea, 2007] and are actions that have been termed aggressive for male ring-tailed lemurs [Jolly, 1966; Schilling, 1974; Budnitz and Dainis, 1975; Mertl, 1976; Gaspari and Crockett, 1984]. This observation of purring in a potentially agonistic context, coupled with the predictions of Morton's [1977] motivation-structural rules that broad-band vocalizations like the purr should be used in aggressive contexts, provides the rationale for further study on purring usage in male ring-tailed lemurs.

Hypothesis: The Male Purr Is Used as an Aggressive Display in Male-Male Agonism

Males may purr as aggressive threat displays in male-male agonistic contexts. If this is the case, then I predict that for the ring-tailed lemur, purring will occur in the seconds before and during intrasexual agonistic acts, and that the male purring rate will be higher during periods of male-male agonism as opposed to contexts without agonism. I further predict that if the purr is an aggressive signal in intrasexual agonism, males with higher purring rates will have higher dominance ranks, and males with higher purring rates during agonistic encounters will also be more likely to win the male-male encounters that purring accompanies. If purring is linked to aggression rather than submission in agonistic encounters, then it follows that males who purr would be winners in those agonistic interactions. Since dominance is determined by agonistic wins, males who purr at higher rates in agonistic encounters would also be expected to have higher dominance ranks.

Methods

Description of Field Site

All data for this study were collected between March 1 and July 1, 2010, at Beza Mahafaly Special Reserve, a protected governmental reserve in Madagascar's south-west (23°30' S lat., 44°40' E long.) which was established in 1978 and has been protected since 1986 [Gould et al., 2003; Sussman and Ratsirarson, 2006; Sussman et al., 2012]. Data collection encompassed the short breeding season, which began in May, but did not include the birthing season.

At the time of this study, approximately 225 free-ranging ring-tailed lemurs in 11 groups lived in parcel I, and within these groups almost all adult lemurs were individually known [Gould and Ziegler, 2007; Sauther and Cuzzo, 2008]. Most individuals were collared and labelled with visible numbers, an identification system dating to the earliest ring-tailed lemur research at the reserve in the late 1980s [Sussman, 1991; Sauther et al., 2002; Cuzzo and Sauther, 2006; Sauther and Cuzzo, 2009; Cuzzo et al., 2010]. The only individuals left uncollared were infants, yearlings and some adult males who had recently migrated from groups outside the reserve. Animals were also identified through patches of black dye in different body areas, sex and size differences. These patches of black dye were added in February 2010 by another researcher as part of another research project.

Description of Study Animals

Focal animal data were collected on 25 adult males from 5 different ring-tailed lemur groups (tables 1, 2), 6 days a week, with each male sampled a minimum of two 30-min intervals a week throughout the study period. Ages for most individuals could be approximated from the decade-long work by researchers [Cuzzo and Sauther, 2006; Sauther and Cuzzo, 2008, 2009; Cuzzo et al., 2010], while age for all individuals with names beginning with 'Umm' (unmarked male, indicating a sexually mature recent immigrant to a study group) was estimated as 3 years or more [Bolt, 2013a].

Table 1. Male ring-tailed lemur study individuals at Beza Mahafaly Special Reserve, March–July 2010

Troop	Individual name	Approximate age, years	Total data time, h
Green	Umm1g	≥4	16.8
Green	Umm2g	≥4	17.6
Green	175	≥8	14.9
Green	Umm3g	≥4	16.8
Green	203	≥8	17.4
Orange	263	≥7	18.6
Orange	259	7	19
Orange	Umm1o	≥4	18.3
Orange	291	≥7	18.3
Orange	318	3	17.4
Orange	226	≥12	18.5
Purple	Umm2p	≥4	14.7
Purple	Umm1p	≥4	15.3
Purple	Umm4p	≥4	15.5
Purple	323	3	15
Purple	322	3	15.5
Purple	Umm3p	≥4	15.9
Red	280	≥6	23.4
Red	273	≥6	24.5
Red	308	3	23.1
Red	307	3	24.6
Yellow	208	≥9	22.4
Yellow	Umm2y	≥4	22.2
Yellow	230	≥8	19.3
Yellow	Umm1y	≥4	20.6

Field Methods

Each focal session lasted for 30 min, with data recorded every 2.5 min using one-zero sampling [Altmann, 1974; Martin and Bateson, 2007]. Data were recorded on a programmed Palm Pilot (Palm Z-22) to document the actions that occurred during the previous period, including the focal individual's purring vocalizations, behaviour (resting, vigilant, allogrooming, autogrooming, feeding, foraging, sunning, scent-marking, tail-waving, travelling, urinating/defecating, other, out of sight), whether or not the focal animal vocalized, and any agonistic interactions involving the focal animal. Animals were watched continuously during the focal period, and the author gathered all focal data. This study was part of a larger study on male ring-tailed lemur vocalization behaviour [Bolt, 2013b]. The ring-tailed lemur ethogram was based on those used by Jolly [1966], Gould [1994], Pereira and Kappeler [1997] and Parga [2006b].

In my study, an agonistic interaction is defined as any behaviour involving contest competition between 2 individuals. This could consist of low-arousal behaviour (e.g. a displacement or lunge-withdraw) or higher-arousal behaviour involving aggressive physical contact (e.g. cuff, bite or jump fight). An agonistic interaction involves 1 or more acts of avoidance, aggression or defence between 2 individuals [Gould, 1994; Pereira and Kappeler, 1997; Parga 2006a, 2009]. Times with male-male agonism were defined as 2.5-min one-zero sampling intervals that contained at least 1 instance of intrasexual agonism involving the focal male, while times without male-male agonism meant a 2.5-min sampling interval that did not contain any instances of male-male agonism involving the focal male.

Table 2. Ring-tailed lemur study group composition (n) at Beza Mahafaly Special Reserve, March–July 2010

Troop name	Total group membership	Adult males aged >3	Natal males aged 1–3	Females aged ≥1	Infants (born 2009)
Green	13	5	1	6	1
Orange	20	6	1	10	3
Purple	15	6	2	5	2
Red	9	2	2	5	0
Yellow	12	4	2	4	2

I used one-zero sampling because I was mainly interested in whether behaviours were present or absent [Gosselin-Ildari and Koenig, 2012], and because one-zero sampling provides an accurate minimum estimate of whether a behaviour is occurring within a given time period [Sarfaty et al., 2012]. The ring-tailed lemur purr vocalization can occur continuously for a long duration and is also of very low amplitude [Macedonia, 1990], making the absolute duration and true rate of this vocalization difficult to accurately determine. For this reason, using one-zero sampling over a relatively long, 2.5-min, sampling interval minimized the chances of missing instances of purring by a focal animal. However, this 2.5-min sampling interval was not so long that individual variation was eliminated. Even if a focal animal was not in close physical proximity at all times while being followed, the chances of missing a purr vocalization were minimal due to the accuracy of this sampling method at providing a reliable minimum estimate of behaviour.

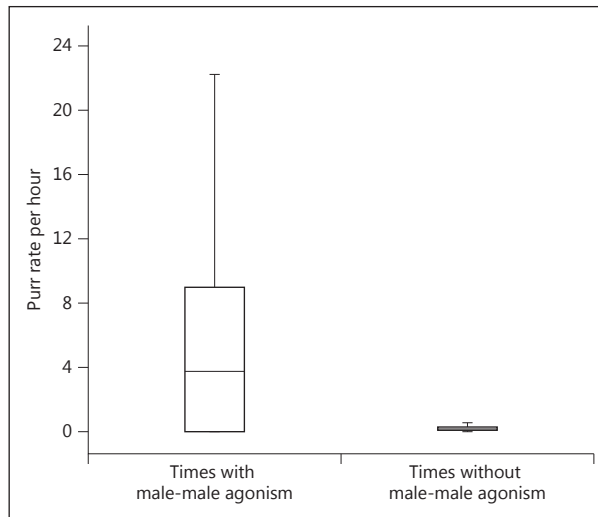
Assessing Male Rank

Although female ring-tailed lemurs are dominant to males [Budnitz and Dainis, 1975; Taylor, 1986; Gould, 1994], males have their own dominance hierarchy, which can be linear or non-linear [Jolly, 1966; Budnitz and Dainis, 1975; Gould, 1994]. The male dominance rank is stable for much of the year [Jolly, 1966], but loses stability during the short breeding season, which my data collection encompassed [Budnitz and Dainis, 1975; Gould, 1994]. During the breeding season, subordinate males may temporarily win agonistic encounters against dominant males [Budnitz and Dainis, 1975; Gould, 1994; Gould and Ziegler, 2007; Parga, 2009]. Dominance was calculated from focal data using dominance index calculations, which tally all decided agonistic and submissive interactions before assigning individual males a dominance percentage within its troop [Zumpe and Michael, 1986]. Dominance indices were determined independently for males in each group. In calculating dominance indices, all agonistic behaviours (e.g. chase, lunge-withdraw, cuff) were treated equally [Gould, 1994]. Male dominance indices were determined using the following equation [Zumpe and Michael, 1986]:

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

In this equation, n signifies the total number of males in the group with whom the male had agonistic interactions, $\%A$ signifies the percentage of aggression given within each male-male dyad, $\%S$ signifies the percentage of submission received within each male-male dyad, and i signifies the summation index. Successive values of i are calculated by adding 1 to the previous value of i , and stopping when i is equal to the total number of males in the group with whom the original male had agonistic interactions (i.e. when $i = n$). Output values approaching 0% indicated low dominance rank, while those approaching 100% indicated high dominance rank. Within each male-male dyad in each group, $\%A$ was determined from the number of aggressive actions given by each male and calculated as a percentage of the total number of aggressive behaviours expressed by both males to one another [Zumpe and Michael, 1986]. For each male-male dyad, $\%S$

Fig. 1. Median male ring-tailed lemur purring rate per hour during periods of male-male agonism versus male purring rate during times without agonism. Boxes represent interquartile ranges, lines represent median values, and whiskers represent maximum and minimum values.



was determined in the same manner 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 determine the dominance index [Zumpe and Michael, 1986]. Males with higher dominance percentages won more fights and had a higher ranking within their troops.

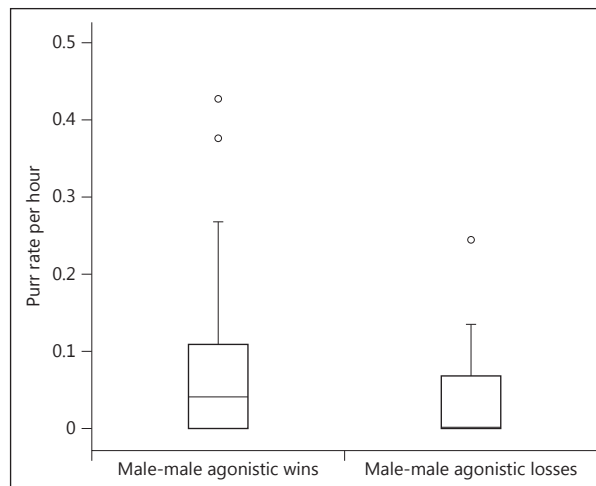
Data Analysis

For each data set used in my study, data were not normally distributed and the sample size was small ($n = 25$ males), requiring the use of non-parametric tests. I used the Wilcoxon signed-rank test to evaluate whether the purring rate was higher during times of male-male agonism when compared to times without agonism, and to evaluate whether the purring rate during winning male-male encounters was higher than that during losing male-male encounters. I used the Spearman rank correlation test to evaluate whether high-ranking males had higher purring rates than lower-ranking males. For comparative purposes, I also used the Spearman test to determine whether high-ranking males had higher overall vocalization rates than lower-ranking males. All tests were two-tailed, and medians (50th percentiles) were reported with quartile deviations (75th–25th percentiles/2). For all tests, the α -level was set to 0.05. All statistical tests were performed using SPSS version 22 (IBM SPSS Statistics, IBM Corporation, Armonk, N.Y., USA, 2013). SPSS identified outliers as data points with a distance from the nearest quartile of more than 1.5 times the interquartile range, and these values were removed when doing recalculations.

Results

Out of all observed instances of male-male agonism, purring occurred in 10.24% of interactions (65/635), a small proportion of total male-male agonistic encounters. However, a large percentage of total purrs, 41.67% (65/156 purrs), were heard in male-male agonistic contexts. Males purred in the seconds before and during these agonistic encounters, as well as during non-agonistic contexts, such as during tail-waving at females (24/156 purrs, or 15.38%), resting (22/156 purrs, or 14.1%), scent-marking (16/156 or 10.26%), feeding (15/156 purrs, or 9.62%), copulation with females during the mating season (9/156 purrs, or 5.77%), grooming (3/156 purrs, or

Fig. 2. Median male ring-tailed lemur purring rate per hour during male-male agonistic wins versus purring rate during male-male agonistic losses. Boxes represent interquartile ranges, lines represent median values, whiskers represent maximum and minimum values, and dots represent outliers.



1.92%) and travelling (2/156 purrs, or 1.28%). Purring was not observed as being associated with specific body postures, and was done with a closed mouth.

There was a significant difference in male purring rates during periods of male-male agonism when compared to periods without male-male agonism (Wilcoxon test: $n = 25$ males, $Z = -3.2$, $p = 0.001$; fig. 1). The median male purring rate was higher during times of male-male agonism (3.75 purrs/h ± 5.35 quartile deviations, $n = 25$ males) than the median male purring rate at times without male-male agonism (0.172 purrs/h ± 0.126 quartile deviations, $n = 25$ males).

While the overall vocalization rate in this species was not correlated with male dominance rank (Spearman test: $n = 25$ males, $r_s = 0.024$, $p = 0.908$), the male purring rate was significantly correlated with the male dominance index (Spearman test: $n = 25$ males, $r_s = 0.56$, $p = 0.004$). However, there was no significant difference in purring rates between winners and losers of male-male encounters (Wilcoxon test: $n = 25$ males, $Z = -1.6$, $p = 0.117$; fig. 2). This result remained non-significant when outliers were removed (Wilcoxon test: $n = 22$ males, $Z = -1.5$, $p = 0.139$).

Discussion

My results indicate that the male purring rate was significantly higher during periods of male-male agonism than at times without male-male agonism, showing that purring plays a role in male-male agonism in the ring-tailed lemur. Although purring happened infrequently in male-male agonistic interactions, the largest proportion of total purrs recorded, 41.67%, was allocated to male-male agonistic behaviours. This proportion is comparable to the 62% of purrs allocated to agonistic contexts (40% to aggressive contexts and 22% to submissive contexts) by both males and females of the close relative of the ring-tailed lemur, the greater bamboo lemur [Bergey and Patel, 2008]. Also like the greater bamboo lemur, the ring-tailed lemur purred in a wide variety of social situations, ranging from affiliation and resting to agonistic

interactions. Within male-male agonistic encounters, ring-tailed lemur males with higher purring rates were higher-ranking animals, which suggests that the purr is an assertive vocalization in intrasexual agonistic contexts. However, lemurs did not purr at significantly higher rates during winning agonistic encounters when compared to losing agonistic encounters. A vocalization linked to high dominance should also be associated with winning in agonistic encounters, given that male-male agonistic wins were the criteria used to determine rank in ring-tailed lemur males. However, there was no significant relationship between purring and winning. The purr was therefore used in contexts of both aggression and submission in agonistic encounters.

There are several possible reasons for this mixed result. One possible explanation involves consideration that in the ring-tailed lemur, male dominance ranks do not always remain stable throughout the annual breeding season [Koyama, 1988; Sauther, 1991; Gould 1994, 1997; Gould and Ziegler, 2007; Parga, 2009], which comprised part of my data collection period. In my study, high-ranking males who won agonistic interactions before and after the mating season did not win consistently throughout [Bolt, 2013c]. Purring could therefore be linked to dominance rank in general, rather than having a specific role as an assertive or submissive signal within agonistic interactions. In the chacma baboon (*Papio ursinus*), the vocalization rate for the male-specific wahoo call has been found to change with changing dominance rank, indicating that for some primate species, the calling rate changes with changing social status and is not bound to intrinsic individual qualities [Kitchen et al., 2003]. For the ring-tailed lemur, the purring rate may similarly be bound to changing dominance rank rather than purrs being associated with agonistic wins, although further research, involving collection of a greater number of data hours and replication of this study over multiple years, is needed to test this speculation.

Another possibility relates to the consideration that a higher purring rate during male-male agonistic encounters could be linked to an increased respiratory rate, since purring is known to occur during both inhalation and exhalation phases of respiration [Peters, 2002]. In the domestic cat, the respiratory rate during purring is approximately 93% higher than that while resting without purring [Remmers and Gautier, 1972]. Although purring energetics research has not been undertaken for other mammals, male ring-tailed lemur intrasexual agonistic encounters are known to be stressful and often involve physical exertion [Cavigelli and Pereira, 2000; Gould et al., 2005; Gould and Ziegler, 2007; Pride, 2005a, b]. It is therefore likely that the ring-tailed lemur respiratory rate during these agonistic interactions would be higher than the resting respiratory rate, suggesting a higher purring rate. Purring may be a physiological occurrence that happens in conjunction with an increased respiration rate, and dominant males could purr more often due to having higher stress levels or being more likely to participate in agonistic encounters. However, behavioural endocrinology and energetics studies are needed to test this speculation.

A third possible explanation for this mixed result is the consideration that my results also indicate that high-ranking males purr at higher rates in general, not just during male-male agonistic encounters. Given that dominant males purr at higher rates than lower-ranking males in contexts ranging from resting to grooming to copulation, it follows that dominant males should also purr at higher rates in agonistic situations. Purring may have little to do with signalling anything specific in particular situations and may not have a 'meaning' in an informational sense at all [Owren and Rendall, 1997]. Vocalizations such as human laughter are difficult to link to particu-

lar motivational states or external circumstances [Owren et al., 2003], and the ring-tailed lemur purr can be described in similar terms. Human laughter occurs in a variety of social contexts and may signal happiness, but may also signal sexual interest, anger, shame, nervousness, submission or self-deprecation [Provine, 1993; Owren and Bachorowski, 2003]. Laughter can therefore have multiple meanings, both broad and specific, in both positive and negative emotional states, 'with little evidence of specific and exclusive connections' [Owren and Bachorowski, 2003, p. 188]. This variety of meanings and usages would also argue against laughter having a specific representational content [Owren and Bachorowski, 2003]. The male ring-tailed lemur purr, with its similarly broad range of usage across social situations, may similarly not convey representational information. Rather, purring may have more to do with intrinsic qualities in individual males, which could make them more frequent vocalizers in all social contexts, ranging from agonism to affiliation [Bradbury and Vehrencamp, 1998]. Dominant ring-tailed lemur males do not have higher overall vocalization rates, but do have higher calling rates for some vocalizations used in agonistic contexts, such as the squeal [Bolt, 2013c] and purr. That the same purr vocalization is used in such widely ranging social contexts would seem to argue against it having distinct, informational functions in each situation. As male ring-tailed lemur purrs heard in agonistic contexts may not communicate either aggression or submission, neither do affiliative purrs necessarily 'express pleasure or satisfaction' or 'communicate non-aggressive intent' [Macedonia, 1990, p. 62]. Instead, a high purring rate may be linked to individual male characteristics, such as health or age, that are likely to result in those same males achieving a high dominance rank [Gould, 2006]. Dominant males may purr at higher rates across social situations in order to influence the behaviour of listening group members, as has been argued for laughter and other signals that do not convey representational information [Owren and Bachorowski, 2003]. High-ranking male lemurs could purr to intimidate other males across social contexts, or to appease and maintain affiliative relationships with lower-ranking male competitors, although these speculations would be difficult to test. Finally, purring in the ring-tailed lemur may be an epiphenomenal sound, made as a byproduct of emotional arousal, with dominant males being more likely to be aroused in general [Peters, 2002].

Conclusions

My study describes the use of the purr as an intrasexual agonistic vocalization by male ring-tailed lemurs, amongst other uses in varied social contexts. Previously, purring had been noted as occurring only during ring-tailed lemur grooming, resting and tail-marking, and was assumed to have strictly affiliative uses in this species [Jolly, 1966; Macedonia, 1990, 1993]. The range of usage of this low-amplitude vocalization is therefore broader than previously documented for the male ring-tailed lemur, with intrasexual agonism as a primary context for male purring. Dominance rank is linked to purring rate for male ring-tailed lemurs, both for purrs heard in agonistic situations as well as more generally across social contexts including affiliation. Given the lack of a significant association with winning or losing in agonistic situations, my results do not convincingly show that agonistic purring functions as an informational signal expressing threat in this species. However, my findings do indicate that in-

dividual differences exist in purring usage amongst ring-tailed lemur males, and that these differences are linked to dominance rank. Although female ring-tailed lemurs were not observed purring in agonistic situations in the present study, the study of female purring at other times of year, such as during the birthing season, may reveal additional contexts of use. Future research should also focus on elucidating the factors behind individual differences in purring usage in this species, as well as examining purring function in a broader range of primate species.

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