ORIGINAL ARTICLE

Agonistic vocalization behaviour in the male ring-tailed lemur (*Lemur catta*)

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Abstract

Vocalizations are used by group-living animals as aggressive and submissive signals during agonistic interactions, and are also used to maintain dominance hierarchies in many species. For gregarious strepsirrhines with large vocal repertoires and differentiated dominance ranks like the ring-tailed lemur (*Lemur catta*), agonistic vocalization use is important to study to better understand their social adaptations.To determine whether ring-tailed lemur vocalizations such as the yip, cackle, twitter, chutter, and plosive bark were used as aggressive or submissive signals during agonism and uttered at different rates by males of differing dominance ranks and ages, 565 h of focal data were collected on 31 individual males aged ≥ 1 year from Beza Mahafaly Special Reserve, Madagascar. Yip, cackle, and twitter vocalizations were consistently used during agonistic submissive interactions with both males and females, chutter vocalizations were used during aggressive agonistic interactions with males and submissive agonistic interactions with males and females, and plosive bark vocalizations were used across behavioural contexts but not particularly during agonism. Males of all ages employed all vocalizations, and while low-ranking males uttered yip calls at higher rates, males of all dominance ranks uttered cackle, twitter, chutter, and plosive bark vocalizations. These results advance our knowledge of how male lemurs utilize agonistic vocalizations to maintain inter-individual relationships with males and females, and improve our overall understanding of the function of different agonistic vocalizations in wild lemurs.

Keywords Aggression · Submission · Agonism · Dominance rank · Vocalization rate · *Lemur catta*

Introduction

In group-living mammals, vocalizations facilitate long-term social relationships, and may be used in social contexts ranging from affiliation to conflict. Conflict can range from intense physical fighting to ritualized display, and interactions often involve vocal signals to help determine the outcome (Bradbury and Vehrencamp 1998). With physical altercations potentially leading to injury or death, it is adaptive for animals to use signals as alternatives to combat when possible (Maynard Smith 1982). Vocal signals, therefore, have evolved to indicate aggression and/or submission during competitive interactions in a number of different animal species, and may help regulate dominance hierarchies (Bradbury and Vehrencamp 1998). Dominant animals win consistently in fights; they consistently receive submissive signals from other group members but rarely give them (Pereira 1995). Dominance is important in the social lives of many mammals, with high rank leading to benefits including better access to food resources for females and better mating opportunities for males (Chapman and Sussman 2004). A wide variety of group-living animal species use forms of communication including vocalizations to maintain intra-group dominance hierarchies. These include the harbor seal [*Phoca vitulina* (Sullivan 1982)], the false vampire bat [*Megaderma lyra* (Bastian and Schmidt 2008)], and primates ranging from the chacma baboon [*Papio ursinus* (Kitchen et al. 2003)] to the common chimpanzee [*Pan troglodytes* (Fedurek et al. 2015)]. Although agonistic vocalizations have been studied widely in primates, their role in inter-individual interactions and in mediating dominance relationships in social strepsirrhines remains poorly understood.

Many lemur species live in groups and are socially complex, with communication systems including large vocal repertoires needed to regulate the myriad forms of interaction

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occurring within and between social groups (Fichtel and Kappeler 2010; Freeberg et al. 2012). Vocalizations are used to mediate these inter-individual relationships, including as aggressive/submissive signals in competitive interactions. Given the similarity between the sociality of extant group-living lemurs and their gregarious human ancestors (Fichtel and Kappeler 2010), it is important to study sociality in lemurs to gain further insight into the evolution of social processes in humans. Amongst social lemur species, the ring-tailed lemur (*Lemur catta*) has the largest vocal repertoire and most complex communicative processes (Kittler et al. 2015), along with female dominance and differentiated rank hierarchies for both males and females, which are associated with high levels of aggressive interactions between individuals (Jolly 1966; Budnitz and Dainis 1975; Taylor 1986; Gould 1994). Additionally, ring-tailed lemurs reportedly use several different vocalizations during competitive interactions (Andrew 1963; Jolly 1966; Macedonia 1990, 1993; Bolt 2013a, c, 2014), suggesting that further study on why this species has evolved so many different vocalizations (Kittler et al. 2015) is warranted. It is important to investigate whether these diverse vocalizations may be used in similar social contexts and therefore function as redundant back-up signals (Johnstone 1996) or are used in diverse social contexts and therefore may have more nuanced adaptive functions. The present study will allow us to better understand the selective pressures operating on communication systems in social strepsirrhines, and in particular, to better understand the vocal communication system of the ring-tailed lemur. In the ring-tailed lemur, the combination of specific behavioural and communicative traits (i.e. their large vocal repertoire, their reported use of multiple different vocalizations during inter-individual competition, and their high levels of inter-individual aggression) suggests that this is an ideal species in which to study the nuances of vocalization usage. Studying the vocalization use of the ring-tailed lemur in detail allows for a better understanding of social strepsirrhine behavioural adaptations and signal evolution.

The ring-tailed lemur lives in groups of up to 27 individuals with approximately equal numbers of males and females (Sussman 1991, 1992; Sauther et al. 1999; Gould et al. 2003). Although adult females outrank males, males have their own dominance hierarchy, which is usually linear (Jolly 1966; Budnitz and Dainis 1975; Taylor 1986; Gould 1994; Nakamichi and Koyama 1997). High rank is advantageous for males, and is associated with better access to food and water, better spatial positioning during group rest and travel, and closer associations with females from their social groups, which may lead to increased mating opportunity during female estrus (Jolly 1966; Sauther 1991, 1993; Sauther and Sussman 1993; Ichino and Koyama 2006). Estrus occurs during an annual breeding season in April–May in Madagascar, with individual females entering asynchronous estrus for

periods of 2–24 h (Jolly 1966; Van Horn and Resko 1977; Taylor and Sussman 1985; Koyama 1988; Sauther 1991; Parga 2006; Walker-Bolton 2017). During this time, male dominance hierarchies become unstable as females mate with multiple males across dominance ranks from within and outside their social groups (Jolly 1966; Koyama 1988; Sauther 1991; Gould 1994; Parga 2009; Bolt 2013c; Walker-Bolton 2017). Males arbitrate their dominance hierarchies through a range of communication modalities, including ritualized displays involving male-specific olfactory and vocal signals (Jolly 1966; Mertl 1976; Macedonia 1990, 1993; Mertl-Millhollen 2006; Bolt 2013a; Walker-Bolton and Parga 2017). Male agonistic behaviour also includes usage of a number of different vocalizations, which may indicate aggression and/or submission during competitive encounters. Male behavioural usage of five vocalizations—the yip, cackle, twitter, chutter, and plosive bark (Macedonia 1990, 1993)—is investigated in the present study.

According to past reports, the yip, cackle, twitter, chutter, and plosive bark vocalizations appear to be used in competitive situations by ring-tailed lemurs, suggesting that they may function as agonistic calls (Andrew 1963; Jolly 1966; Macedonia 1990, 1993; Pereira and Kappeler 1997). The yip and cackle may function as agonistic submissive calls, while the twitter, chutter and plosive bark may function as agonistic aggressive calls (Andrew 1963; Jolly 1966; Macedonia 1990; Pereira and Kappeler 1997; for spectrograms of all five vocalizations see Macedonia 1993, p. 194). Most previous investigations inferred the behavioural function of vocalizations from qualitative observations but did not systematically investigate usage (Andrew 1963; Jolly 1966; Macedonia 1990, 1993). Pereira and Kappeler (1997) examined agonistic vocalization use in ring-tailed lemurs from a quantitative perspective, but did so in a captive environment and using a small sample size. This is the first study to quantitatively investigate, using a large sample size, the usage of the yip, cackle, twitter, chutter, and plosive bark vocalizations in a wild population of ring-tailed lemurs.

In previous investigations, the yip, cackle, twitter, chutter, and plosive bark vocalizations have been referred to by various alternative terms [cf. yip—light yip, spat call; cackle—high-intensity yip, deep spat call; twitter—huh; chutter—huff; plosive bark—explosive voiced grunt, bark (Andrew 1963; Jolly 1966; Pereira and Kappeler 1997], but this study follows the nomenclature used by Macedonia (1990, 1993). These five vocalizations are used by both males and females, but given that males have larger vocal repertoires than females (Jolly 1966; Macedonia 1990, 1993), a broader range of vocalization usage (Bolt 2013c, 2014), and use a variety of vocalizations during agonistic encounters (Jolly 1966; Pereira and Kappeler 1997), this provides the rationale for a male-focused study of agonistic vocalization usage.

Hypothesis 1: vocalizations are used as aggressive and submissive signals during agonistic social interactions

Of the six ring-tailed lemur vocalizations identified as being potentially agonistic in previous reports [squeal, yip, cackle, twitter, chutter, plosive bark (Macedonia 1993; Pereira and Kappeler 1997)], the behavioural usage of the squeal has already been examined (Bolt 2013a). The male-specific squeal vocalization was found to be agonistic and used in both aggressive and submissive competitive interactions (Bolt 2013a). Another ring-tailed lemur vocalization, the purr, was used as an affiliative vocalization by males and females (Macedonia 1993), but was additionally uttered at high rates by males during both aggressive and submissive agonistic interactions (Bolt 2014). This study assesses the function of the five other vocalizations classified as potentially agonistic (Macedonia 1993)—yip, cackle, twitter, chutter, and plosive bark calls—through examining their possible usage as aggressive and/or submissive signals during agonistic encounters.

If the yip, cackle, twitter, chutter, and plosive bark vocalizations are used in agonistic interactions, I predict that they should be uttered at higher rates during agonistic contexts as opposed to behavioural contexts without agonism. Because rates of male agonism are known to be higher during female estrus (Budnitz and Dainis 1975; Koyama 1988; Sauther 1991; Gould 1994; Gould and Zeigler 2007; Parga 2009; Walker-Bolton 2017), I also test whether agonistic vocalization rates are higher on days of known estrus compared to days without estrus. To assess whether these vocalizations are used in aggressive, submissive, or both aggressive/submissive contexts during agonism, I also investigate whether vocalizations are associated with winning or losing during competitive interactions. To further assess the nuances of male vocalization use during agonism, I test whether yip, cackle, twitter, chutter, and plosive bark vocalizations show differential usage when directed towards males vs. females. Specifically, I examine vocalization rates during male-male and male–female agonism compared to non-agonism, and during losing male-male vs. male–female agonistic encounters in order to determine whether the sex of an agonistic partner may impact vocalization use. I predict that the yip and cackle vocalizations will be generally associated with agonistic submissive behaviour and uttered at lower rates during winning agonistic encounters and higher rates during losing agonistic encounters, while twitter, chutter, and plosive bark vocalizations will be associated with agonistic aggressive behaviour and uttered at higher rates during winning agonistic encounters and lower rates during losing agonistic encounters.

Hypothesis 2: individual differences in vocalization rate relate to dominance rank and age class

The individual differences hypothesis (Bolt and Tennenhouse 2017; Bolt 2020a) predicts that individual male characteristics such as dominance index and age class will influence vocalization rate. This relationship has been shown in other animals, including chickadees [*Poecile atricapillus* (Otter et al. 1997)], deer [*Cervus elaphus* (Clutton-Brock and Albon 1979)], toads [*Bufo bufo* (Davies and Halliday 1978)], common chimpanzees (Clark 1993), and chacma baboons (Kitchen et al. 2003). In the ring-tailed lemur, previous research on male vocalizations used in agonistic contexts (squeal and purr) found links between male dominance rank and vocalization rate, with higher-ranking males calling at higher rates (Bolt 2013a, 2014). The relationship between calling rate and age was not investigated, nor were other potentially agonistic vocalizations [yip, cackle, twitter, chutter, and plosive bark calls (Macedonia 1993)] with respect to male qualities.

Based on previous findings for other agonistic vocalizations (Bolt 2013a, 2014), I predict that yip, cackle, twitter, chutter, and plosive bark vocalization rates will similarly show relationships with male dominance rank, with yip and cackle vocalizations (i.e. vocalizations expected to be uttered in submissive agonistic contexts) uttered at higher rates by lower-ranking males, and twitter, chutter, and plosive bark vocalizations (i.e. vocalizations expected to be uttered in aggressive agonistic contexts) uttered at higher rates by higher-ranking males (Macedonia 1990, 1993; Pereira and Kappeler 1997). A past study also noted a correlation between male ring-tailed lemur age and dominance rank (Bolt and Tennenhouse 2017), with old males (aged ≥ 8 years) and prime aged males (aged 4–7 years) having higher dominance ranks than subadult males (aged 1–2 years) and young adult (aged 3 years) males. Given these previous results, I therefore predict that younger males will utter yip and cackle vocalizations at higher rates than older males, while younger males will utter twitter, chutter and plosive bark vocalizations at lower rates than older males.

Methods

Field site

Focal data were collected from March-July 2010 in the Parcel I riverine forest at Beza Mahafaly Special Reserve, Madagascar (23°30′S, 44°40′E), a site that has been governmentally protected since 1986 (Gould et al. 2003; Sussman and Ratsirarson 2006; Sussman et al. 2012). Due to its remote location and limited environmental noise, Beza

Mahafaly is a model field site for collecting data on lemur vocalization behaviour.

Study animals

Approximately 225 ring-tailed lemurs from 11 troops lived in the Parcel I forest, and most adults in these groups could be individually identified using visible numbers hanging from collars, a system of identification in continuous usage at Beza Mahafaly since ring-tailed lemur research began in the late 1980s (Sussman 1991; Sauther et al. 2002; Cuozzo and Sauther 2006; Gould and Ziegler 2007; Sauther and Cuozzo 2008, 2009; Cuozzo et al. 2010). Any individual lemurs without collars could be identified using black dye spots on different body areas (O'Mara 2012).

Data were collected on 31 males aged ≥ 1 year from five different ring-tailed lemur groups (green, orange, purple, red, and yellow groups); 565 h of male focal data were collected as part of a large-scale study on ring-tailed lemur vocalization behaviour (Bolt 2013c). Individual males were sampled for between 14.45 and 24.5 h each, with total sampling time during agonism ranging from 1 to 2.8 h per male, total sampling time during non-agonism ranging from 12.5 to 22.2 h per male, total sampling time during winning agonistic encounters ranging from 0.04 to 1.3 h per male, total sampling time during losing agonistic encounters ranging from 0.8 to 2.3 h per male, total sampling during estrus days ranging from 0 to 2 h per male, total sampling time during non estrus days ranging from 14 to 23.3 h per male, total sampling time during inter-group encounters ranging from 0.08 to 2.1 h per male, and total sampling time during non inter-group encounters ranging from 14.3 to 23.2 h per male. Age data for most lemurs were obtained from published accounts (Cuozzo and Sauther 2006; Sauther and Cuozzo 2008, 2009; Cuozzo et al. 2010) or provided by Sauther and Cuozzo (unpublished data), while the ages for all sexually mature, non-natal males with unknown birthdates were estimated as being 4–7 years (Bolt and Tennenhouse 2017; Bolt 2020a), since males typically disperse from social groups for the first time at age 3–4 years, and have a high mortality rate in the wild, with few reaching old age (Sussman 1991, 1992). Focal males were assigned to one of the following four age classes based on established age class estimates by other researchers (Sussman 1992; Gould 1994, 1997; Sauther et al. 2002; Gould and Ziegler 2007; Parga 2013): sub-adult (1–2 years old, natal group member and sexually immature), young adult (3 years old, natal group member and sexually mature), prime adult (4–7 years old, non-natal group member and sexually mature), or old adult (≥ 8 years old, non-natal group member and sexually mature) (Bolt and Tennenhouse 2017; Bolt 2020a).

Field methods

Individual male ring-tailed lemurs were followed for 30 min at a time during focal sampling, with data recorded for each 2.5-min interval on a programmed palm pilot (Palm Z-22). Instantaneous sampling (Altmann 1974) and one-zero sampling (Martin and Bateson 2007) were performed concurrently. Instantaneous sampling was used to record the identity of the focal individual and their state behaviour [resting, foraging (including feeding), travelling, vigilant, other (including allogrooming)] at the start of each 2.5-min sampling interval. One-zero samples for individual males were recorded at the end of each 2.5-min interval to note whether or not the animal vocalized during the preceding time period, which vocalization types the focal animal uttered of 18 different vocalizations [moan, hmm, purr, chirp, wail, squeal, yip, cackle, twitter, chutter, plosive bark, gulp, rasp, shriek, click, click series, yap, howl; following Macedonia (1990, 1993) and Bolt (2013c)], whether males uttered yip, cackle, twitter, chutter, or plosive bark calls; any agonistic interactions involving the focal animal; and any inter-group encounters [i.e. another ring-tailed lemur group was within 20 m and in visual range of the focal group (Bolt 2013b, c)].

Estrus days were noted opportunistically during the study period, and were recorded using ad libitum sampling on estrous females (Altmann 1974) in addition to one-zero sampling on individual males. Female estrus was defined as a period of time when females copulated with and made proceptive gestures towards males (Beach 1976; Bolt 2013a, b, c; Walker-Bolton 2017).

One-zero sampling has been characterized as a problematic data collection method (e.g. Altmann 1974), but has also been demonstrated as effective for data collection on primate behavioural rates (Leger 1977; Rhine and Linville 1980; Suen and Ary 1984; Sarfaty et al. 2012). It has also been used in many other studies on primate vocalizations (e.g. Suzuki and Sugiura 2011; Clarke et al. 2012; Bolt 2013a, c, 2014, 2020a; Bolt et al. 2015; Bolt and Tennenhouse 2017). The present study used one-zero sampling following Bernstein (1991), who recommended that one-zero scoring should be used when behavioural acts are clustered and the bout is of interest, rather than each act. As several ring-tailed lemur vocalizations can occur repeatedly within a short time (e.g. yip, cackle, twitter), are of low amplitude (e.g. twitter, chutter, plosive bark), and/or can transition from one vocalization type to another [e.g. yip transitions to cackle (Macedonia 1990, 1993)], making it difficult to determine the total number of each discrete type of vocalization, one-zero sampling was considered an appropriate method for providing a reliable minimum estimate of whether a behaviour occurred within a given time period. Reducing each yip, cackle, twitter, chutter, and plosive bark vocalization bout

to a single, independent data point allowed for individual variation to be more accurately represented, and for social factors influencing patterns of use for vocalizations to be more accurately discerned.

Agonistic behaviour included interactions classified as both low arousal (e.g. stare/look away or approach/withdraw) and high arousal (e.g. cuff/jump away, chase/flee, attack/retreat or stalk/cower) (Gould 1994; Pereira and Kappeler 1997; Parga 2006, 2009). Individual male dominance scores were determined from these data following methods described in detail by Bolt (2013a, b, c, 2014), using dominance index calculations (Zumpe and Michael 1986), which take all aggressive and submissive interactions in each group into account before assigning an individual dominance percentage to each individual based on the relative number of agonistic wins and losses. High dominance percentages correlate with high dominance levels, while low dominance percentages correlate with low dominance levels. Only decided agonistic interactions with clear winners and losers were used to determine male dominance rankings.

Data analysis

As the sample size of each data set was small ($n = 31$ males; Table 1) and the data were not normally distributed, nonparametric tests were used for the statistical analyses.

To test the usage of yip, cackle, twitter, chutter, and plosive bark vocalizations as aggressive and/or submissive signals during agonistic interactions (hypothesis 1), the Wilcoxon signed-rank test was used to determine vocalization rates during 2.5-min sampling intervals containing agonism (i.e. intervals in which the focal animal gave or received agonism) when compared to sampling intervals without agonism (i.e. intervals in which the focal animal did not give or receive agonism). Wilcoxon-signed rank tests were further used to determine vocalization rates during periods of male-male agonism (i.e. intervals in which the focal animal participated in agonistic interactions with other males) compared to sampling intervals without agonism, and during periods of male–female agonism (i.e. intervals in which the focal animal participated in agonistic interactions with

females) compared to sampling intervals without agonism. I also used the Wilcoxon signed-rank test to examine whether vocalization rates for yip, cackle, twitter, chutter, and plosive bark vocalizations were higher during winning agonistic interactions as opposed to during losing agonistic interactions, during winning male-male agonistic interactions (NB: all winning interactions occurred in the context of male-male agonistic interactions in this female-dominant species) compared to losing male-male agonistic interactions, and during male-male agonistic losses compared to male–female agonistic losses. Finally, the Wilcoxon signed-rank test was used to determine if males uttered agonistic vocalizations at higher rates on days of known female estrus compared to days without known estrus (Bolt 2013a, b, c). Males were excluded from analysis if estrus was not observed in their group or they were sampled for less than 30 min during estrus days ($n = 17$ males excluded).

For vocalizations that were uttered at low rates during the study period and/or did not show clear results for usage during agonism compared to non-agonism (i.e. chutter and plosive bark vocalizations; Table 1), additional tests were performed to elucidate behavioural contexts for vocalization use. Repeated measures ANOVA tests followed by post hoc pairwise t-tests were performed to compare the rates at which males uttered chutter and plosive bark calls across behavioural contexts. Wilcoxon signed-rank tests were performed to see if chutter and plosive bark vocalization rates differed during sampling intervals containing inter-group encounters compared to sampling intervals without intergroup encounters.

In order to test the effects of dominance index and age class on calling rates (hypothesis 2) for the yip, cackle, twitter, chutter, and plosive bark vocalizations, multiple regressions were used to test average hourly rates for each vocalization type for each focal male. To determine differences in vocalization rates for each agonistic call across social groups, Kruskal–Wallis tests were used to compare individuals across different groups. For significant values, I performed pairwise asymptotic (two-sided) post hoc tests with significance adjusted by the Bonferroni correction for multiple tests to test which social groups differed in vocalization rates.

All statistical tests were performed using SPSS version 26 (IBM SPSS Statistics; IBM, Armonk, NY). An α-level of 0.05 was adopted.

Results

Hypothesis 1: yip vocalization

The yip vocalization was uttered at significantly higher mean rates during agonistic contexts compared to sampling

Table 1 Male ring-tailed lemur (*Lemur catta*) vocalization rates at Beza Mahafaly Special Reserve

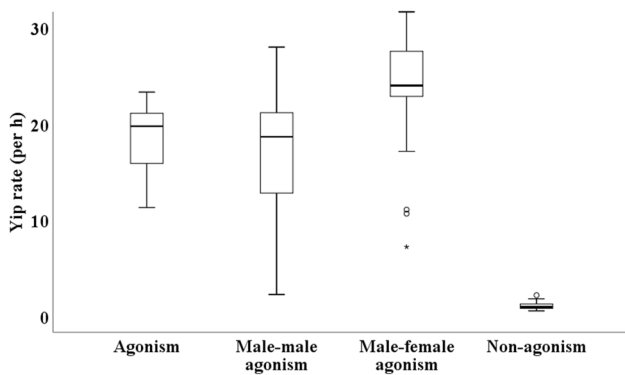| Vocalization	Mean rate (vocalizations per hour)	SD	Range (vocalizations per hour)
Yip	2.70	0.56	1.64–4.05
Cackle	0.24	0.23	0–0.93
Twitter	0.05	0.06	0–0.22
Chutter	0.03	0.06	0–0.24
Plosive bark	0.03	0.04	0–0.14

Fig. 1 Male yip rate during sampling intervals with agonism versus during intervals without agonism. Mean yip rate was significantly higher during agonistic contexts ($p < 0.001$), during male-male agonistic contexts ($p < 0.001$), and during male–female agonistic contexts ($p < 0.001$) compared to intervals without agonism. *Boxes* represent inter-quartile ranges, *lines* represent median values, *whiskers* represent maximum and minimum values, *white circles* represent outliers, and the *star* represents an extreme outlier

Fig. 2 Male yip rate during agonistic wins versus during agonistic losses. Compared to agonistic wins, mean yip rate was significantly higher during agonistic losses ($p < 0.001$) and during male-male agonistic losses ($p < 0.001$). *Boxes* represent inter-quartile ranges, *lines* represent median values, *whiskers* represent maximum and minimum values, *white circles* represent outliers, and *stars* represent extreme outliers

intervals without agonism (18.3 vs. 1.07 yips/h and 64% vs. 36% of total yips, $z = -4.86$, $n = 31$ males, $p < 0.001$; Fig. 1), during male-male agonistic contexts compared to sampling intervals without agonism (17.8 vs. 1.07 yips/h and 32.2% vs. 36% of total yips, $z = -4.86$, $n = 31$ males, $p < 0.001$; Fig. 1), and during male–female agonistic contexts compared to sampling intervals without agonism (23.8 vs. 1.07 yips/h and 31.8% vs. 36% of total yips, $z = -4.86$, $n = 31$ males, $p < 0.001$; Fig. 1). The yip vocalization was also uttered at higher rates during losing agonistic interactions compared to during winning agonistic interactions [21.3 vs. 6.4 yips/h and 91.3% vs. 8.7% of yips during agonism (41.6% during agonistic losses to males, 49.7% of yips during agonistic losses to females, and 8.7% during agonistic wins against males), $z = -4.8$, $n = 31$ males, $p < 0.001$; Fig. 2], and during losing male-male agonistic interactions compared to during winning agonistic interactions (23.9 vs. 6.4 yips/h and 82.7% vs. 17.3% of yips during male-male agonism, $z = -4.8$, $n = 31$ males, $p < 0.001$; Fig. 2). There was no significant difference in male yip utterance when rates during male-male and male–female agonistic losses were compared (23.9 vs. 23.8 yips/h and 45.5% vs. 54.5% of yips during agonistic losses, $z = -1.9$, $n = 31$ males, $p = 0.053$; Fig. 2), nor was there a difference in male yip rate on days of known female estrus compared to days when female estrus was not observed (3.33 vs. 2.69 yips/h and 4.2% vs. 95.8% of total yips, $z = -0.22$, $n = 14$ males, $p = 0.83$).

Hypothesis 2: yip vocalization

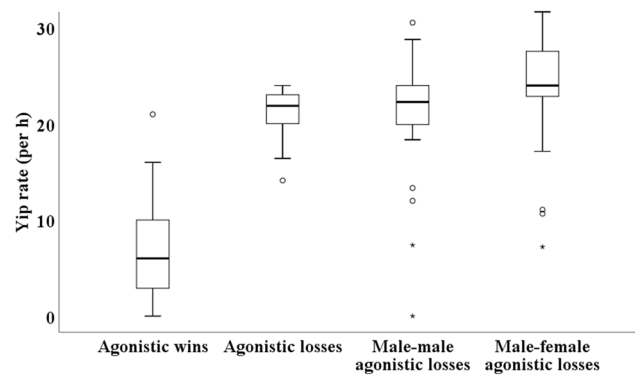There was a significant negative relationship between yip vocalization rate and dominance rank ($p = 0.02$; Table 2),

with yip calls uttered at higher rates by lower-ranking males (Fig. 3). However, there was no relationship between yip rate and age (Table 2). Mean yip rate did not show significant relationships across social groups ($H_4 = 2.80$, $n = 31$ males, $p = 0.59$).

Hypothesis 1: cackle vocalization

Like the yip vocalization, the cackle vocalization was uttered at significantly higher mean rates during sampling intervals containing agonism compared to sampling intervals without agonism (2.24 vs. 0.02 cackles/h and 92.6% vs. 7.4% of total cackles, $z = -4.7$, $n = 31$ males, $p < 0.001$; Fig. 4), during male-male agonistic contexts compared to sampling intervals without agonism (1.93 vs. 0.02 cackles/h and 43.7% vs. 7.4% of total cackles, $z = -3.9$, $n = 31$ males, $p < 0.001$; Fig. 4), and during male–female agonistic contexts compared to sampling intervals without agonism (3.02 vs. 0.02 cackles/h and 48.1% vs. 7.4% of total cackles, $z = -4.5$, $n = 31$ males, $p < 0.001$; Fig. 4). Of total cackles, the remaining 0.8% occurred during agonism with individuals that could not be identified as male or female. The cackle vocalization was also uttered at higher rates during losing agonistic interactions compared to during winning agonistic interactions [2.74 vs. 0.10 cackles/h and 99.2% vs. 0.8% of cackles during agonism (46.4% of cackles during agonistic losses to males, 52% during agonistic losses to females, 0.8% during agonistic losses to individuals that could not be identified as male or female, and 0.8% during agonistic wins against males), $z = -4.6$, $n = 31$ males, $p < 0.001$; Fig. 5] and during losing male-male agonistic interactions compared to during winning interactions (2.89 vs. 0.10 cackles/h and 98.3% vs. 1.7% of cackles during male-male agonism, $z = -3.9$, $n = 31$

Table 2 Linear regression values for male ring-tailed lemur (*L. catta*) vocalization rates in relation to dominance index and age class

Vocalization name	Characteristic	Unstandardized β	SE	t-value	p-value
Yip	Dominance index	− 0.01	0.00	− 2.48	0.02*
	Age class	0.20	0.14	1.48	0.15
Cackle	Dominance index	− 0.00	0.00	− 0.66	0.52
	Age class	0.09	0.05	1.66	0.11
Twitter	Dominance index	0.00	0.00	− 0.40	0.69
	Age class	− 0.00	0.02	− 0.07	0.95
Chutter	Dominance index	0.00	0.00	1.56	0.13
	Age class	−0.01	0.02	− 0.70	0.49
Plosive bark	Dominance index	0 .00	0.00	0.87	0.39
	Age class	− 0.01	0.01	− 1.04	0.31
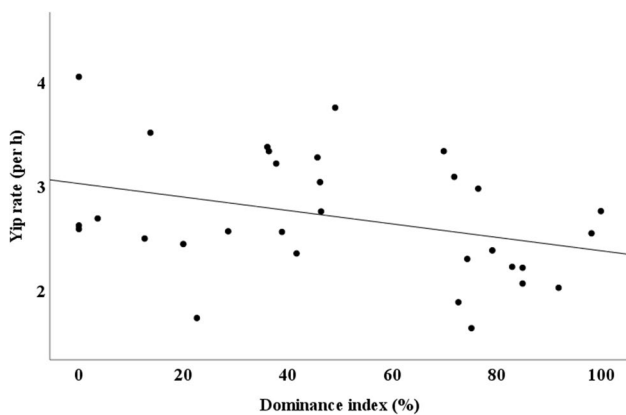
Fig. 3 Correlation between male ring-tailed lemur dominance index score and yip vocalization rate, with linear regression. Males with lower dominance ranks uttered yip vocalizations at higher rates ($p=0.02$). *Individual dots* represent individual males
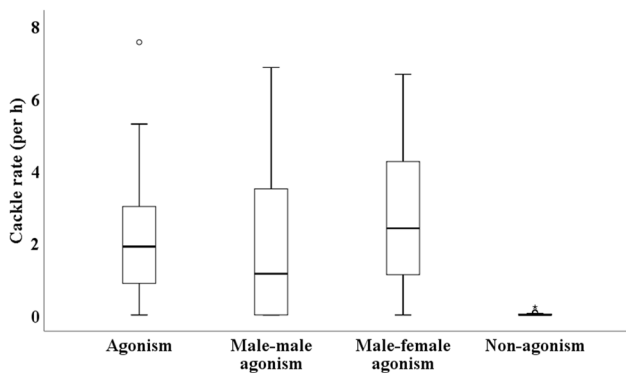
Fig. 4 Male cackle rate during sampling intervals with agonism versus during intervals without agonism. Mean cackle rate was significantly higher during agonistic contexts ($p<0.001$), during male-male agonistic contexts ($p<0.001$), and during male–female agonistic contexts ($p<0.001$) compared to intervals without agonism. *Boxes* represent inter-quartile ranges, *lines* represent median values, *whiskers* represent maximum and minimum values, *white circles* represent outliers, and the *star* represents an extreme outlier
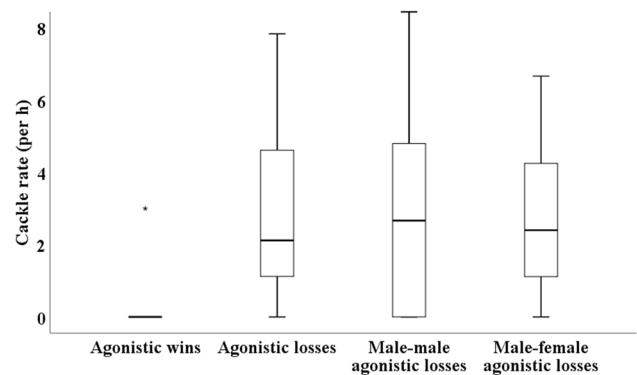

Fig. 5 Male cackle rate during agonistic wins versus during agonistic losses. Compared to agonistic wins, mean cackle rate was significantly higher during agonistic losses ($p<0.001$), and during male-male agonistic losses ($p<0.001$). *Boxes* represent inter-quartile ranges, *lines* represent median values, *whiskers* represent maximum and minimum values, and the *star* represents an extreme outlier

males, $p<0.001$; Fig. 5). There was no significant difference in male cackle utterance when rates during male-male and male–female agonistic losses were compared [2.89 vs. 3.02 cackles/h and 46.8% vs. 52.4% of cackles during agonistic losses (the remaining 0.8% of cackles were uttered during agonistic losses to unidentified individuals), $z=−0.22$, $n=31$ males, $p=0.83$; Fig. 5], nor was there a significant difference in male cackle rate on known female estrus days compared to days when female estrus was not observed (0.33 vs. 0.22 cackles/h and 10.4% vs. 89.6% of total cackles, $z=−0.85$, $n=14$ males, $p=0.40$).

Hypothesis 2: cackle vocalization

There were no significant relationships between cackle rate and male dominance rank or between cackle rate and age (Table 2). Mean cackle rate did not show significant relationships across social groups ($H_4=2.75$, $n=31$ males, $p=0.6$).

Hypothesis 1: twitter vocalization

Like the yip and cackle vocalizations, the twitter vocalization was uttered at significantly higher mean rates during agonistic contexts compared to contexts without agonism (0.46 vs. 0.01 twitters/h and 79.3% vs. 20.7% of total twitters, $z = -3.4$, $n = 31$ males, $p = 0.001$; Fig. 6), during male-male agonistic contexts compared to sampling intervals without agonism (0.48 vs. 0.01 twitters/h and 41.4% vs. 20.7% of total twitters, $z = -2.8$, $n = 31$ males, $p = 0.005$; Fig. 6), and during male–female agonistic contexts compared to sampling intervals without agonism (0.65 vs. 0.01 twitters/h and 37.9% vs. 20.7% of total twitters, $z = -2.8$, $n = 31$ males, $p = 0.005$; Fig. 6). The twitter vocalization was also uttered at higher rates during losing agonistic interactions compared to during winning agonistic interactions [0.56 vs. 0.02 twitters/h and 95.7% vs. 4.3% of twitters during agonism (47.8% of twitters during agonistic losses to males, 47.8% during agonistic losses to females, and 4.4% during agonistic wins against males), $z = -3.3$, $n = 31$ males, $p = 0.001$; Fig. 7], and during losing male-male agonistic interactions compared to during winning interactions (0.59 vs. 0.02 twitters/h and 91.7% vs. 8.3% of twitters during male-male agonism, $z = -2.8$, $n = 31$ males, $p = 0.006$; Fig. 7). However, there was no significant difference in male twitter utterance when rates during male-male and male–female agonistic losses were compared (0.59 vs. 0.65 twitters/h and 50% vs. 50% of twitters during agonistic losses, $z = -0.37$, $n = 31$ males, $p = 0.71$; Fig. 7), nor was there a significant difference in male twitter rate on known female estrus days compared to days when female estrus was
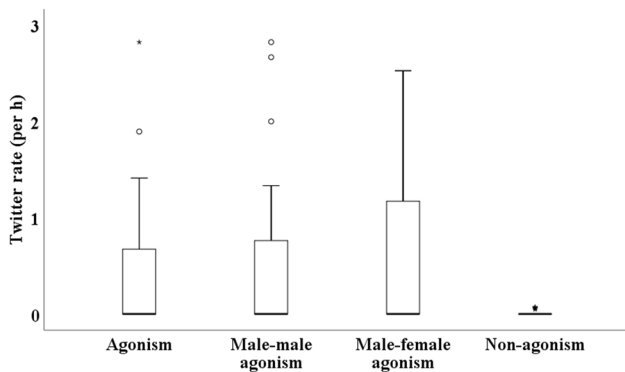

Fig. 6 Male twitter rate during sampling intervals with agonism versus during intervals without agonism. Mean twitter rate was significantly higher during agonistic contexts ($p = 0.001$), during male-male agonistic contexts ($p = 0.005$), and during male–female agonistic contexts ($p = 0.005$) compared to intervals without agonism. *Boxes* represent inter-quartile ranges, *lines* represent median values, *whiskers* represent maximum and minimum values, *white circles* represent outliers, and *stars* represent extreme outliers
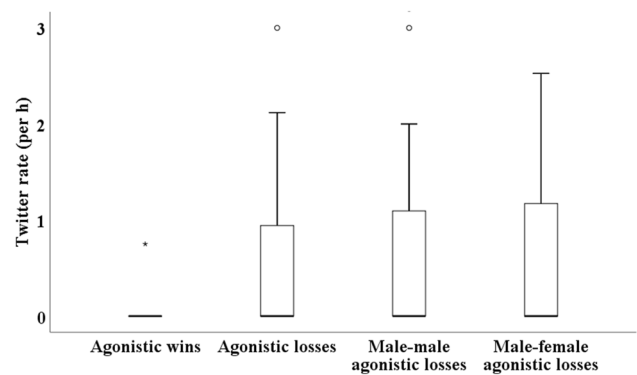

Fig. 7 Male twitter rate during agonistic wins versus during agonistic losses. Compared to agonistic wins, mean twitter rate was significantly higher during agonistic losses ($p = 0.001$), and during male-male agonistic losses ($p = 0.006$). *Boxes* represent inter-quartile ranges, *lines* represent median values, *whiskers* represent maximum and minimum values, *white circles* represent outliers, and the *star* represents an extreme outlier

not observed (0.06 vs. 0.04 twitters/h and 3.2% vs. 96.8% of total twitters, $z = -1.18$, $n = 14$ males, $p = 0.24$).

Hypothesis 2: twitter vocalization

There were no significant relationships between twitter vocalization rate and dominance rank or between twitter rate and age (Table 2). Mean twitter rate did not show significant relationships across social groups ($H_4 = 4.88$, $n = 31$ males, $p = 0.3$).

Hypothesis 1: chutter vocalization

Mean chutter rate was higher during agonism compared to contexts without agonism (0.20 vs. 0.01 chutters/h and 66.7% vs. 33.3% of total chutters, $z = -2.1$, $n = 31$ males, $p = 0.04$), but was not significantly different during male-male agonism compared to contexts without agonism (0.22 vs. 0.01 chutters/h and 38.9% vs. 33.3% of total chutters, $z = -1.7$, $n = 31$ males, $p = 0.09$) or during male–female agonism compared to contexts without agonism (0.19 vs. 0.01 chutters/h and 27.8% vs. 33.3% of total chutters, $z = -1.2$, $n = 31$ males, $p = 0.23$). Mean chutter rate showed no difference during losing and winning agonistic interactions [0.15 vs. 0.72 chutters/h and 50% vs. 50% of chutters during agonism (8.3% of chutters during agonistic losses to males, 41.7% during agonistic losses to females, and 50% during agonistic wins against males), $z = -1.6$, $n = 31$ males, $p = 0.12$], but chutters were uttered at significantly lower rates during losing male-male agonistic interactions compared to during winning agonistic interactions (0.05 vs. 0.72 chutters/h and 14.3% vs. 85.7% of chutters during male-male agonism, $z = -2.0$, $n = 31$ males, $p = 0.04$). Chutters

were not uttered at significantly different rates during losing male-male or male–female agonistic interactions (0.05 vs. 0.19 chutters/h and 16.7% vs. 83.3% of chutters during agonistic losses, $z = -1.1$, $n = 31$ males, $p = 0.27$), and no chutter vocalizations were recorded during focal samples on days of known female estrus.

When further tested, chutter vocalizations were used during foraging (47.1% of chutters), vigilance (29.4% of chutters), travelling (17.6% of chutters), and allogrooming behaviours (5.9% of chutters), but were not uttered at different rates across these behavioural contexts ($F_{3,90} = 0.43$, $p = 0.73$). Chutter vocalizations were used during inter-group encounters, but were not uttered at higher or lower rates during inter-group encounters compared to sampling periods without inter-group encounters (0.01 vs. 0.02 chutters/h and 29.4% vs. 70.6% of chutters, $z = -0.4$, $n = 31$ males, $p = 0.67$).

Hypothesis 2: chutter vocalization

There were no significant relationships between chutter vocalization rate and dominance rank or between chutter rate and age (Table 2). Mean chutter rate did not show significant relationships across social groups ($H_4 = 4.45$, $n = 31$ males, $p = 0.35$).

Hypothesis 1: plosive bark vocalization

The plosive bark vocalization showed no difference in rate when used in agonistic contexts as opposed to non-agonistic behavioural contexts (0.07 vs. 0.03 plosive barks/h and 13.3% vs. 86.7% of total plosive barks, $z = -1.4$, $n = 31$ males, $p = 0.15$), or during male-male agonistic contexts as opposed to non-agonistic contexts (0.11 vs. 0.03 plosive barks/h and 13.3% vs. 86.7% of total plosive barks, $z = -1.4$, $n = 31$ males, $p = 0.15$), but was used at significantly lower rates during male–female agonistic contexts as opposed to non-agonistic contexts (0 vs. 0.03 plosive barks/h and 0% vs. 86.7% of total plosive barks, $z = -2.9$, $n = 31$ males, $p = 0.003$). The plosive bark showed no significant differences in rate when used in losing or winning agonistic interactions [0.07 vs. 0 plosive barks/h and 100% vs. 0% of plosive barks during agonism (100% of plosive barks during agonistic losses to males, 0% during agonistic losses to females, and 0% during agonistic wins against males), $z = -1.3$, $n = 31$ males, $p = 0.18$] or when used in losing or winning male-male agonistic interactions (0.13 vs. 0 plosive barks/h and 100% vs. 0% of plosive barks during male-male agonism, $z = -1.3$, $n = 31$ males, $p = 0.18$). Similarly, plosive barks were not uttered at significantly different rates during losing male-male or male–female agonistic interactions (0.13 vs. 0 plosive barks/h and 100% of plosive barks during agonistic losses, $z = -1.3$, $n = 31$ males,

$p = 0.18$), and no plosive bark vocalizations were recorded during focal samples on days of female estrus.

When further tested, plosive bark vocalizations were uttered during foraging (40% of plosive barks), vigilance (26.7% of plosive barks), travelling (20% of plosive barks), and resting behaviours (13.3% of plosive barks), but were not uttered at different rates across these behavioural contexts ($F_{3,90} = 0.66$, $p = 0.58$). Males did not utter plosive bark vocalizations during any inter-group encounters.

Hypothesis 2: plosive bark vocalization

There were no significant relationships between plosive bark vocalization rate and dominance rank or between plosive bark rate and age (Table 2). However, mean male plosive bark rate differed significantly across social groups ($H_4 = 16.3$, $n = 31$ males, $p = 0.003$; Fig. 8). Male plosive bark rate in the purple group was significantly higher than in all other social groups (0.07 plosive barks/h, SD = 0.04, range = 0–0.14, $n = 8$ males; purple vs. green group, $p = 0.002$, purple vs. orange group, $p = 0.001$, purple vs. red group, $p = 0.006$, purple vs. yellow group, $p = 0.02$; Fig. 8). Other groups did not differ from one another in mean plosive bark rate.

Discussion

Hypothesis 1 and hypothesis 2: yip vocalization

The results indicated strong support for the hypothesis that the yip vocalization is an agonistic signal (hypothesis 1), with higher rates during overall agonism as well as during male-male and male–female agonism compared to other behavioural contexts (Fig. 1). The yip was also uttered at
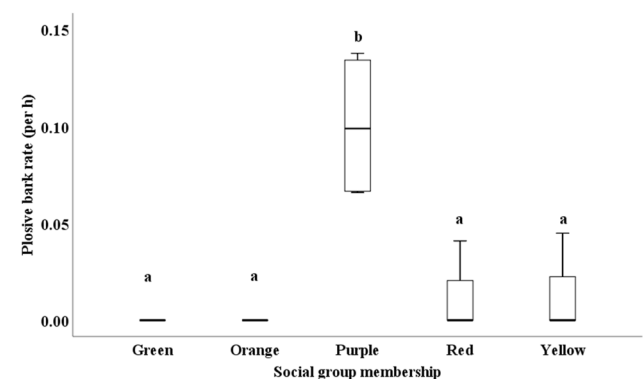

Fig. 8 Male plosive bark rate across social groups at Beza Mahafaly Special Reserve ($p = 0.003$). *Boxes* represent inter-quartile ranges, *lines* represent median values, and *whiskers* represent maximum and minimum values. Means indicated by *different letters* are significantly different according to pairwise *t*-tests

significantly higher rates during losing agonistic encounters compared to winning encounters and during losing male-male agonistic encounters compared to winning encounters (Fig. 2), suggesting that the yip is a vocalization used to indicate submission, as predicted. It was used consistently as a submissive vocalization across the study period, including during agonistic encounters with both males and females and on days of known female estrus. The findings also indicated support for the individual differences hypothesis (hypothesis 2), with males with lower dominance ranks making yip calls at higher rates than males with higher dominance ranks (Fig. 3), although male age showed no relationship with yip call usage (Table 2). The yip was therefore used consistently by lower-ranking males of all ages to signal submission during agonistic encounters with both males and females.

For the female-dominant ring-tailed lemur, all males are lower-ranking than all adult females (Jolly 1966; Sussman 1992; Sauther 1993). This means that the highest-ranking males would be expected to utter submissive vocalizations like yips toward females, while lower-ranking males would be expected to utter submissive yips to both females and higher-ranking males. As generally low-ranking group members, males would therefore be expected to utter submissive vocalizations such as the yip at high rates, with males that are at the bottom of the male-specific dominance hierarchy expected to utter submissive vocalizations at the very highest rates. I found that males uttered yips at comparable rates during losing agonistic interactions with males and with females (Fig. 2), suggesting that this signal indicates submission in both male-male and male–female interactions in this species. Males may utter yip vocalizations at higher rates to signal peaceful intent and to encourage increased tolerance from both higher-ranking males and females in their social groups, as has been suggested for the affiliative hmm call in the ring-tailed lemur (Bolt and Tennenhouse 2017). If males utter submissive yip vocalizations towards approaching higher-ranking individuals, this may lessen the chances that these high-ranking individuals will cuff the caller or otherwise engage in physical fighting. It is advantageous for low-ranking males to minimize their chances of receiving agonism whenever possible, since agonism is stressful and can result in injury or even death (Beehner et al. 2005; Pride 2005; Gould and Ziegler 2007; Tennenhouse 2016; Tennenhouse et al. 2017). The usage of some vocalizations in lessening a caller's chances of receiving violence from a conspecific has also been suggested in other primate species, including the wedge-capped capuchin [*Cebus olivaceus* (Robinson 1982)], the stump-tailed macaque [*Macaca arctoides* (Bauers 1993)], the chacma baboon (Cheney et al. 1995), the red-fronted lemur [*Eulemur rufifrons* (Pflüger and Fichtel 2012)], and the ring-tailed lemur [hmm call (Bolt and Tennenhouse 2017)]. The yip vocalization may have similar

behavioural usage as a submissive agonistic call in the male ring-tailed lemur.

Hypothesis 1 and hypothesis 2: cackle and twitter vocalizations

The results similarly indicated strong support for the cackle and twitter vocalizations being used as submissive signals during agonism (hypothesis 1), but their usage appears to be more dependent on behavioural context than usage of the yip vocalization. The cackle and twitter were used during agonism, including male-male and male–female agonism, at significantly higher rates compared to non-agonism (Figs. 4, 6). They were also uttered at higher rates during losing agonistic interactions and losing male-male agonistic interactions compared to winning interactions (Figs. 5, 7); however, contrary to predictions, there were no differences in cackle or twitter rates between individuals with different dominance ranks and ages (hypothesis 2; Table 2), suggesting that males of all ranks and ages consistently utter these vocalizations. Taken together, these results suggest that cackle and twitter vocalizations are situation-dependent submissive signals, used by both high- and low-ranking males at times when they are losing agonistic interactions to both males and females. Similarly to the yip vocalization, the cackle and twitter vocalizations were uttered at comparable rates during losing agonistic interactions with both males and females (Figs. 4, 6), suggesting that these signals generally indicate submission within both male-male and male–female agonistic encounters in this species.

The findings for both cackle and the twitter usage can be understood in light of male ring-tailed lemur behavioural adaptations. While the male dominance hierarchy is largely stable for much of the year in the ring-tailed lemur (Jolly 1966), it is unstable during the mating season each April–May in Madagascar, when the male-male agonism rate increases and males fight one another for sexual access to estrous females (Budnitz and Dainis 1975; Koyama 1988; Sauther 1991; Gould 1994; Gould and Zeigler 2007; Parga 2009; Walker-Bolton 2017). Because females mate with multiple males from both within and outside their social groups, temporary male rank reversals often occur during female estrus, allowing males across varying dominance ranks the chance to mate (Jolly 1966; Van Horn and Resko 1977; Taylor and Sussman 1985; Sussman 1992; Parga 2006; Walker-Bolton 2017). The 4-month study period encompassed the mating season, and males likely uttered both cackle and twitter vocalizations to show submission to other males in agonistic interactions during such periods of rank instability. Although the cackle and twitter were not uttered at higher rates on known estrus days, both vocalizations were used consistently throughout the study period including during female estrus, and were used routinely in

submissive interactions with both males and females. This may help explain why the cackle and twitter were consistently uttered during losing agonistic interactions and seemed to indicate submission, yet were not uttered at higher rates by lower-ranking males.

Hypothesis 1 and hypothesis 2: chutter vocalization

As predicted, the results indicated that chutter vocalizations were uttered at higher rates during agonism compared to non-agonistic contexts (hypothesis 1), but this relationship did not hold when chutter rates during male-male and male–female agonism were compared to rates during contexts without agonism. Chutter vocalizations were used during both winning and losing agonistic interactions, and at higher rates during winning male-male interactions compared to during losing male-male interactions. These findings suggest that chutters were uttered during agonistic interactions with both males and females: during winning encounters against other males, during losing encounters with females, and less frequently during losing encounters with other males. Although chutters were not used at significantly different rates during losing male-male vs. male–female encounters, the vast majority of submissive agonistic chutters were produced during male–female interactions compared to male-male interactions (83.3% vs. 16.7% of chutters uttered during losing agonistic interactions). Past qualitative observations on chutter usage (Macedonia 1990, 1993) suggest that the chutter is a low-intensity threat vocalization directed from higher-ranking individuals towards lower-ranking individuals to reinforce the dominance hierarchy. The present study's results for chutter usage within male-male agonistic interactions support this idea, with significantly more male-male agonistic chutters uttered during winning interactions than during losing interactions against other males (85.7% vs. 14.3% of male-male agonistic chutters). However, males also vocalized a large percentage (41.7%) of overall agonistic chutters during submissive interactions with females. Males may use chutters as advertisement calls towards females, to display their health and high rank and to entice females to mate with them, as has been suggested for the male-specific agonistic squeal vocalization in the ring-tailed lemur (Bolt 2013a, 2020b). However, unlike the squeal vocalization rate, the chutter vocalization rate showed no relationship with male dominance rank or age (hypothesis 2; Table 2) and was not higher on known estrus days, as would be expected for a vocalization used to advertise male attributes to females. Taken together, the results suggest that the chutter is an agonistic vocalization in the male ring-tailed lemur, but is used across both winning and losing interactions, particularly when an individual is winning against another male or losing against a female.

The chutter was additionally used during foraging, vigilance, travelling, and allogrooming behaviours, but was not uttered at a higher rate in any particular social context. Although chutter vocalizations were produced during intergroup encounters, which suggests that they could play some role in territory or resource defence in this species (Mertl-Millhollen et al. 1979; Gould et al. 2003), chutters were not uttered at higher rates when other lemur groups were present and within visual range compared to other sampling periods. Overall, these findings suggest that, in addition to primary usage during agonism, the chutter vocalization is used across behavioural contexts by males of all ages and dominance ranks including during inter-group encounters.

Hypothesis 1 and hypothesis 2: plosive bark vocalization

Contrary to predictions, rates of plosive bark vocalizations were not higher during agonism, aggression, or submission (hypothesis 1). Instead, plosive barks were uttered across both agonistic and non-agonistic contexts. The plosive bark was not produced by males during male–female agonistic interactions, was not heard during focal sampling on known estrus days, and was not uttered during inter-group encounters, further suggesting a lack of usage as an agonistic vocalization. Male dominance rank and age also had no relationship with plosive bark rate (hypothesis 2; Table 2), although the plosive bark was used at higher rates by one social group (purple) compared to the other social groups (Fig. 8). The plosive bark was used during foraging, vigilance, travelling, and resting behaviours, but was not used at higher rates during any single activity. Overall, the results suggest that the plosive bark was used across behavioural contexts by males of all ages and dominance ranks, but was not used primarily as an agonistic vocalization.

The result that one social group (purple) had higher rates of plosive bark utterance compared to other groups is suggestive of the idea that the plosive bark may play some role as an anti-predator vocalization. This idea is further supported by an observation by Macedonia (1990, 1993), who noticed lemurs using the plosive bark towards perched raptors in a semi-free ranging captive environment. Past study at Beza Mahafaly Special Reserve (Bolt et al. 2015) showed that the purple group at this site ranged entirely within a forest area with higher predator abundance than other study groups, and also uttered higher rates of anti-predator yap and shriek vocalizations. This higher predation pressure influenced lemurs, with males making anti-predator vocalizations at higher rates in areas where predators were more likely to be observed (Bolt et al. 2015). The plosive bark was uttered at higher rates by the purple group in this higher-risk forest area (Bolt et al. 2015), and so may have similarly been used as an anti-predator vocalization. However, it was not used

at higher rates during vigilance behaviour than in other contexts, as would be expected for an anti-predator vocalization. Although this study's results did not clearly support anti-predator usage of the plosive bark, future research should further evaluate its use in anti-predator interactions in the wild, including through experiments using vocalization playbacks and predator models.

Conclusions

Overall, I found that of the five vocalizations tested, the yip, cackle, and twitter calls were used as agonistic submissive vocalizations for the male ring-tailed lemur, the chutter call was used as both an aggressive and submissive agonistic vocalization for the male ring-tailed lemur, and the plosive bark call was used across behavioural contexts but not primarily during agonism (hypothesis 1). When used during agonism, yip, cackle, and twitter vocalizations did not show rate differences when used in male-male vs. male–female interactions, suggesting that these vocalizations indicate agonistic submission during interactions with both sexes. The rate of the chutter vocalization was higher during agonism compared to non-agonism and during winning compared to losing during male-male agonistic interactions, suggesting that the chutter may indicate agonistic aggression when directed towards males. There was also a statistically non-significant tendency for the chutter to be used more often during losing agonistic interactions against females compared to during losing interactions against males, suggesting that the chutter may indicate agonistic submission when directed towards females. However, further research is needed to test whether the chutter vocalization has differential usage when directed towards males vs. females. Low-ranking males uttered yip vocalizations at higher rates, although there was no relationship between yip rate and male age, or between dominance rank, age, or calling rate for the other four vocalizations (hypothesis 2). The yip, cackle, twitter, chutter, and plosive bark were therefore used by males of all ages. The function of the plosive bark vocalization should be further examined in future research, with plosive bark use investigated during predator encounters.

Data were collected on yip, cackle, twitter, chutter, and plosive bark vocalizations over a 4-month sampling period encompassing the annual mating season, but were not examined during other seasons, such as during male migration or the austral summer. Studying vocalization use at other times of the year may reveal a broader range of adaptive functions in different contexts. Additionally, vocalization rates were likely underestimated due to the use of one-zero sampling during data collection, so should not be compared to those from studies on other primate species where rates were determined from all calls produced. This study was also focused on male usage of five vocalizations, which may differ from female usage of these vocalizations. Finally, twitter, chutter, and plosive bark vocalizations had low rates of utterance (Table 1), so may have been uttered at increased rates over a longer study period. However, previous reports (Jolly 1966; Macedonia 1990, 1993) found these vocalizations to be uttered infrequently overall (twitter), infrequently by males (chutter), or infrequently by adults (plosive bark), suggesting that a longer study period may not have yielded higher rates or different results.

As the ring-tailed lemur has a large vocal repertoire including several different vocalizations identified as agonistic (Andrew 1963; Jolly 1966; Macedonia 1990, 1993; Pereira and Kappeler 1997; Bolt 2013a , c, 2014, this study), it is important to study the range of behavioural usage for each vocalization as a way of better understanding patterns of signal evolution in social primates. Such investigations can also provide insight into why this species may have evolved so many different types of agonistic vocalization. Of the ring-tailed lemur vocalizations evaluated in this study (yip, cackle, twitter, chutter, plosive bark), four show evidence of being used primarily during agonism (yip, cackle, twitter, chutter), while one does not (plosive bark). The different acoustic features of these different agonistic vocalizations (Macedonia 1990, 1993) may facilitate their audibility for other group members in different social contexts; for example, among ring-tailed lemur agonistic submissive vocalizations, yip and cackle vocalizations have higher amplitudes (i.e. are louder) than twitter vocalizations, which means that they can likely be heard by conspecifics located at greater distances from the focal animal. Additionally, the different agonistic calls used by the focal animal may communicate the severity of agonistic interaction, with, as suggested by Macedonia (1993), more intense physical agonistic interactions (e.g. cuff/jump away) using higher-arousal vocalizations (e.g. chutter), and less intense, non-physical agonistic interactions (e.g. stare/look away) using lower-arousal vocalizations (e.g. yip). While the present study did not differentiate between more and less intense types of agonistic interaction during data collection and so could not relate the severity of agonistic interaction to the type of agonistic vocalization used, future research should do so. Understanding how dominance relationships and agonistic interactions are mediated by agonistic vocal signals in the ring-tailed lemur helps us to better discern the range of selective pressures shaping the vocal repertoires of group-living strepsirrhines, and enables us to better understand why this species has evolved multiple different types of agonistic vocalization.

Compliance with ethical standards

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