

The Relationship Between Dominance and Vocal  
Communication in the Male Ring-Tailed Lemur (*Lemur catta*)

by

Laura McLachlan Bolt

A thesis submitted in conformity with the requirements  
for the degree of Doctor of Philosophy

Department of Anthropology  
University of Toronto

© Copyright by Laura McLachlan Bolt, 2013

# The Relationship Between Dominance and Vocal Communication in the Male Ring-Tailed Lemur (*Lemur catta*)

Laura McLachlan Bolt

Doctor of Philosophy

Department of Anthropology  
University of Toronto

2013

## **Abstract**

Sex-specific calls are used in male-male agonistic encounters and male-female courtship in many animal species. The ring-tailed lemur (*Lemur catta*) is a gregarious Malagasy strepsirhine with twenty-two distinct vocalizations for adults, including two male-specific vocalizations and an additional vocalization with male-specific functions: the howl, the squeal, and the purr. Proposed intra-sexual agonistic functions for these three vocalizations have never been empirically tested. This study's purpose was to investigate the functions of howling, squealing, and purring in the ring-tailed lemur, and to assess the relationships between the rates of these vocalizations and male dominance. From March to July 2010, I collected 600 hours of total data and 480 hours of focal data on male ring-tailed lemurs aged three and older at Beza Mahafaly Special Reserve, Madagascar. I observed each male continuously for 30 minutes at a time and noted behaviours including all vocalizations and all agonism using one-zero sampling at 2.5-min intervals. I calculated male dominance rank and vocalization rates from these data. My results indicated that male dominance rank is correlated with male purring rate and with squealing rate, but not with howling rate. Male purring rate increased during intra-sexual agonism and was associated with aggression in agonistic encounters. Squealing rate increased during male-male agonism and indicated both aggression and submission in male-male encounters. Howling rate increased

during inter-group encounters and a greater number of males participated in multi-male howling choruses when non-group members were present. Purring and squealing are agonistic vocalizations and used in male-male agonism in the ring-tailed lemur, while howling is used in inter-group encounters.

## **Acknowledgments**

I am grateful to many people and organizations for their help with this project. Firstly, I thank my supervisory committee for their contributions. I am very grateful to my academic supervisors, Shawn Lehman and Joyce Parga. I am aware of how much support and help they each provided me with throughout this process, and I thank them sincerely for the numerous ways in which they contributed to my dissertation. Due to their helpful feedback and great suggestions for improvement on each of my chapters, I completed a stronger doctoral project. I thank Esteban Parra, Michael Schillaci, and Dan Sellen for their feedback on my written dissertation and thoughtful questions during my defence. I am grateful to Drew Rendall for serving as my external examiner, and for his various helpful suggestions. I also thank the faculty and staff in the University of Toronto anthropology department for all of their help throughout my PhD program, particularly Natalia Krencil and Jack Sidnell.

I am appreciative of all of my fellow graduate students and other colleagues from University of Toronto's anthropology department. Your help and feedback about my project has been invaluable, while your friendship and comraderie has contributed immeasurably to my graduate student experience. In particular, I thank Iulia Bădescu, Katherine Bannar-Martin, Ryan Burke, Brooke Crowley, Cadell Last, Keriann McGoogan, Catherine Merritt, Mike Reid, Abigail Ross, Travis Steffens, Erica Tennenhouse, Kim Valenta, and Amber Walker-Bolton. The scintillating conversations and copious e-mails of the anthropology "Meet 'N Eat" group have kept me well-entertained over the years, and I thank Rastko Cvekic, Daniella Jofre, Dean Langan, Eugenia Tsao and all the others most sincerely for their food, fun, and friendship.

Beyond the University of Toronto, I am grateful to many influential teachers from all stages of my education. I thank them all, and in particular acknowledge Sinikka Valila Chantler, Muriel Kent, Brenda Ravenscroft, Nancy Stormes, and Mary Lousie and David A. White.

I was fortunate to have the opportunity to undertake field research in Madagascar for this dissertation. For their great support and facilitation of my project in Madagascar, I thank Andry Randrianandrasana and Jacky Ibrahim Antho Youssouf at the Beza Mahafaly Special Reserve. My appreciation goes to Jeannin Rainavanosy and Joel Ratsirarson of the Département des Eaux et Forêts de l'Ecole Supérieure des Sciences Agronomiques (ESSA) and Madagascar National

Parks (MNP) for permission to work at Beza Mahafaly, and to Madagascar Institut pour la Conservation des Ecosystèmes Tropicaux (MICET) staff, including director Benjamin Andriamihaja for their help with logistics. I thank Elahavelo, Efitiria, Enafa, Edouard, Ralaevo, and Monja of the Beza Mahafaly Ecological Monitoring team for field assistance, and Lala, Delaprairie, Voola, Etala, Efmoeza, Veloke and the rest of the reserve staff for their aid and kindness during my stay. Teague O'Mara and his assistants Ayden Sherritt and Cathriona Hickey provided invaluable help with my orientation at Beza Mahafaly. I am also grateful to Stephanie Meredith for her advice about what to expect at Beza. Finally, Michelle Sauther and Frank Cuozzo kindly provided me with ring-tailed lemur age data and have encouraged my work at Beza Mahafaly, for which I'm extremely grateful.

I had the opportunity to complete pilot research for this project on St. Catherines Island, USA. I thank the late president Frank Larkin, the Larkin and Smith families, and the SCI foundation board for allowing researchers to study both native and non-native wildlife on SCI. I am very grateful to the St. Catherines Island Foundation for their permission to conduct this research, as well as for providing me with housing and transportation while on the island. The Wildlife Conservation Society staff of the Wildlife Survival Centre on SCI aided my research, and I am grateful to WCF staff members and Timothy Keith-Lucas for their help. I also thank the SCI staff, especially superintendant Royce Hayes. They were all instrumental in facilitating my project. Finally, I thank Anna McFaul for providing me with field assistance while on SCI.

Shannon Digweed and Drew Rendall provided me with invaluable field experience early in my PhD, and I thank them for allowing me to assist in their red squirrel project. They introduced me to acoustic research and gave me practical experience in using the field techniques common to animal behaviour study, for which I am very grateful.

This dissertation was funded by an Alexander Graham Bell Canada Graduate Scholarship (CGS-D) from the Natural Sciences and Engineering Research Council of Canada (NSERC), Ontario Graduate Scholarships (OGS), the American Museum of Natural History, the Edward J. Noble Foundation, the St. Catherines Island Foundation, and various awards, fellowships, and research grants from the University of Toronto. I thank all of these funding bodies for their generous support.

My success would not have been possible without the support and encouragement of my friends and family. C.S. Lewis says, “friendship is unnecessary, like philosophy, like art... It has no survival value; rather it is one of those things which give value to survival.” I am grateful to the many good friends who have helped me in practical ways throughout this dissertation. Salina Morrow and Anya and Bob Willis provided me with housing when I first arrived in Toronto. When my 2009 field season in Madagascar was postponed due to political unrest, Susitna Banerjee generously provided me with a place to live. Several others, including Kirsten and Kevin Martin, have offered me their basements in case I need a place to live in the future. Other friends have kindly provided me with transportation, including Amy and James Allingham, Julie Johnson and Mark Chown, Paula Morritt, and Anya Willis. Ryan Janzen aided me tremendously by advising me about many technical aspects of my project and helping with logistical issues while I was at remote field sites. Others sent encouraging notes and care packages to me at my field sites, including Amy Allingham, Ryan Janzen, Ruth Kiang, and Tristan Rhys Williams. Friends including Ian Begg, Nick Collins, Ryan Janzen, Chloe Valenti, and Tristan Rhys Williams have all provided me with valuable academic and professional advice. Finally, I am privileged to have great friends near and far who have helped me to live a rich and varied life beyond academia. For their friendship and support through the years, I thank Amy and James Allingham, Susitna Banerjee and Debu Sen, Sarah Berry, Scott Brubacher, Laura Grace Conlon, Michael Chan and Maria Jose Sandi, Michelle Chan, Natalie Cheung, Nick Collins, Lelia Fry, Lisa and Mario Greco, Suzanne Grossman, Heather Hummel, Ryan Janzen, Julie Johnson and Mark Chown, Ruth and Paul Kiang, Tiffany Krahn and TJ Wry, Vincent Lai, Grayden Laing, Moray McGill, Kirsten and Kevin Martin, Paula Morritt, Salina Morrow and Kyu Shim, Angie and Jamie Nelson, Tina Roberts and Nicolas Bossile, Colleen Savage, Rachel Schmucker, Adelle Spouge, Chloe Valenti, Rebecca Walker, Marjorie and Ron Walker, Tristan Rhys Williams, Angela and Emyr Williams, Huw and Felicity Williams, Anya and Bob Willis, Jon and Nicole Wise, and anyone I have neglected to mention.

Ryan Janzen has tirelessly supported me through this dissertation, from its conception to the finished product, while his unflappable optimism has encouraged me throughout the process. He has aided me in ways too numerous and varied to list. I am deeply appreciative of his input, and thank him profusely. I am fortunate to have him in my life.

Finally, I am deeply grateful to my family. My grandparents and great-grandparents were always very supportive of my academic endeavours, and would have been very proud to see me complete a doctorate. I think of Mary Olive Cunningham, Jack Wallace Cunningham, Lucille Mabel Bolt, Douglas Kitchener Bolt, Gordon Cecil Barber, Barbara Sherwood Barber, and Nellie Astles. I also thank my extended family for their support, and especially acknowledge my brother Jonathan Bolt, who has always been proud of my academic accomplishments, and my parents, Brian and Mary-Ellen Bolt. My parents have been unflagging supporters through all stages of my education, and I owe much of my success to their fortitude. They were a huge source of encouragement through my PhD program, and I am deeply appreciative of their myriad contributions. I am fortunate to have grown up in a household where education was valued and encouraged, and to live at a time and in a place with no limits imposed on my academic achievement. I think of my brave and hard-working ancestors, who lacked the educational opportunities available to my generation. From this long line of ancestors, my parents were each the first of their forebears to graduate from university, while I am the first to earn a PhD.

This dissertation is dedicated to my parents, Brian Douglas Bolt and Mary-Ellen Bolt.

## Table of Contents

<b>Abstract</b>	<b>ii</b>
<b>Acknowledgements</b>	<b>iv</b>
<b>Table of Contents</b>	<b>viii</b>
<b>List of Tables</b>	<b>x</b>
<b>List of Figures</b>	<b>xi</b>
<b>List of Appendices</b>	<b>xiii</b>
<b>Chapter 1: Vocal Communication in the Ring-tailed Lemur</b>	<b>1</b>
Dissertation Overview	6
References	7
<b>Chapter 2: Male-specific Use of the Purr in the Ring-tailed Lemur</b>	<b>15</b>
Abstract	15
Introduction	15
Methods	25
Results	30
Discussion	31
References	34
<b>Chapter 3: The Function of Howling in the Ring-tailed Lemur</b>	<b>50</b>
Abstract	50
Introduction	50

Methods	59
Results	65
Discussion	68
References	74
<b>Chapter 4: Squealing Rate Indicates Dominance Rank in the Ring-tailed Lemur</b>	<b>88</b>
Abstract	88
Introduction	88
Methods	96
Results	103
Discussion	104
References	107
<b>Chapter 5: Conclusions and Future Directions</b>	<b>122</b>
Summary of Findings	122
Implications of my Findings and Directions for Future Study	124
References	126
<b>Appendix I</b>	<b>128</b>
<b>Appendix II</b>	<b>129</b>
<b>Appendix III</b>	<b>130</b>
<b>Copyright Acknowledgements</b>	<b>131</b>

## **List of Tables**

<b>Chapter 1: Vocal Communication in the Ring-tailed Lemur</b>	<b>1</b>
Table I. Ring-tailed lemur vocal repertoire as described by Macedonia (1990)	12
<b>Chapter 2: Male-specific Use of the Purr in the Ring-tailed Lemur</b>	<b>15</b>
Table I. Male ring-tailed lemur study individuals at Beza Mahafaly Special Reserve, March-July 2010	44
<b>Chapter 3: The Function of Howling in the Ring-tailed Lemur</b>	<b>50</b>
Table I. Male ring-tailed lemur study individuals at Beza Mahafaly Special Reserve, March-July 2010	81
<b>Chapter 4: Squealing Rate Indicates Dominance Rank in the Ring-tailed Lemur</b>	<b>88</b>
Table I. Male ring-tailed lemur study individuals at Beza Mahafaly Special Reserve, March-July 2010	115
<b>Chapter 5: Conclusions and Future Directions</b>	<b>122</b>

## List of Figures

<b>Chapter 1: Vocal Communication in the Ring-tailed Lemur</b>	<b>1</b>
<b>Chapter 2: Male-specific Use of the Purr in the Ring-tailed Lemur</b>	<b>15</b>
Figure 1: Sound spectrogram of a male ring-tailed lemur purr	45
Figure 2: Mean male ring-tailed lemur purring rate per hour during periods of male-male agonism versus male purring rate during times without agonism	46
Figure 3: Male ring-tailed lemur purr allocation during male-male agonism and outcome of the agonistic interaction	47
Figure 4: Correlation between male ring-tailed lemur dominance index score and mean male purring rate, with linear regression	48
Figure 5: Correlation between male ring-tailed lemur dominance index score and mean rate for purrs given during male-male agonism, with linear regression	49
<b>Chapter 3: The Function of Howling in the Ring-tailed Lemur</b>	<b>50</b>
Figure 1: Sound spectrogram of a male ring-tailed lemur howl bout	82
Figure 2: Sound spectrogram of a ring-tailed lemur howling chorus, with howls from two males	83
Figure 3: Correlation between male ring-tailed lemur dominance index score and mean male howling rate, with polynomial regression	84
Figure 4: Correlation between male ring-tailed lemur dominance index score and mean number of howls in a howling bout, with polynomial regression	85
Figure 5: Male howling rate per hour during periods when non-group ring-tailed lemurs were present versus male howling rate when no non-group members were present	86
Figure 6: Mean male ring-tailed lemur howling rate on days of known female estrus versus mean howling rate on days without known estrus	87

<b>Chapter 4: Squealing Rate Indicates Dominance Rank in the Ring-tailed Lemur</b>	<b>88</b>
Figure 1: Sound spectrogram of male ring-tailed lemur squeal	116
Figure 2: Correlation between male ring-tailed lemur dominance index score and mean male squealing rate, with linear regression	117
Figure 3: Correlation between male ring-tailed lemur dominance index score and mean rate for squeals given during male-male agonism, with linear regression	118
Figure 4: Mean male ring-tailed lemur squealing rate per hour during periods of male-male agonism versus male squealing rate during times without agonism	119
Figure 5: Mean male squealing rate per hour during male-male agonistic wins versus squealing rate during male-male agonistic losses	120
Figure 6: The frequency of observed versus expected dyadic squealing incidents involving ring-tailed lemur males separated by varying numbers of positions in the dominance rank hierarchy	121
<b>Chapter 5: Conclusions and Future Directions</b>	<b>122</b>

## **List of Appendices**

<b>Appendix I: Individual ring-tailed lemur purring rates and standard deviations</b>	<b>128</b>
<b>Appendix II: Individual ring-tailed lemur howling rates and standard deviations</b>	<b>129</b>
<b>Appendix III: Individual ring-tailed lemur squealing rates and standard deviations</b>	<b>130</b>

## **Chapter 1: Vocal communication in the ring-tailed lemur**

### **Sexual selection and male vocalizations**

In group-living animals, social relationships are mediated by a variety of signals (Bradbury and Vehrencamp, 1998). While many signals are used by both sexes, vocal signals related to mate attraction, copulation, and competition are often male-specific and have functions related to sexual selection (Andersson, 1994; Darwin, 1871). Sexual selection is a form of natural selection which operates between individuals of the same sex as they compete against one another for access to copulatory partners, and between members of the opposite sex as individuals make themselves attractive to potential mates (Darwin, 1871). According to the predictions of sexual selection theory, male vocalizations are thought to display individual strength, health, genetic quality, and suitability as an inseminator to females, while females are thought to choose males based on the quality and quantity of their vocalizations (Darwin, 1871; Snowdon, 2004). Male vocalizations also display these qualities to other males, and show that the caller could win in a fight if challenged (Darwin, 1871). In this way, intra- and inter-sexual selection act on male vocalizations (Snowdon, 2004).

### **Male vocalization rate as an indicator of dominance rank**

Male-specific vocalizations are also known to have rates indicating individual dominance rank or fighting ability (Delgado, 2006). In male red deer (*Cervus elaphus*), high roaring rate indicates superior fighting ability (Clutton-Brock and Albon, 1979), while in male gray mouse lemurs (*Microcebus murinus*), higher rate of trill calls on days of female estrus indicates higher dominance rank (Zimmermann and Lerch, 1993), and in chacma baboons (*Papio ursinus*), dominant males produce “wahoo” calls of longer duration, at higher rates, and with higher pitch than lower ranking males (Fischer et al., 2004; Kitchen et al., 2003). In these and other animal species, dominant males produce vocal signals which work to advertise and maintain their high social status.

A dominant animal is one who wins consistently in fights and other agonistic encounters; they consistently receive submissive signals from other group members but rarely give them (Pereira, 1995). Such animals are usually privileged with respect to feeding sites, sexual access

to breeding partners, in affiliative behaviours such as grooming, and in sleeping site access (Chapman and Sussman, 2004). Dominant males are more likely to be healthy, strong, well-provisioned, and able to win at physical combat if challenged, and can therefore risk sparing the energetic investment necessary for the production of vocal signals associated with dominance (Maynard Smith and Harper, 2003; Zahavi and Zahavi, 1997). Because only healthy and robust males would be able to incur the social and production costs associated with signals indicating high rank, it is likely that vocalizations associated with dominance can be considered handicap signals and reliable indicators of an animal's fitness (Zahavi, 1975; Zahavi and Zahavi, 1997). The present study will assess the relationship between male vocalizations and dominance rank in a strepsirhine primate, the ring-tailed lemur (*Lemur catta*).

### **Background on the ring-tailed lemur**

The ring-tailed lemur is a group-living and highly social strepsirhine endemic to southern Madagascar (Jolly, 1966). It is a female-dominant species, meaning that all sexually mature females have higher dominance ranks than all males (Jolly, 1966; Sussman, 1991). The ring-tailed lemur is female philopatric and lives in troops comprised of up to twenty-seven animals (Gould et al., 2003; Jolly, 1966; Pride, 2005; Sussman, 1991). Each troop is territorial and defends a home range (Ichino and Koyama, 2006; Jolly et al., 1993; Oda, 2001). In Madagascar, the breeding season of the ring-tailed lemur is in May, with females in asynchronous estrus for between 3.25 and 24 hours each, and mating only while in estrus (Jolly, 1966; Sauther, 1991). Multi-male, multi-female mating, where both males and females copulate with multiple partners, occurs during the breeding season (Koyama, 1988; Sauther, 1991; Sussman, 1992; Taylor and Sussman, 1985).

Male ring-tailed lemurs disperse from their natal group at the age of three or four, and stay with each new group for around three years before migrating to the next (Gould, 2006; Koyama et al., 2002; Sussman, 1992). Although females are universally dominant to males, males have their own separate dominance hierarchy (Gould, 1994). There is often a single, non-natal dominant male and a clear linear dominance order amongst the other males, which is maintained through physical aggression (Budnitz and Dainis, 1975; Gould, 1994; Taylor, 1986). Male-male aggression is at its height during the annual breeding season and especially the first week of matings (Gould and Ziegler, 2007; Jolly, 1966; Koyama, 1988). The competition

between males for sexual access to females can result in near-fatal wounds or death for competing males (Gould and Ziegler, 2007; Jolly, 1966; Sauther, 1991).

Despite these potentially high costs, dominance holds many advantages for male ring-tailed lemurs (Gould, 1994; Jolly, 1966). Agonistically dominant males usually hold spatial positions of privilege within a group, commanding a place in the group's centre while resting, feeding, or foraging (Sauther, 1991). High-ranking males feed more than low-ranking males, are allowed a greater amount of high-quality foods, and have greater drinking site access (Sauther, 1993; White et al., 2007). High-ranking males are known to interact with females at greater rates and to receive earlier-mating opportunity during female estrus (Ichino and Koyama, 2006; Koyama, 1988; Parga, 2006; Sauther, 1991; Sauther and Sussman, 1993). Paternity data on captive ring-tailed lemurs suggests a first-male mating advantage (Pereira and Weiss, 1991), although further data from wild populations are needed. High status for males may translate into greater reproductive success, and therefore greater fitness. Male status in the ring-tailed lemur is advertised by signals including vocalizations (Jolly, 1966).

### **Study of ring-tailed lemur vocalizations**

Ring-tailed lemur vocalizations were first described briefly by Andrew (1963), then expanded on by Jolly (1966), who outlined the ring-tailed lemur vocal repertoire in qualitative terms in the context of her large-scale project detailing ring-tailed lemur behaviour. Throughout the 1970's and 1980's, other researchers further elucidated the contexts for ring-tailed lemur vocalizations and produced qualitative and some quantitative data about vocalization characteristics (Petter and Charles-Dominique, 1979; Sauther, 1989); however, none of these researchers focused on vocal communication.

The most comprehensive study undertaken to date on ring-tailed lemur vocalizations was that performed by Macedonia in the late 1980's (Macedonia, 1986, 1990, 1993). Macedonia described the vocalizations of the ring-tailed lemur both qualitatively and quantitatively, revealing the spectral parameters and social contexts common to each vocalization type (Macedonia, 1990, 1993). His study was undertaken from 1985-1989 in a semi- free-ranging captive environment at the Duke University Primate Center (which has since been renamed the Duke Lemur Center) (Macedonia, 1990). Through quantitative analysis, Macedonia identified

twenty-two distinct vocalizations for adult ring-tailed lemurs, two of which are male-specific, and an additional six vocalizations for infants (Macedonia, 1990, 1993; summarized in **Table 1**).

### **Goals of my study and vocalizations of interest: purr, howl, and squeal**

My study will examine the rates and uses of three vocalizations by male ring-tailed lemurs — the purr, the howl, and the squeal — and will investigate whether these vocalizations show potential to be the product of sexual selection. The purr is a short-range affiliative vocalization mainly used by adult females while grooming infants (Macedonia, 1990), but is also used by adults when allogrooming, by males when tail-marking, and by infants when being groomed (Jolly, 1966). In contrast, the howl is a tonal, long-range, male-specific call advertising the presence and location of the ring-tailed lemur troop (Jolly, 1966; Macedonia, 1993), and can be repeated ten times or more when uttered (Andrew, 1963). Males howl in response to other howls or recurring loud sounds (Andrew, 1963), in addition to changes of light and before sleeping (Jolly, 1966). Howling also occurs more frequently during the breeding season (Jolly, 1966). Finally, the squeal is a male-specific, agonistic sharp call used to assert status during male tail-waving displays (Macedonia, 1993). Males squeal when chasing inferiors who are subordinate in rank (Andrew, 1963), while tail-marking and aggressively staring towards another male (Jolly, 1966), and as a courtship display towards females (Macedonia, 1993).

Because the howl and squeal vocalizations of the ring-tailed lemur are male-specific and usually uttered by sexually mature animals (Jolly, 1966; Macedonia, 1993), they are good candidates for further investigation with reference to sexual selection theory. In addition, past research has suggested that both the howl and squeal are used in contexts of mate attraction, copulation, and/or male-male competition (Jolly, 1966; Koyama, 1988; Macedonia, 1993), which further supports the likelihood of sexual selection having acted on these vocalizations. The purr, while not male-specific, has been reported to have male-specific uses, such as during scent marking and prior to tail-waving (Jolly, 1966), which are behaviours that have been termed aggressive and related to intra-sexual agonism in male ring-tailed lemurs (Budnitz and Dainis, 1974; Gaspari and Crockett, 1984; Jolly, 1966; Mertl, 1976; Schilling, 1974). Due to this sex-specific usage in intra-sexual competition, the purr is also a good candidate for evaluation with relation to sexual selection.

## **Rationale for my study**

Macedonia's (1990) large-scale study describing the ring-tailed lemur vocal repertoire, and several studies undertaken since have elucidated many of the forms and functions of ring-tailed lemur vocalizations (Nunn, 2000; Oda, 1996, 1999, 2002). However, none of these studies have focused on the uniquely male vocalizations of ring-tailed lemurs, or addressed how male-female relationships (i.e. mating) and male-male relationships (i.e. dominance) are related to male vocal behaviour.

No previous projects have examined ring-tailed lemur vocalization rates and their relationship with individual characteristics, such as dominance rank. Although previous work has linked male dominance rank to vocalization rate in other species, including red deer, mouse lemurs, and chacma baboons (Clutton-Brock and Albon, 1979; Kitchen et al., 2003; Zimmermann and Lerch, 1993), my study is the second to measure vocalization rates and their relationship with dominance in a strepsirhine primate, and one of only a handful of studies exploring the relationship between vocalization rate and dominance in the primate order in general. My study on male ring-tailed lemur vocalizations and vocalization rate will augment existing knowledge of both strepsirhine and species-specific vocalization behaviour for the ring-tailed lemur.

Additionally, to date no quantitative vocalization studies have been undertaken on ring-tailed lemurs in the wild. According to Patel et al. (2005), "...there has never been a quantitative vocal repertoire study of any wild diurnal lemur" (p. 48). Patel et al.'s (2005) preliminary examinations of the vocal repertoire of the diademed sifaka (*Propithecus diadema*) and Bergey and Patel's (2008) examination of the greater bamboo lemur's (*Prolemur simus*) vocal repertoire were the first, and my study will supplement existing knowledge of wild diurnal lemur vocalizations by presenting the first quantitative data on wild ring-tailed lemur vocalization rates.

Macedonia's (1990) large-scale study on ring-tailed lemur vocalizations, while extremely useful in detailing the vocal repertoire of the ring-tailed lemur, was undertaken in a captive environment at the Duke Lemur Center with forcible separation between groups and without free access between individuals during the mating season. In addition, proportionately fewer non-natal males were present in each group than are typically found in the wild, with sex ratios

approximating 2:1 or 3:1 (female: male) at Duke and wild sex ratios approximating 1:1 (Jolly, 1966, Macedonia, 1990; Sauther et al., 1999; Sussman, 1992). This difference in sex ratio could potentially impact male vocalization behaviour. Male-specific vocalizations can depend on the presence of male competitors and/or estrous females for utterance (Snowdon, 2004), and it is well-known that primates in indigenous environments typically demonstrate a broader range of behaviours than primates in various captive situations (Hosey, 2005). Male-specific vocalizations such as the howl and squeal may demonstrate greater variance in rates as well as a broader range of utterance in the wild in Madagascar. The purr vocalization was uttered rarely by males in Macedonia's (1990) study, but according to observations by Jolly (1966), is more widely used by males and has more various functions for males in the wild. My study will complement Macedonia's (1990, 1993) work by examining male ring-tailed lemur use and rate for these three vocalizations — the purr, the howl, and the squeal — in an indigenous environment, at Beza Mahafaly Special Reserve in Madagascar (Sussman and Ratsirarson, 2006).

### **Dissertation overview**

My dissertation is a collection of independent manuscripts relating male ring-tailed lemur vocalizations and vocalization rate to male dominance rank, and contextualizing results in sexual selection theory. Chapter 2 explores the male-specific functions of the ring-tailed lemur purr vocalization, and also investigates the relationship between purring rate and dominance rank in males. Chapter 3 evaluates the usage of the male-specific howl vocalization, and evaluates whether the mate defense and mate attraction hypotheses for male long calls (reviewed in Wich and Nunn, 2002) are supported in this species. Chapter 4 examines the usage of the male-specific squeal vocalization and assesses the relationship between squealing rate and dominance rank in males. Finally, Chapter 5 concludes this examination of male ring-tailed lemur vocalizations with reference to dominance and sexual selection, and explores the implications of my findings while detailing directions for future research.

## References

- Andersson, M. (1994). *Sexual Selection*. Princeton, NJ: Princeton University Press.
- Andrew, R. (1963). The origins and evolution of calls and facial expressions of the primates. *Behaviour* 20: 1-109.
- Bergey, C., and Patel, E. (2008). A preliminary vocal repertoire of the greater bamboo lemur (*Prolemur simus*). *Nexus* 1: 69-84.
- Bradbury, J., and Vehrencamp, S. (1998). *Principles of animal communication*. Sunderland, MA: Sinauer Associates.
- Budnitz, N. and Dainis, K. (1975). *Lemur catta*: Ecology and behavior. In: *Lemur biology*. Tattersall, I., and Sussman, R. (eds.). New York: Plenum Press, pp. 219-235.
- Chapman, A., and Sussman, R. Eds. (2004). *The Origins and Nature of Sociality*. New York: Aldine de Gruyter.
- Clutton-Brock, T., and Albon, S. (1979). The roaring of red deer and the evolution of honest advertisement. *Behaviour* 69: 145–169.
- Darwin, C. (1871). *The descent of man, and selection in relation to sex*, 1<sup>st</sup> ed. London: John Murray.
- Delgado, R. (2006). Sexual selection in the loud calls of male primates: signal content and function. *International Journal of Primatology* 27: 5-25.
- Fischer, J., Kitchen, D., Seyfarth, R., and Cheney, D. (2004). Baboon loud calls advertise male quality: acoustic features and their relation to rank, age, and exhaustion. *Behavioral Ecology and Sociobiology* 56: 140-148.
- Gaspari, M., and Crockett, C. (1984) The role of scent marking in *Lemur catta* agonistic behavior. *Zoo Biology* 3: 123–132.
- Gould, L. (1994) Patterns of affiliative behavior in adult male ringtailed lemurs (*Lemur catta*) at the Beza-Mahafaly Reserve, Madagascar. Ph.D. Dissertation; Washington University, St. Louis.
- Gould, L. (2006). Male sociality and integration during the dispersal process in *L. catta*: a case study. In: Jolly, A., Sussman, R., Koyama, N., and Rasamimanana, H. (eds.), *Ringtailed Lemur Biology*. Springer, New York, pp. 296-310.
- Gould, L., Sussman, R., and Sauther, M. (2003). Demographic and life-history patterns in

- a population of ring-tailed lemurs (*Lemur catta*) at Beza Mahafaly Reserve, Madagascar: A 15-year perspective. *American Journal of Physical Anthropology* 120: 182-194.
- Gould, L., and Zeigler, T. (2007). Variation in fecal testosterone levels, inter-male aggression, dominance rank and age during mating and post-mating periods in wild adult male ring-tailed lemurs (*Lemur catta*). *American Journal of Primatology* 69: 1325-1339.
- Hosey, G. (2005). How does the zoo environment affect the behaviour of captive primates? *Applied Animal Behaviour Science* 90: 107-129.
- Ichino, S., and Koyama, N. (2006). Social changes in a wild population of ringtailed lemurs (*Lemur catta*) at Berenty, Madagascar. In: Jolly, A., Sussman, R., Koyama, N., and Rasamimanana, H. (eds.), Ringtailed Lemur Biology. Springer, New York, pp. 233-244.
- Jolly, A. (1966). *Lemur Behavior: A Madagascar Field Study*. London: University of Chicago Press.
- Jolly, A., Rasamimanana, H., Kinnaird, M., O'Brien, T., Crowley, H., Harcourt, C., Gardner, S., and Davidson, J. (1993). Territoriality in *Lemur catta* groups during the birth season at Berenty, Madagascar. In: Kappeler, P. and Ganzhorn, J. (eds.), *Lemur Social Systems and their Ecological Basis*. New York: Plenum Press, pp. 85-110.
- Kitchen, D., Seyfarth, R., Fischer, J., and Cheney, D. (2003). Loud calls as indicators of dominance in male baboons (*Papio cynocephalus ursinus*). *Behavioral Ecology and Sociobiology* 53:374-384.
- Koyama, N. (1988) Mating behavior of ring-tailed lemurs (*Lemur catta*) at Berenty, Madagascar. *Primates* 29: 163-175.
- Koyama, N.; Nakamichi, M.; Ichino, S., and Takahata, Y. (2002). Population and social dynamics changes in ring-tailed lemur troops at Berenty, Madagascar between 1989-1999. *Primates* 43: 291-314.
- Macedonia, J. (1986). Individuality in a contact call of the ringtailed lemur. *American Journal of Primatology* 11: 163-179.
- Macedonia, J. (1990). Vocal communication and antipredator behavior in the ringtailed lemur (*Lemur catta*). PhD Dissertation: Duke University.
- Macedonia, J. (1993). The vocal repertoire of the ringtailed lemur (*Lemur catta*). *Folia Primatologica* 61:186-217.
- Maynard Smith, J., and Harper, D. (2003). *Animal Signals*. Oxford: Oxford University Press.
- Mertl, A. (1976). Olfactory and visual cues in social interactions of *Lemur catta*. *Folia*

- Primatologica* 26: 151-161.
- Nunn, C. (2000). Maternal recognition of infant calls in ring-tailed lemurs. *Folia Primatologica* 71: 142-146.
- Oda, R. (1996). Effects of contextual and social variables on contact call production in free-ranging ringtailed lemurs (*Lemur catta*). *International Journal of Primatology* 17: 191-205.
- Oda, R. (1999). Scent marking and contact call production in ringtailed lemurs (*Lemur catta*). *Folia Primatologica* 70: 121-124.
- Oda, R. (2001). Lemur vocal communication and the origin of human language. In: Matsuzawa, T. (ed.), *Primate Origins of Human Cognition and Behaviour*. Springer-Verlag, Tokyo, pp. 115-134.
- Oda, R. (2002). Individual distinctiveness of the contact calls of ringtailed lemurs. *Folia Primatologica* 73:132-136.
- Parga, J. (2006). Sexual selection in the ringtailed lemur (*Lemur catta*): female choice, male mating strategies, and male mating success in a female dominant primate. Ph.D. dissertation: University of Texas at Austin, Texas.
- Patel, E., Anderson, J., Irwin, M., and Owren, M. (2005). Quantifying the vocal repertoire of wild adult diademed sifakas (*Propithecus diadema diadema*) in Madagascar. *American Journal of Primatology* 66: 48 [abstract]
- Pereira, M. (1995). Development and social dominance among group-living primates. *American Journal of Primatology* 37: 143-175.
- Pereira, M., and Weiss, M. (1991). Female mate choice, male migration, and the threat of infanticide in ring-tailed lemurs. *Behavioral Ecology and Sociobiology* 28: 141–152.
- Petter, J., and Charles-Dominique, P. 1979. Vocal communication in prosimians. In: Doyle, G., and Martin, R. (eds.). *The study of prosimian behavior*. New York: Academic press, pp. 247-305.
- Pride, R. (2005). Optimal group size and seasonal stress in ring-tailed lemurs (*Lemur catta*). *Behavioral Ecology* 16: 550-560.
- Sauther, M. (1989). Antipredator behavior in troops of free-ranging *Lemur catta* at Beza Mahafaly special reserve, Madagascar. *International Journal of Primatology* 10: 595-606.
- Sauther, M. (1991). Reproductive behavior of free-ranging *Lemur catta* at Beza Mahafaly

- Special Reserve, Madagascar. *American Journal of Physical Anthropology* 84: 463-477.
- Sauther, M. (1993). The dynamics of feeding competition in wild populations of ring-tailed lemurs (*Lemur catta*). In: Kappeler, P., and Ganzhorn, J. (eds.). *Lemur social systems and their ecological basis*. London: Plenum Press, pp. 135-152.
- Sauther, M., and Sussman, R. (1993). A new interpretation of the social organization and mating system of the ringtailed lemur (*Lemur catta*). In: Kappeler, P., and Ganzhorn, J. (eds.). *Lemur Social Systems and their Ecological Basis*. London: Plenum Press, pp. 111-122.
- Sauther, M., Sussman, R., and Gould, L. (1999) The socioecology of the ringtailed lemur: thirty-five years of research. *Evolutionary Anthropology* 8: 120-132.
- Schilling, A. (1974). A study of marking behavior in *Lemur catta*. In: *Prosimian biology*. Doyle, G., Martin, R., and Walker, A. (eds.). Pittsburg: University of Pittsburgh Press, pp. 347-362.
- Snowdon, C. (2004). Sexual selection and communication. In: *Sexual selection in primates: New and comparative perspectives*. Kappeler, P., and van Schaik, C. (eds.). Cambridge: Cambridge University Press, pp. 57–70.
- Sussman, R. (1991) Demography and social organization of free-ranging *Lemur catta* in the Beza Mahafaly Reserve, Madagascar. *American Journal of Physical Anthropology* 84: 43-58.
- Sussman, R. (1992) Male life history and intergroup mobility among ringtailed lemurs (*Lemur catta*). *International Journal of Primatology* 13: 395-413.
- Sussman, R., and Ratsirarson, J. (2006). Beza Mahafaly Special Reserve: A research site in southwestern Madagascar. In: *Ringtailed lemur biology: Lemur catta in Madagascar*. Jolly, A., Sussman, R., Koyama, N., Rasamimanana, H. (eds.). New York: Springer, pp. 43-51.
- Taylor, L. (1986). Kinship, dominance, and social organization in a semi-free ranging group of ringtailed lemurs (*Lemur catta*). Ph.D. Dissertation: Washington University, Missouri.
- Taylor, L., and Sussman, R. (1985) A preliminary study of kinship and social organization in a semi-free ranging group of *Lemur catta*. *International Journal of Primatology* 6: 601-614.
- White, F., Overdorff, D., Keith-Lucas, T., Rasmussen, M., Kallam, W., and Forward, Z. (2007). Female dominance and feeding priority in a prosimian primate: experimental manipulation of feeding competition. *American Journal of Primatology* 69: 295–304.

- Wich, S., and Nunn, C. (2002). Do male “long-distance calls” function in mate defense? A comparative study of long-distance calls in primates. *Behavioral Ecology and Sociobiology* 52: 474-484.
- Zahavi, A. (1975) Male selection - a selection for a handicap. *Journal of Theoretical Biology* 53: 205-214.
- Zahavi, A., and Zahavi, A. (1997). The handicap principle: A missing piece of Darwin’s puzzle. Oxford: Oxford University Press.
- Zimmermann, E., and Lerch, C. (1993). The complex acoustic design of an advertisement call in male mouse lemurs (*Microcebus murinus*, Prosimii, Primates) and sources of its variation. *Ethology* 93: 211–224.

**Table 1. Ring-tailed lemur vocal repertoire as described by Macedonia (1990)**

<b>Vocalization class and call type</b>	<b>Call name</b>	<b>Social context used</b>	<b>Arousal level</b>	<b>Age and sex-class using this vocalization</b>	<b>Call synonyms in previous descriptions</b>
Affiliative; contact call	Moan	Promotes group cohesion	Low/moderate	All lemurs older than 14 weeks	“Moan” <sup>a</sup> “mew” <sup>b</sup> “Cohesion miaouw” <sup>d</sup> “Cohesion call” <sup>c</sup>
Affiliative; contact call	Wail variant 1, early-high wail	Promotes group cohesion	Moderate/high	All lemurs older than 6-8 weeks	“Wail” <sup>a</sup> “me-ow” <sup>b</sup>
Affiliative; contact call	Wail variant 2, late-high wail	Promotes group cohesion	High	Usually non-infant females, more rarely males	“Wail” <sup>a</sup> “me-ow” <sup>b</sup>
Affiliative; male long call	Howl*	Broadcasts the presence and location of the group	Moderate/high	Only males older than infancy	“Howl” <sup>a, b</sup>
Affiliative; cohesion grunt	Hmm	Promotes group cohesion during slow relocation	Low	All lemurs older than 5 weeks	“Cohesion Grunt” <sup>d</sup>
Affiliative; cohesion grunt	Huh	Emitted in same contexts as hmm, but less frequently	Low	Usually given by lemurs 3 months old or older and by male juveniles or adolescents, rarely given by adults	None
Affiliative; acoustic beacon	Chirp	Promotes group cohesion during rapid movement	Moderate	All lemurs older than 3 weeks	None
Affiliative	Purr*	Given by adults and juveniles when grooming infants and by infants when being groomed	Low	Given by both sexes of all age classes, but most frequently given by adult females	“Purr” <sup>b</sup>
Agonistic; submissive	Yip	Used by subordinates when near dominants	Low/moderate	All non-infants except alpha females	“Yip” <sup>a</sup> “Light yip”, “spat call” <sup>b</sup>
Agonistic; submissive defensive display	Cackle	Used by subordinates in agonistic situations	Moderate/high	Adults of both sexes	“High-intensity yip” <sup>a</sup> “Deep spat” <sup>b</sup>
Agonistic; submissive and aggressive display	Twitter	Used by subordinates to show both submission and aggression	Moderate	All lemurs older than 6 months	“Twitter” <sup>b</sup>
Agonistic; male “status assertion: vocal display	Squeal*	Occurs only during male tail-waving display, when asserting status toward male or toward female (as part of courtship)	Moderate/high	Only adult males and sometimes juvenile males	“Squeal” <sup>b</sup> “Sharp call” <sup>a, d</sup>

**Table 1 (continued): Ring-tailed lemur vocal repertoire as described by Macedonia (1990)**

<b>Vocalization class and call type</b>	<b>Call name</b>	<b>Social context used</b>	<b>Arousal level</b>	<b>Age and sex-class using this vocalization</b>	<b>Call synonyms in previous descriptions</b>
Agonistic; threat vocalization	Plosive bark	Uttered as a vocal threat	High	Both sexes of all age classes	“Explosive voiced grunt” <sup>b</sup>
Agonistic; threat vocalization	Chutter	Uttered when a dominant lunges toward a subordinate	Low/moderate	Dominant adults toward subordinates of all ages	None
Antipredator; alerting aerial predator vocalization	Gulp	Given in response to startling aerial visual or acoustic stimuli	Low/moderate	All lemurs greater than 14 weeks old	None
Antipredator; aerial predator vocalization	Rasp	Uttered on perception of potential aerial predator	Moderate	All non-infants	None
Antipredator; aerial predator vocalization	Shriek variant 1 (single frequency sweep)	Uttered in response to low-flying, large birds	High	All non-infants	“Shriek” <sup>a, b</sup> “Oua-oua” <sup>d</sup>
Antipredator; aerial predator vocalization	Shriek variant 2 (multiple frequency sweeps)	Uttered when under direct attack from an aerial predator	Highest	All non-infants	“Shriek” <sup>a, b</sup> “Oua-oua” <sup>d</sup>
Antipredator; terrestrial predator vocalization	Click	Given in response to startling terrestrial stimuli	Low	All lemurs older than 2 weeks	“Click” <sup>a</sup> “Click-grunt” <sup>b</sup>
Antipredator; terrestrial predator vocalization	Closed-mouth click series	Given in response to terrestrial predators	Moderate	All lemurs older than 2 months	“Click series” <sup>b</sup>
Antipredator; terrestrial predator vocalization	Open-mouth click series	Given in response to terrestrial predators	High	All non-infants	“Click series” <sup>b</sup>
Antipredator; terrestrial predator mobbing call	Yap	Mobbing call to nearby terrestrial predators	Highest	All non-infants	“Yap” <sup>b</sup> “Bark” <sup>a, d</sup>

**Table 1 (continued): Ring-tailed lemur vocal repertoire as described by Macedonia (1990)**

<b>Vocalization class and call type</b>	<b>Call name</b>	<b>Social context used</b>	<b>Arousal level</b>	<b>Age and sex-class using this vocalization</b>	<b>Call synonyms in previous descriptions</b>
Affiliative; contact call	Infant contact call	Elicits maternal attention	Low/moderate	Infants from birth to 6 months	None
Affiliative; contact call	Trill 1	Given during physical contact	Low/moderate	Infants from birth to 6 months	None
Affiliative; contact call	Trill 2	Given during ano-genital grooming by an adult	Moderate/high	Infants from birth to 6 months	None
Distress; distress call	Whit variant 1	Given during physical discomfort	Moderate	Infants from birth to 6 months	“Infant squeaks” <sup>b</sup>
Distress; distress call	Whit variant 2	Given during great physical discomfort	High	Infants from birth to 6 months	None
Distress; lost call	Yelp	Given when separated from their mother	High	Infants only, first heard at week 4	“High-pitched, modulated plaintive call” <sup>d</sup>

\*vocalizations addressed in my study

<sup>a</sup>Andrew, 1963.

<sup>b</sup>Jolly, 1966.

<sup>c</sup>Macedonia, 1986.

<sup>d</sup>Petter and Charles-Dominique, 1979.

## **Chapter 2: Male-specific use of the purr in the ring-tailed lemur (*Lemur catta*)**

### **Abstract**

In mammals, purring has been described in mostly affiliative contexts. In the ring-tailed lemur (*Lemur catta*), both males and females purr, but males appear to purr in contexts additional to affiliation. In order to determine why and when male ring-tailed lemurs purr, 480 hours of focal data were collected on 25 males aged three and older from Beza Mahafaly Special Reserve, Madagascar from March-July 2010. Throughout the sampling period, males were followed for 30 minutes at a time and their behaviour including purring vocalizations and agonistic interactions were noted each 2.5 minutes using one-zero sampling. Male purring rate increased during periods of male-male agonism when compared with times without intra-sexual agonism, and purring rate was positively correlated with male dominance rank. Males who purred during agonistic encounters were more likely to win that encounter. My results indicate that the ring-tailed lemur male purr is used primarily in assertive contexts within male-male agonistic encounters.

### **Introduction**

Sexual selection is a form of natural selection dependent on an individual's ability to attract and successfully copulate with a mate (Darwin, 1871). Sexual selection takes two forms: intra-sexual selection, where individuals compete with same-sex individuals for mates, and inter-sexual selection, where the traits and behaviours of individuals cause opposite-sex individuals to preferentially mate with them (Andersson, 1994; Darwin, 1871). Vocalizations have long been documented as tools used in both forms of sexual selection, particularly by males (Bradbury and Vehrencamp, 1998; Darwin, 1871). Males in many animal species use vocalizations as sexual displays to attract females, and as assertive displays to repel and out-compete other males (Andersson, 1994; Darwin, 1871; Snowdon, 2004; Wiley, 1991). In animals as diverse as amphibians, birds, and mammals, the structure of vocal displays is thought to encode information about fighting ability, size, health, and social rank of an individual, while vocalization rate and high repetition of a vocalization indicates male condition (amphibians: Davies and Halliday, 1978; Lode and LeJacques, 2003; birds: Catchpole and Slater, 1995; Forester and Czarnowsky, 1985; mammals: Kunc and Wolf, 2008; Reby and McComb, 2003).

Zahavi (1975) proposed the handicap principle as the means by which honesty is maintained in animal communication. Leading theoretical models predict that the honesty of most vocalization properties must be ensured in order for a communication system to remain evolutionarily stable (Fitch and Hauser, 2003). The handicap principle states that in order for a signal to remain honest over evolutionary time, it must be heritable as well as costly such that it “handicaps” the signaling individual’s fitness (Zahavi, 1975). Further, the honest signal must have lower costs for high-quality individuals and higher costs for low-quality individuals (Grafen, 1990; Iwasa et al., 1991; Zahavi, 1975; Zahavi and Zahavi, 1997). Over generations, high-quality signalers will have higher fitness since they will be better able to bear the costs associated with the honest signal (Grafen, 1990; Zahavi, 1975; Zahavi and Zahavi, 1997).

Two main criticisms have been made of the handicap principle: firstly, that there is insufficient variety in the fitness of individuals to warrant handicap signaling, and secondly, that the burden of “handicap” genes on offspring would outweigh any genetic advantage to mating with a fitter male (Pomiankowski and Iwasa, 1998). The first criticism has been shown to be unfounded, since all potential male qualities which could underlie the handicap - both genetic and phenotypic - have large enough variation to make handicap signaling plausible (Burt, 1995; Pomiankowski and Møller, 1995). The second criticism, raised and mathematically modeled by Maynard Smith (1976, 1978) and others (Bell, 1978; Eshel, 1978), states that under normal conditions, the cost of having handicap genes would outweigh any genetic benefit to reproducing with a fitter male. This early model was called the “pure epistasis” model (Maynard Smith, 1985; Iwasa et al., 1991), and objections to it raised by Maynard Smith (1976, 1978) and others (Bell, 1978; Eshel, 1978) are still valid. However, when this epistasis model is modified to include condition-dependent signaling, the handicap process becomes more plausible (Andersson, 1986; Pomiankowski, 1987a, 1987b; Pomiankowski and Iwasa, 1998). Condition-dependent signaling suggests that the expression of the handicap trait depends on male quality, such that only high-quality males produce handicap signals, although many lower-quality males also have the ability to produce handicap signals (Pomiankowski, 1987b). Since only fit males express handicap signals, the benefits of mating with these males outweigh the potential costs of inheriting the handicap (Pomiankowski and Iwasa, 1998). These more recent models have therefore quieted early criticisms, and the general point of the handicap principle is now widely accepted as applicable to most aspects of animal signaling behaviour (Johnstone, 1997). Most researchers

now agree that reliable signaling of individual quality is ensured through differential signaling costs (Grafen, 1990; Iwasa et al., 1991), which is the root of Zahavi's (1975) handicap hypothesis.

Zahavi's (1975) handicap principle can be particularly demonstrated in courtship and threat situations, because these are risky contexts in which males have more opportunity than in regular situations to demonstrate their superior quality (Bradbury and Vehrencamp, 1998). Courtship and threat signals reveal accurate information about the vocalizing individual (Snowdon, 2004). Rival males may determine whether they could beat a vocalizing male in combat based solely on how and the rate at which he vocalizes, while females are known to base mate choice on male vocalization quantity and spectral characteristics (e.g. Briefer et al., 2010; Forester and Czarnowsky, 1985; McComb, 1991; Reid et al., 2004). Vocal displays are thus thought to indicate male quality (Zahavi, 1975).

Previous studies have investigated the role that long-range, male-specific vocalizations play with respect to male quality in a range of animal species (birds: Alatalo et al., 1990; Radesater et al., 1987; insects and anurans: Prestwich, 1994; mammals: Clutton-Brock and Albon, 1979; Delgado, 2006; McComb, 1991). For some animals with male-specific long calls, such as red deer (*Cervus elaphus*) and pied flycatchers (*Ficedula hypoleuca*), quality is indicated by high call repetition rate (pied flycatcher: Alatalo et al., 1990; red deer: Clutton-Brock and Albon, 1979). For others, such as chacma baboons (*Papio ursinus*), male quality is reflected by the spectral characteristics of long calls, with dominant males calling with higher fundamental frequencies than lower-ranking males (Fischer et al., 2004). Long-range calls made by birds, amphibians, and mammals can carry for distances of up to 2.5 kilometres in some species, and they serve as long-distance advertisements of a male's presence in a certain location (Delgado, 2006). Studies of signal energetic in birds suggest that vocal production carries physiological costs (Eberhardt, 1994; McCarthy, 1996). Vocalizations may also put a signaling male at higher risk of being attacked or predated (Andersson, 1994; Cade, 1975), but could decrease a signaler's risk of harm by demonstrating high health levels and consequent ability to evade predation (Martin and Lopez, 2001; Zuberbühler et al., 1999). Either way, long-range calls are considered energetically expensive to produce, are generally produced at higher rates by fitter males, and are thus acknowledged as honest indicators of male fitness (Delgado, 2006; Zahavi, 1975; Zahavi and Zahavi, 1997).

In contrast, few studies have investigated whether short-range calls may also be honest signals of male quality (but see Anderson et al., 2008; Titus, 1998; Zimmermann and Lerch, 1993). Short-range calls are generally only audible by individuals in close proximity to the caller, such as within 20 metres for the common ringtail possum (*Pseudocheirus peregrinus*) and 9 metres for the pygmy marmoset (*Cebuella pygmaea*) (common ringtail possum: Wintle et al., 2005; pygmy marmoset: de la Torre and Snowdon, 2002), with many short-range calls only audible at lesser distances than these. Examples of short-range vocalizations include contact calls termed “trills” and “J-calls” in the pygmy marmoset, which are used by both sexes of marmosets to maintain group cohesion and regulate interactions between group members (Pola and Snowdon, 1975; Snowdon and Hodun, 1981). Short-range vocalizations have also been studied in other animal orders, including birds. Song sparrows (*Melospiza melodia*) have a low-amplitude vocalization termed “soft song”, which is male-specific (Anderson et al., 2008). Male sparrows sing short-range songs during male-male agonistic interactions, suggesting this vocalization type to be an aggressive intra-sexual signal (Searcy et al., 2006). Although such low amplitude vocalizations may seem less likely to be functional in intra-sexual aggressive signaling, they are found in several bird species. In other bird species, such as the blackbird (*Turdus merula*) and the dark-eyed junco (*Junco hyemalis*), male-specific, low-amplitude songs are given in similar intra-sexual agonistic contexts, as well as during inter-sexual display contexts (Anderson et al., 2008; Dabelsteen et al., 1998; Dabelsteen and Pedersen, 1990; Titus, 1998). Given these consistent reports of inter- and intra-sexual use of low-amplitude calls by males in a range of avian species, it is remarkable that short-range vocalizations have rarely been investigated with reference to sexual selection. Clearly, how sexual selection may function with respect to short-range vocalizations in birds and other animal species has not been adequately studied. As with long-distance calls in other animal species and low-amplitude calls in birds, other short-range vocalizations, such as the mammalian purr, may also advertise a caller’s qualities to intra-sexual competitors or potential mates.

### **Background on purring**

A purr is a uniquely mammalian broadband vocalization characterized by very low amplitude (Bradbury and Vehrencamp, 1998; Peters, 2002). When visually represented on a spectrogram, a purr consists of a tightly-spaced series of very narrow columns of noise, which would sound like a series of very fast clicks (Andrew, 1962; **Figure 1**). The very low amplitude

of a purr makes it audible only at very close range for most mammals, such as within 3 metres for domestic cats (*Felis catus*), which is compounded by the purr's highest amplitude component typically being at the lower limit of species' hearing capability (Frazer Sissom et al., 1991; Heffner and Heffner, 1985; Peters, 2002). For many animals that purr, sound is produced during both inhalation and exhalation phases of respiration, and purr rate is thought to reflect the animal's breathing rate. Purring is known to be a vocalization with physiological costs (Peters, 2002). In the domestic cat, respiratory rate during purring is approximately 93% higher than respiratory rate while resting without purring (Remmers and Gautier, 1972). Although purring energetics research has not been undertaken for other mammals, it is likely that the respiratory rate for other mammals would also be increased during purring. Purring rate may therefore have the potential to honestly indicate male energy level and health to conspecific males and females, and thus signal male quality (Zahavi, 1975; Zahavi and Zahavi, 1997). Although the purr has been most thoroughly studied in the domestic cat, a variety of mammals have purr or purr-like vocalizations. These include species as diverse as cats, rodents, bears, civets, peccaries, bats, Old World monkeys, New World monkeys, hominids, and strepsirhine primates (reviewed in Peters, 2002).

### **Social contexts for purring**

Purring and purr-like vocalizations have been described in relation to a limited suite of behaviours throughout mammals, and all in contexts that could be termed consummatory or affiliative (Bradbury and Vehrencamp, 1998). These include infants suckling, females nursing, feeding, prior to copulation, during copulation, cuddling, juveniles and adults huddled together in close proximity, grooming, soliciting grooming, play, affiliative approach, and courtship (Peters, 2002). As Peters (2002) notes, in all of these behavioural contexts, the purring animal is likely to be in a mood that is "relaxed, friendly and probably reassuring/soothing" (p. 264). He concludes therefore that the signaler wishes to advertise their comfort and contentedness to a nearby recipient (Peters, 2002). According to Bradbury and Vehrencamp (1998), purring is a "satisfaction signal" for mammals, conveying "pleasure and contentment" as well as "self-confidence" (pp. 809-810).

As in other mammals, in primates, purring is used in contexts that can be interpreted as affiliative, with few exceptions (Peters, 2002). Three species of Old World monkeys, twelve

species of New World monkeys, one ape, and eight species of strepsirhine are known to purr. Amongst these species, purring is heard in largely affiliative contexts, the most common being in mother-infant interaction (Old World monkeys: rhesus macaque [*Macaca mulatta*], Jürgens, 1979, Rowell and Hinde, 1962; vervet monkey [*Chlorocebus aethiops*], Struhsaker, 1967; New World monkeys: red titi monkey [*Callicebus cupreus*], Maestripiéri and Call, 1996; red-bellied titi monkey [*Callicebus moloch*], Fragaszy et al., 1982; Moynihan, 1966; common squirrel monkey [*Saimiri sciureus*], Jürgens, 1979; Winter et al., 1966; central American squirrel monkey [*Saimiri oerstedii*], Baldwin and Baldwin, 1981; mantled howler monkey [*Alouatta palliata*], Carpenter, 1934; red howler monkey [*Alouatta seniculus*], Neville et al., 1988; white-faced capuchin monkey [*Cebus capucinus*], Freese and Oppenheimer, 1981; weeper capuchin monkey (*Cebus olivaceus*), Freese and Oppenheimer, 1981; bald uakari monkey [*Cacajao calvus*], Fontaine, 1981; strepsirhines: eastern woolly lemur [*Avahi laniger*], gray mouse lemur [*Microcebus murinus*], Coquerel's mouse lemur [*Microcebus coquereli*], sifaka [*Propithecus* spp.], brown lemur [*Eulemur fulvus*], black lemur [*Eulemur macaco*], and lesser bamboo lemur [*Haplemur griseus*], Petter and Charles-Dominique, 1979). Purring is also heard in contexts such as during infant play (vervet monkey, Struhsaker, 1967), during genital display and mating (central American squirrel monkey, Baldwin and Baldwin, 1981; common squirrel monkey, Jürgens, 1979, Winter et al., 1966), during adult reciprocal grooming (gray mouse lemur, Charles-Dominique and Martin, 1972, Scheumann et al., 2007; brown lemur, black lemur, Petter and Charles-Dominique, 1979), during and after eating (mountain gorilla [*Gorilla beringei beringei*], Schaller, 1963; golden lion tamarin [*Leontopithecus rosalia*], Boinski et al., 1994, Kleiman et al., 1988), as a low-intensity alarm call prior to group movement (black-and-white colobus monkey [*Colobus guereza*], Marler, 1972), and as a call heard in a range of situations, from affiliation to aggression (greater bamboo lemur [*Prolemur simus*], Bergey and Patel, 2008).

### **Purring as a display of aggression**

Although purring is thought to be a contented vocalization and used in largely affiliative social contexts (Bradbury and Vehrencamp, 1998), purring is also an assertive display in some primates. Various vocalizations have been called purrs, but these purrs may be very different from one another in form and function in different species. For the greater bamboo lemur, Bergey and Patel (2008) reported that 40% of total purr vocalizations were heard in aggressive contexts. The black-and-white colobus monkey is known to purr during group movement, and

this is thought to help coordinate the group as well as being a low-intensity alarm call (Marler, 1972). Although Peters (2002) regarded this colobus monkey purring context as affiliative, a vocalization serving as an alarm call and influencing group movement can be interpreted more intuitively as non-affiliative, and even assertive. The common squirrel monkey purrs in a number of different contexts (Jürgens, 1979), and in some of these contexts, purring is thought to reflect “preparedness for aggression” (Baldwin and Baldwin, 1981, p. 316). Jürgens (1979) and Peters (2002) perceived common squirrel monkey purring during adult genital display and infant suckling as affiliative, but Winter et al. (1966) thought that the purr displayed an aggressive motivation in these contexts. This (Winter et al., 1966) interpretation of squirrel monkey infant suckling and adult genital display as aggressive has implications for the function of purring in all mammalian infants who purr while suckling, and all adults who purr while making sexual displays. If this descriptor is extended to all mammals, then a great many species from a variety of taxonomic orders can be said to purr in aggressive contexts.

### **Motivational-Structural rules and acoustic design expectations for purring**

The acoustic structure of the purr vocalization also has more features common to vocalizations heard in aggressive contexts, rather than affiliative. According to leading theoretical models for acoustic design, there is a strong relationship between the structure of sounds and their function because natural selection has resulted in the structural convergence of all animal vocalizations used for common functions (Morton, 1977). Morton’s motivational-structural (MS) rules (1977) apply to all close-range vocalizations of birds and mammals and can be used to link the structure of signals to their function and motivation. Morton’s MS rules can be summarized as follows:

1. Affiliative or appeasing vocalizations used in friendly contexts are usually pure, high-pitched, tonal sounds. An animal making these sounds is friendly or submissive, and will not be hostile if approached. The greater the sound’s tonality, the greater the friendly/submissive motivation of the caller.
2. Agonistic vocalizations used in hostile contexts are usually harsh-sounding, broadband, low-frequency sounds. An animal making these sounds is likely to attack if the receiver comes closer or remains close by. The greater the sound’s harshness, the greater the aggressive motivation of the caller.

3. Vocalizations may have gradations, such that a single vocalization type may transition from friendly to hostile given the motivation of the caller at a given moment. Sounds rising in frequency indicate lower hostility or increasing appeasement or fear, while sounds decreasing in frequency indicate an increasingly hostile motivation.

These MS rules predict that broadband, low-frequency vocalizations, like the mammalian purr, should be associated with aggressive social contexts. If the purr is used in affiliation, it should instead be tonal and high-frequency (Morton, 1977). Researchers have noticed this disparity between theoretical predictions for the purr's form (i.e. aggressive) and probable function (i.e. affiliative), and have suggested amendments to Morton's MS rules (1977) to account for these differences (Peters, 2002). Peters (2002) thought that despite the purr's spectral properties which suggest agonism, the high repetition rate and low intensity of purring are features which mark the purr as an affiliative vocalization. This recent adjustment of theoretical models allows the mammalian purr vocalization to be classified as affiliative in acoustic design (Shuemann et al., 2007). However, this classification of the purr is controversial in that Morton's MS rules (1977) have been supported by research for vocalizations given in social contexts other than affiliation (August and Anderson, 1987; reviewed in Shuemann et al., 2007). In particular, the acoustic design of close-contact aggressive mammalian vocalizations has been found to strongly adhere to Morton's MS rule hypothesis (1977) in fifty species (reviewed in August and Anderson, 1987), suggesting the purr to be quite an anomaly. The purr's largely affiliative usage throughout the mammalian order violates Morton's predictions for signal design (1977), and since purring bears many of the spectral features of an aggressive signal (August and Anderson, 1987; Peters, 2002), and particularly since some mammals do purr in aggressive contexts (greater bamboo lemur: Bergey and Patel, 2008; common squirrel monkey: Baldwin and Baldwin, 1981; Winter et al., 1966), purring use should be investigated as an open question in each species without *a priori* assumptions made. My study investigates the purr vocalization in a Malagasy strepsirhine, the ring-tailed lemur (*Lemur catta*).

### **Background on the ring-tailed lemur**

The ring-tailed lemur is a female-dominant strepsirhine primate endemic to southern Madagascar (Jolly, 1966). It is a gregarious animal that lives in multi-male, multi-female groups

of up to twenty-seven animals (Gould et al., 2003; Pride, 2005; Sussman, 1991). Males disperse from their natal group at 3-4 years of age and disperse to new groups approximately every three years, while females usually remain in their natal groups for their entire lives (Budnitz and Dainis, 1975; Jones, 1983; Sussman, 1992).

The ring-tailed lemur has an annual breeding season that begins in May in Madagascar, with females in asynchronous estrus (Jolly, 1966). Each female stays in estrus for 3.25 to 24 hours in total, and during this time usually mates with multiple males (Jolly, 1966; Parga, 2006a; Sauther, 1991; Van Horn and Resko, 1977). Mating opportunities are usually restricted to non-natal males who are sexually mature and unrelated to group females (Parga, 2010; Sauther, 1991; Taylor and Sussman, 1985). The competition between non-natal males for mates leads to a high degree of male-male aggression during the breeding season, and can lead to severe injuries and even death (Gould and Ziegler, 2007; Jolly, 1966; Sauther 1991). Although females are dominant, males have their own dominance hierarchy, which is often linear (Budnitz and Dainis, 1975; Gould, 1994; Taylor, 1986). Dominance confers social advantages for high-ranking males, typically including first sexual access to group females when they are in estrus (Koyama, 1988; Parga, 2006b; Sauther, 1991; but see Gould, 1994). Being an earlier-mating male during female estrus may also provide a fertilization advantage (Pereira and Weiss, 1991). Dominance is therefore an extremely desirable characteristic for ring-tailed lemur males.

Males maintain their dominance hierarchy through physical combat as well as through ritualized scent marking and tail waving displays (Gould, 1994; Gould and Ziegler, 2007; Palagi et al., 2003; Scordato and Drea, 2007). When a male tail waves, he rubs his high-contrast ringed tail across scent glands located on his wrists and shoulders, then lifts his tail over his head and waves his tail repeatedly to waft his scent towards a rival male, who is 1-3 metres away (Gould, 1994; Jolly, 1966; Mertl, 1976). The rival male may retreat, reciprocate, or attack in response (Jolly, 1966).

In addition to tail-waving and scent marking, vocalizations mediate male ring-tailed lemur behaviour, and have been studied by a number of researchers (Andrew, 1963; Jolly, 1966; Macedonia, 1986, 1990, 1993; Oda, 1996; Petter and Charles-Dominique, 1979; Sauther, 1989). As a highly social strepsirhine, the ring-tailed lemur has a large vocal repertoire composed of 22 distinct vocalizations for adults (Macedonia, 1990). These consist of 8 calls used in affiliative

interactions, 6 calls used in agonistic behaviour, and 8 anti-predator vocalizations (Macedonia, 1990). Of these 22 calls, several are long-range, two are male-specific, and some are known to be individually distinctive (Jolly, 1966; Macedonia, 1986, 1990, 1993). My study focuses on one affiliative vocalization, the purr (Jolly, 1966). Although this vocalization is used by adult males and females as well as infants (Jolly, 1966; Macedonia, 1990, 1993), my study will concentrate on adult male use of purring.

### **Purring in the ring-tailed lemur**

In the ring-tailed lemur, the purr vocalization is known to be an affiliative call used by both males and females (Jolly, 1966; Macedonia, 1990, 1993). Like purring in other mammals, ring-tailed lemur purrs are seen spectrally as a fairly constant series of broadband vertical ridges, which may be produced during both inhalation and exhalation phases of breathing (**Figure 1**; Macedonia, 1990; but see Peters, 2002). As a very short-range vocalization, it is only audible to the human ear within 1 metre (Jolly, 1966). Past studies have noted that the purr is made most often by adult females as they groom infants (Macedonia, 1990), but that all age classes and both sexes sometimes purr (Jolly, 1966). Adults purr while allogrooming and resting, and infants purr while being groomed or licked by their mother (Jolly, 1966; Petter and Charles-Dominique, 1979). 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).

Jolly (1966) also noted that males often purred while rubbing their tails across their scent glands while tail-marking, prior to tail-waving. Tail marking and tail waving are behaviours that have been termed aggressive for male ring-tailed lemurs (Budnitz and Dainis, 1974; Gaspari and Crockett, 1984; Jolly, 1966; Mertl, 1976; Schilling, 1974). These social contexts for male purring are therefore not affiliative, but agonistic. For this reason, further study as to when and why male ring-tailed lemurs purr is warranted.

### **Hypothesis: The male purr is used as an aggressive display in male-male agonism**

My study investigates contexts in which the purr vocalization occurs in male ring-tailed lemurs. In particular, the goal of my study is to clarify the male-specific function of the purr vocalization with reference to intra-sexual selection. Although male purring has been noted

anecdotally in various social contexts, this has not been empirically tested. I predict that male purring rate will be higher during periods of male-male agonism as opposed to contexts without agonism. If purring is used as an aggressive display in male-male agonism and has some role in intra-sexual selection, it follows that males should purr more at times when they are engaged in agonism with other males. Conversely, the null hypothesis predicts that there will be no difference in male purring rate between times with and without male-male agonism.

Further to this hypothesis are several associated questions. If males do purr during intra-sexual agonistic interactions, is the male purr associated with male-male agonistic wins or with losses? Finally, is overall male purring rate associated with high dominance ranking?

## **Methods**

### **Description of field site**

All data for this study were collected between March 1-July 1, 2010 at Beza Mahafaly Special Reserve, a protected governmental reserve in Madagascar's southwest (23°30'S lat., 44°40'E long.) (Sussman and Ratsirarson, 2006; Sussman et al., 2012). This reserve was established in 1978 and has been protected since 1986 (Gould et al., 2003; Sussman et al., 2012). It consists of two non-contiguous forest types, dry forest in the western area of the reserve (Parcel II, 500 ha) and riverine forest on the eastern side (Parcel I, 80 ha) (Sussman and Ratsirarson, 2006). However, the two non-contiguous parcels have recently been connected in an expansion of the reserve to now nearly 4000ha (Sauther, pers. Comm.). A system of labeled trails roughly divided Parcel I into 100m<sup>2</sup> squares, making this forest easy to navigate. Beza Mahafaly was an optimal site for recording primate vocalizations and collecting high-quality behavioural data because of its secluded location away from major roads. The small number of motorized vehicles in the area limited environmental noise.

Approximately 225 free-ranging ring-tailed lemurs in eleven 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 labeled with visible numbers, an identification system dating to the earliest ring-tailed lemur research at the reserve in the late 1980s (Cuzzo and Sauther, 2006; Cuzzo et al., 2010; Sauther and Cuzzo, 2009;

Sauther et al., 2002; Sussman, 1991). The only individuals left uncollared were infants, yearlings, and some adult males who had recently migrated from groups outside of the reserve.

Any uncollared animals could be easily individually identified due to patches of black dye in different body areas on each animal, in addition to sex and size differences. Five groups from Parcel I were the focus of this study.

### **Description of study animals**

Behavioural focal follows were performed six days per week from dawn until dusk on all males aged three and older from five ring-tailed lemur troops (green, orange, purple, red, and yellow troops). Only one group was followed per day. Each group was studied 1-2 days per week. Resident males were sampled using the focal animal sampling method from dawn until dusk on a randomized, rotational basis (Altmann, 1974).

Focal data were collected from 25 sexually mature males in total (**Table 1**). Ages for most individuals are known from the decade-long work by researchers, who identify lemurs as subadults (second year of age) when first captured, with age determined from a series of variables including dental development, sexual maturity (or lack thereof), body mass, and somatic development (Cuozzo and Sauther, 2006; Cuozzo et al., 2010; Sauther and Cuozzo, 2008, 2009). Thus collared lemurs aged two or greater are of known age. I estimated the age for all individuals with names beginning with “UMM” (unmarked male) as three or more. All “UMM” individuals were sexually mature males who were known to be new, non-natal members to collared study groups in Parcel I within the last year (Beza Mahafaly Special Reserve unpublished data). Both natal and non-natal male group members were included in all statistical analyses because some natal males were observed mating with female group members (Bolt, unpublished data). At Beza Mahafaly Special Reserve, ring-tailed lemur study group size ranged from 9-20 individuals, with 4-8 males, 4-10 females, and 0-3 infants present per group.

### **Field methods**

During focal sampling, each male subject was followed for thirty minutes at a time, with data recorded every 2.5 minutes on a programmed palm pilot (Palm Z-22) using one-zero sampling (Martin and Bateson, 2007) to document the actions that occurred during the previous

time period, including the focal individual's behaviour (resting, vigilant, allogrooming, autogrooming, feeding, foraging, sunning, playing, attacking, fleeing, wrist marking, shoulder marking, genital marking, tail marking, tail waving, travelling, urinating/defecating, mounting, licking scent mark, other, out of sight), whether they were engaged in behaviour with others, and the identity of other individual(s) involved (if applicable). During focal sampling, the following vocalization types were recorded: moan, wail, howl, hmm, huh, purr, chirp, yip, cackle, squeal, twitter, plosive bark, chatter, gulp, rasp, shriek, click, click series, yap (following Macedonia, 1990). Animals were watched continuously during the focal period, and I collected all focal data. The ring-tailed lemur ethogram was based on those used by Gould (1994), Jolly (1966), Parga (2006b), and Pereira and Kappeler (1997).

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). Although one-zero sampling has received criticism (e.g. Altmann, 1974), this sampling method has also been empirically shown to be an effective technique for collecting data on primate behavioural rates (Leger, 1977; Suen and Ary, 1984), and provides an equally accurate measure of behaviour as more widely used sampling methods (reviewed in Rhine and Linville, 1980). One-zero sampling has been used in other studies of primate vocalizations as a means of measuring the rate of a short, repetitive vocalization (Suzuki and Sugiura, 2011) or to determine whether vocalizations occurred or not within a given time period (Clarke 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 absolute duration and rate of this vocalization difficult to accurately determine. For this reason, one-zero sampling provided an accurate minimum estimate of behaviour, allowing for high quality data to be recorded.

Vocal recordings were made of all utterances by the focal animal during each focal follow when possible, using a Sennheiser ME66 directional microphone (Sennheiser Electronic GmbH and Company, KG) and digital Marantz PMD660 recorder (Marantz Corporation, New York, USA). Recordings were made with a 44.1kHz sampling rate, 16-bit sample depth, and 64 kilobits/second MP3 compression. The sampling rate refers to the number of digital sound samples taken in per second, while the 16-bit sample depth refers to 65 536 different levels of quantization recorded (Oppenheim et al., 1996). MP3 compression was necessary due to storage

space limitations on the digital recorder. Sound spectrograms for purrs were produced using Cool Edit Pro v.2.1 (Syntrillium Software, USA, 2003), with the spectrogram created using a Blackman window with 2048 frequency bins. A Blackman window is a mathematical function used in spectral analysis and used to generate spectrograms, while the number of frequency bins refers to the frequency resolution of the spectrogram, with 2048 values in total of different frequencies that are measured and used to generate the spectrogram (Oppenheim et al., 1996). 2048 frequency bins allowed for optimal frequency and time resolution of the ring-tailed lemur purr vocalization, based on a visual inspection.

In my study, an agonistic interaction is defined as any behaviour involving contest competition between two individuals. This could consist of low-arousal behaviour (e.g. a displacement or lunge-withdraw) or higher-arousal behaviour (e.g. cuff, bite, or jump fight). An agonistic interaction involves one or more acts of avoidance, aggression, or defense between two individuals. A period without male-male agonism is defined as a time without contest competition between individuals.

### **Calculating male rank**

The male dominance hierarchy in a ring-tailed lemur troop is often linear, but is sometimes non-linear (Budnitz and Dainis, 1975; Gould, 1994; Jolly, 1966). In my study, dominance was determined from focal data using dominance index calculations, which take all decided agonistic and submissive interactions into account before assigning each male an individual dominance percentage within its troop (Zumpe and Michael, 1986). In my study, dominance index was calculated using the following equation:

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

In this equation,  $n$  represents the total number of males in the group with whom the male had agonistic interactions,  $\%A$  represents the percent aggression given within each male-male dyad,  $\%S$  represents submission received within each male-male dyad, and  $i$  represents the index of summation. Successive values of  $i$  are determined by adding 1 to the previous value of  $i$ , stopping when  $i$  is equal to the total number of males in the group with whom the male in question had agonistic interactions (i.e. when  $i=n$ ). Output values approaching 100% indicated

high dominance rank, while those approaching 0% indicated comparatively low dominance rank. Within each male-male dyad in each group, %A was calculated from the number of aggressive actions expressed by each male and calculated as a percentage of the total number of aggressive behaviours given by both males to one another (Zumpe and Michael, 1986). For each male-male dyad, %S was calculated in the same way as %A. For each male, the %A and %S scores were added, then divided by the total number of males in the group with whom the male had agonistic interactions to produce a dominance index (Zumpe and Michael, 1986).

In calculating dominance indices, all agonistic behaviours (e.g. chase, lunge-withdraw, cuff) were treated equally (following Gould, 1994). Dominance indices were calculated separately for males in each group. Males with higher dominance percentages won more fights and had a higher ranking within their troops. Dominance index calculations for all males in each troop are presented in **Table 1**.

### **Data analysis**

For each separate data set analyzed to address my hypothesis, preliminary Shapiro-Wilk tests were performed and Q-Q plots were created to assess normality values (McDonald, 2009; Sokal and Rohlf, 1995). The Shapiro-Wilk test is a recommended normality assessment for sample sizes less than fifty, and therefore appropriate for assessing normality in my study (McDonald, 2009). The Q-Q plot is a graphical test for normality, and can be used in conjunction with the Shapiro-Wilks test to show whether or not data are likely to be normally distributed (McDonald, 2009; Sokal and Rohlf, 1995). For each data set used in my study, data were not normally distributed, requiring the use of non-parametric tests. In addition, the sample size was small (n=25 males), making non-parametric tests appropriate. For this reason, analyses in my study were performed using non-parametric statistics, such as Wilcoxon signed-rank tests, one-sample binomial tests, and Spearman rank correlations.

In my study, the Wilcoxon signed-rank test was used to evaluate a prediction from my hypothesis, that purring rate will be higher during times of male-male agonism. The Wilcoxon signed-rank test allows for the testing of differences between two nominal variables (e.g. individual and time of agonism versus time without agonism) and a measurement variable (e.g. purring rate) (McDonald, 2009; Sokal and Rohlf, 1995). The null hypothesis for the Wilcoxon signed-rank test states that the median difference between pairs of observation is zero

(McDonald, 2009; Sokal and Rohlf, 1995). Under the null hypothesis, smaller values of  $z$  are less likely (McDonald, 2009; Sokal and Rohlf, 1995). The dependent variable was ring-tailed lemur purring rate, and the independent variable was time (i.e. at a time of male-male agonism versus at a time without male-male agonism).

In my study, the binomial test was used to determine if males who purr before or during intra-sexual agonism are more likely to win the agonistic interaction that purring accompanies. The one-sample binomial test allows for the testing of whether the proportion of successes on a two-level categorical dependent variable (e.g. wins while purring versus losses while purring) significantly differs from a hypothesized, predicted value (McDonald, 2009; Sokal and Rohlf, 1995). For the binomial test, the statistical null hypothesis states that categorical values should be equally represented, or do not differ significantly from 50% (McDonald, 2009; Sokal and Rohlf, 1995). For this test, the two-level categorical dependent variables for male purring during agonism were winning versus losing.

In my study, the Spearman rank correlation test was used to evaluate whether high-ranking males have higher purring rates than lower-ranking males. The Spearman rank correlation test is used when there are two measurement variables (e.g. squealing rate and dominance index) and one nominal variable (e.g. individual) which groups measurement variables into pairs (McDonald, 2009; Sokal and Rohlf, 1995). The null hypothesis for the Spearman rank test states that the ranks of one measurement variable do not co-vary with the ranks of the other measurement variable (i.e. as one variable increases, the other is not more likely to increase or decrease) (McDonald, 2009; Sokal and Rohlf, 1995). For this test, the two variables were male purring rate and dominance index. When the Spearman rank correlation test was performed, linear regression was also performed in order to visually summarize the relationship between the variables (McDonald, 2009).

All tests were two-tailed, and means were reported with standard deviations (SD). For all tests, the alpha level was set to 0.05. All statistical tests were performed using SPSS version 20 (IBM SPSS Statistics, IBM Corporation, Armonk, NY, USA, 2011).

## **Results**

There was a significant difference in male purring rate during periods of male-male agonism when compared to periods without male-male agonism (Wilcoxon signed-rank test:  $z = -3.2$ ,  $n = 25$  males,  $p = 0.001$ ; **Figure 2**). Mean male purring rate was higher during times of male-male agonism (5.564 purrs per hour  $\pm$  6.507,  $n = 25$  males) than mean male purring rate at times without male-male agonism (0.201 purrs per hour  $\pm$  0.157,  $n = 25$  males). See **Appendix I** for data on individual male purring rates, which were quite variable.

Out of all observed instances of male-male agonism, purring occurred in 10.27% of interactions (65/633), a small proportion out of total male-male agonistic encounters. However, a large percentage of total purrs, 41.67% (65/156) of total purrs, were heard in male-male agonistic contexts. Of total purrs heard during male-male agonism ( $n = 65$  purrs in male-male agonistic contexts), 67.7% (44/65) of purrs were given by males while winning male-male agonistic encounters, while 32.3% (21/65) of purrs were given by males while losing male-male agonistic encounters. Although purrs were given by both winning and losing males before and during agonistic encounters, purrs were much more likely to be given by winning males (binomial test:  $z = 2.9$ ,  $n = 65$  purrs,  $x = 44$  purrs,  $p = 0.006$ ; **Figure 3**). Further, male purring rate was significantly correlated with male dominance index, such that males with higher overall purring rates had higher dominance status (Spearman rank correlation:  $r_s = 0.56$ ,  $n = 25$  males,  $p = 0.004$ ; linear regression:  $r^2 = 0.37$ ,  $df = 23$ ,  $p = 0.001$ , **Figure 4**). In addition to male dominance rank being correlated with overall purring rate, this correlation was significant when purring rate using only purrs given during male-male agonism were considered (Spearman rank correlation:  $r_s = 0.48$ ,  $n = 25$  males,  $p = 0.015$ ; linear regression:  $r^2 = 0.265$ ,  $df = 23$ ,  $p = 0.008$ , **Figure 5**).

## Discussion

In my study, male purring rate was significantly higher during periods of male-male agonism than at times without male-male agonism. This indicates that purring plays some role in male-male agonistic behaviour in the ring-tailed lemur. Although purring happened infrequently in male-male agonistic interactions, a large proportion of total purrs recorded, 41.67%, were allocated to male-male agonistic behaviours, with the other 58.33% of purrs were allocated to non-agonistic social contexts. This proportion is very similar to the 40% of purrs allocated to aggressive contexts by the close relative of the ring-tailed lemur, the greater bamboo lemur (Bergey and Patel, 2008). Within male-male agonistic encounters, ring-tailed lemur males with

higher purring rates were higher ranking animals and more likely to win in the agonistic interactions that purring accompanied. In the majority of male-male agonistic interactions in ring-tailed lemurs where purring occurs, purring rate seemed to honestly indicate male dominance rank and agonistic ability, making it possible for other males to assess these qualities in a purring male. However, results should be interpreted with caution in that not all winning or high ranking males purred, and not all purring males won agonistic interactions or were high ranking.

In the ring-tailed lemur, the purr call fits the predictions of Morton's MS rules (1977) for an agonistic vocalization. The purr is not a pure, high-pitched, tonal call, as would be expected of a friendly or submissive call, but instead bears the spectral characteristics expected of an aggressive vocalization given at close range (August and Anderson, 1987; Morton, 1977). As is the rule for agonistic calls, the purr is low frequency, broadband, and accompanies intense competition between individuals at close range (Morton, 1977).

### **Comparing study results to previous research on ring-tailed lemur purring function**

My study describes the use of the purr as an intra-sexual threat vocalization by male ring-tailed lemurs, a context for ring-tailed lemur purr use that has not been previously reported. Purring had only been previously described as occurring during ring-tailed lemur grooming, resting, and tail-marking (Jolly, 1966; Macedonia, 1990, 1993). Purrs are used in non-affiliative contexts by a few other mammals (reviewed in Peters, 2002), in situations including aggression (greater bamboo lemur: Bergey and Patel, 2008; black-and-white colobus monkey: Marler, 1972; common squirrel monkey: Baldwin and Baldwin, 1981; Winter et al., 1966), discomfort, and pain (domestic cat: Beaver, 1992; Leyhausen, 1979; red-bellied titi monkey: Moynihan, 1966). In these situations, purring may act as an appeasement signal (Peters, 2002). 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 advertisement of helplessness towards a nearby individual (Beaver, 1992; Leyhausen, 1979), or as an "autocommunicatory signal" which allows the animal to self-soothe (Peters, 2002, p. 264). Red-bellied titi monkey infants purr when in physical contact with surrogate mothers, which Moynihan (1966) suggested expresses infant discomfort at being carried by a potentially threatening non-parent. Similarly to cats, titi monkey infants may also purr to self-soothe or to signal appeasement. Aggressive, agonistic situations

can also be stressful to animals (Summers and Winberg, 2006), and mammals who purr in these contexts may also do so as a form of self-comfort. In the ring-tailed lemur, some purring may also occur as a result of similar motivation. Ring-tailed lemur males purred in some situations of male-male agonism, which are known to be stressful (Cavigelli and Pereira, 2000; Gould et al., 2005; Gould and Ziegler, 2007; Pride, 2005a, 2005b). In these situations, ring-tailed lemur males may purr to self-soothe and/or to signal appeasement, similarly to cats and titi monkeys.

## **Conclusions**

Ring-tailed lemur males purr in some intra-sexual agonistic contexts. Purring rate escalates during periods of male-male agonism, and high purring rate is linked to both high dominance rank and a greater likelihood of winning in male-male agonistic encounters for ring-tailed lemurs. Purring is not only used in male-male agonism in the ring-tailed lemur, but also conforms to signal design expectations for aggressive vocalizations. Male-male agonistic use of the purr vocalization has not been previously reported in this species. The male purr as an agonistic signal can be added to the suite of known vocalization behaviours for the ring-tailed lemur.

## References

- Alatalo, R., Glynn, D., and Lundberg, A. (1990). Singing rate and female attraction in the pied flycatcher: An experiment. *Animal Behavior* 39: 601-603.
- Altmann, J. (1974). Observational study of behavior: sampling methods. *Behaviour* 49: 227-265.
- Anderson, R., Searcy, W., Peters, S., and Nowicki, S. (2008). Soft song in song sparrows: Acoustic structure and implications for signal function. *Ethology* 114: 662-676.
- Andersson, M. (1986). Evolution of condition-dependent sex ornaments and mating preferences: sexual selection based on viability differences. *Evolution* 40: 804-816.
- Andersson, M. (1994). Sexual selection. Princeton, NJ: Princeton University Press.
- Andrew, R. (1962). The situations that evoke vocalization in primates. *Annals of the New York Academy of Sciences* 102: 296-315.
- Andrew, R. (1963). The origins and evolution of calls and facial expressions of the primates. *Behaviour* 20: 1-109.
- August, P., and Anderson, J. (1987). Mammal sounds and motivation-structural rules: A test of the hypothesis. *Journal of Mammalogy* 68: 1-9.
- Baldwin, J., and Baldwin, J. (1981). The squirrel monkeys, genus *Saimiri*. In: Ecology and behavior of neotropical primates. Coimbra-Filho, A., and Mittermeier, R. (eds.). Rio de Janeiro, Brazil: Academic Brasileira de Ciências, pp. 277-330.
- Beaver, B. (1992). Feline behavior: A guide for veterinarians. St. Louis, Miss.: CV Mosby.
- Bell, G. (1978). The handicap principle in sexual selection. *Journal of Theoretical Biology* 32: 872-885.
- Bergey, C., and Patel, E. (2008). A preliminary vocal repertoire of the greater bamboo lemur (*Prolemur simus*). *Nexus* 1: 69-84.
- Boinski, S., Moraes, E., Kleiman, D., Dietz, J., and Baker, A. (1994). Intra-group vocal behaviour in wild golden lion tamarins, *Leontopithecus rosalia*: honest communication of individual activity. *Behaviour* 130: 53-75.
- Bradbury, J., and Vehrencamp, S. (1998). Principles of animal communication. Sunderland, Mass.: Sinauer Associates.
- Briefer, E., Vannoni, E., and McElligott, A. (2010). Quality prevails over identity in the sexually selected vocalizations of an ageing mammal. *BMC Biology* 8:1-15.
- Budnitz, N. and Dainis, K. (1975). *Lemur catta*: Ecology and behavior. In: Lemur biology.

- Tattersall, I., and Sussman, R. (eds.). New York: Plenum Press, pp. 219-235.
- Burt, A. (1995). Perspective: the evolution of fitness. *Evolution* 49: 1-8.
- Cade, W. (1975). Acoustically orienting parasitoids: fly phonotaxis to cricket song. *Science* 190: 1312-1313.
- Carpenter, C. (1934). A field study of the behavior and social relations of the howling monkeys (*Alouatta palliata*). *Comparative Psychological Monographs* 10: 1-68.
- Catchpole, C. and Slater, P. (1995). Bird song: Biological themes and variations. Cambridge, UK: Cambridge University Press.
- Cavigelli, S., and Pereira, M. (2000). Mating season aggression and fecal testosterone levels in male ring-tailed lemurs (*Lemur catta*). *Hormones and Behavior* 37: 246-255.
- Charles-Dominique, P., and Martin, R. (1972). Behaviour and ecology of nocturnal prosimians: Field studies in Gabon and Madagascar. *Advances in Ethology: Supplements to Journal of Comparative Ethology* 9: 1-89.
- Clarke, E., Reichard, U., and Zuberbühler, K. (2012). The anti-predator behavior of wild white-handed gibbons (*Hylobates lar*). *Behavioral Ecology and Sociobiology* 66: 85-96.
- Clutton-Brock, T., and Albon, S. (1979). The roaring of red deer and the evolution of honest advertisement. *Behaviour* 69: 145-170.
- Cuozzo, F., and Sauther M. (2006). Severe wear and tooth loss in wild ring-tailed lemurs (*Lemur catta*): a function of feeding ecology, dental structure, and individual life history. *Journal of Human Evolution* 51:490-505.
- Cuozzo, F., Sauther, M., Gould, L., Sussman, R., Villers, L., and Lent, C. (2010). Variation in dental wear and tooth loss in known-aged, older ring-tailed lemurs (*Lemur catta*): A comparison between wild and captive individuals. *American Journal of Primatology* 72:1026-1037.
- Dabelsteen, T., McGregor, P., Lampe, H., Langmore, N., and Holland, J. (1998). Quiet song in song birds: an overlooked phenomenon. *Bioacoustics* 9: 89-105.
- Dabelsteen, T., and Pedersen, S. (1990). Song and information about aggressive responses of blackbirds, *Turdus merula* - evidence from interactive playback experiments with territory owners. *Animal Behaviour* 40: 1158-1168.
- Darwin, C. (1871). The descent of man, and selection in relation to sex, 1<sup>st</sup> ed. London: John Murray.
- Davies, N. and Halliday, T. (1978). Deep croaks and fighting assessment in toads (*Bufo bufo*).

- Nature* 274: 683-685.
- De la Torre, S., and Snowdon, C. (2002). Environmental correlates of vocal communication of wild pygmy marmosets *Cebuella pygmaea*. *Animal Behaviour* 63: 847-856.
- Delgado, R. (2006). Sexual selection in the loud calls of male primates: signal content and function. *International Journal of Primatology* 27: 5-25.
- Eberhardt, L. (1994). Oxygen consumption during singing by male Carolina wrens (*Thryothorus ludovicianus*). *The Auk* 111: 124-130.
- Eshel, I. (1978). On the handicap principle: A critical defence. *Journal of Theoretical Biology* 70: 245-250.
- Fischer, J., Kitchen, D., Seyfarth, R., and Cheney, D. (2004). Baboon loud calls advertise male quality: acoustic features and their relation to rank, age, and exhaustion. *Behavioral Ecology and Sociobiology* 56: 140-148.
- Fitch, W., and Hauser, M. (2003). Unpacking “honesty”: vertebrate vocal production and the evolution of acoustic signals. In: *Acoustic communication: Springer handbook of auditory research*, vol. 16. Simmons, A., Popper, A., and Fay, R. (eds.). New York: Springer, pp. 65-137.
- Fontaine, R. (1981). The uakaris, genus *Cacajao*. In: *Ecology and behavior of neotropical primates*. Coimbra-Filho, A., and Mittermeier, R. (eds.). Rio de Janeiro, Brazil: Academic Brasileira de Ciências, pp. 443-93.
- Forester, D., and Czarrowsky, R. (1985). Sexual selection in the spring peeper, *Hyla crucifer* (*Amphibia, anura*): role of the advertisement call. *Behaviour* 92: 112-128.
- Fragaszy, D., Schwarz, S., and Shimosaka, D. (1982). Longitudinal observations of care and development of infant titi monkeys (*Callicebus moloch*). *American Journal of Primatology* 2: 191-200.
- Frazer Sissom, D., Rice, D., and Peters, G. (1991). How cats purr. *Journal of Zoology* 223: 67-78.
- Freese, C., and Oppenheimer, J. (1981). The Capuchin monkeys, genus *Cebus*. In: *Ecology and behavior of neotropical primates*. Coimbra-Filho, A., and Mittermeier, R. (eds.). Rio de Janeiro, Brazil: Academic Brasileira de Ciências, pp. 331-390.
- Gaspari, M., and Crockett, C. (1984). The role of scent marking in *Lemur catta* agonistic behavior. *Zoo Biology* 3: 123-132.

- Gosselin-Ildari, A., and Koenig, A. (2012). The effects of group size and reproductive status on vigilance in captive *Callithrix jacchus*. *American Journal of Primatology* 74: 613-621.
- Gould, L. (1994). Patterns of affiliative behavior in adult male ringtailed lemurs (*Lemur catta*) at the Beza-Mahafaly Reserve, Madagascar. Ph.D. dissertation: Washington University, Missouri.
- Gould, L., Sussman, R., and Sauther, M. (2003). Demographic and life-history patterns in a population of ring-tailed lemurs (*Lemur catta*) at Beza Mahafaly Reserve, Madagascar: A 15-year perspective. *American Journal of Physical Anthropology* 120: 182-194.
- Gould, L., and Zeigler, T. (2007). Variation in fecal testosterone levels, inter-male aggression, dominance rank and age during mating and post-mating periods in wild adult male ring-tailed lemurs (*Lemur catta*). *American Journal of Primatology* 69: 1325-1339.
- Gould, L., Ziegler, T., and Wittwer, D. (2005). Effects of reproductive and social variables on fecal glucocorticoid levels in a sample of adult male ring-tailed lemurs (*Lemur catta*) at the Beza Mahafaly reserve, Madagascar. *American Journal of Primatology* 67: 5-23.
- Grafen, A. (1990). Biological signals as handicaps. *Journal of Theoretical Biology* 144: 475-546.
- Heffner, R., and Heffner, H. (1985). Hearing range of the domestic cat. *Hearing Research* 19: 85-88.
- Iwasa, Y., Pomiankowski, A., and Nee, S. (1991). The evolution of costly mate preference. II. The “handicap” principle. *Evolution* 45: 1431-1442.
- Johnstone, R. (1997). The evolution of animal signals. In: Behavioural ecology, an evolutionary approach, 4<sup>th</sup> edition. Krebs, J., and Davies, N. (eds). Oxford, UK: Blackwell, pp. 155-178.
- Jolly, A. (1966). Lemur behavior: A Madagascar field study. London: University of Chicago Press.
- Jones, K. (1983). Inter-troop transfer of *Lemur catta* males at Berenty, Madagascar. *Folia Primatologica* 40: 145-160.
- Jürgens, U. (1979). Vocalization as an emotional indicator: a neuroethological study in the squirrel monkey. *Behaviour* 69: 88-117.
- Kleiman, D, Hoage, R., and Green, K. (1988). The lion tamarins, genus *Leontopithecus*. In: Ecology and Behavior of Neotropical Primates, Vol. 2. Mittermeier, R., Rylands, A., Coimbra-Filho, A., and da Fonseca, G. (eds). Washington, D.C: World Wildlife Fund, pp. 299-347.

- Koyama, N. (1988). Mating behavior of ring-tailed lemurs (*Lemur catta*) at Berenty, Madagascar. *Primates* 29: 163-175.
- Kunc, H., and Wolf, J. (2008) Seasonal changes of vocal rates and their relation to territorial status in male Galápagos sea lions (*Zalophus wollebaeki*) *Ethology* 114: 381-388.
- Leger, D. (1977). An empirical evaluation of instantaneous and one-zero sampling of chimpanzee behavior. *Primates* 18: 387-393.
- Leyhausen, P. (1979). Cat behavior: The predatory and social behavior of domestic and wild cats. New York and London: STPM Garland Press.
- Lode, T. and Le Jacques, D. (2003). Influence of advertisement calls on reproductive success in the male midwife toad *Alytes obstetricans*. *Behaviour* 140: 885-898.
- Macedonia, J. (1986). Individuality in a contact call of the ringtailed lemur. *American Journal of Primatology* 11: 163-179.
- Macedonia, J. (1990). Vocal communication and antipredator behavior in the ringtailed lemur (*Lemur catta*). Ph.D. dissertation: Duke University, North Carolina.
- Macedonia, J. (1993). The vocal repertoire of the ringtailed lemur (*Lemur catta*). *Folia Primatologica* 61:186-217.
- Maestripietri, D., and Call, J. (1996). Mother-infant communication in primates. *Advances in the Study of Behavior* 25: 613- 642.
- Marler, P. (1972). Vocalizations of east African monkeys. II: Black and white colobus. *Behaviour* 42: 175-197.
- Martin, J., and Lopez, P. (2001). Are fleeing “noisy” lizards signaling to predators? *Acta Ethologica* 3: 95-100.
- Martin, P., and Bateson, P. (2007). *Measuring Behavior: An Introductory Guide*. 3rd ed. Cambridge, UK: Cambridge University Press.
- Maynard Smith, J. (1976). Sexual selection and the handicap principle. *Journal of Theoretical Biology* 57: 239-242.
- Maynard Smith, J. (1978). *The evolution of sex*. Cambridge, UK: Cambridge University Press.
- Maynard Smith, J. (1985). Mini review: Sexual selection, handicaps, and true fitness. *Journal of Theoretical Biology* 115: 1-8.
- McCarthy, J. (1996). The energetic cost of begging in nestling passerines. *The Auk* 113: 178-188.
- McComb, K. (1991). Female choice for high roaring rates in red deer, *Cervus elaphus*. *Animal Behavior* 41: 79-88.

- McDonald, J. (2009). Handbook of biological statistics 2<sup>nd</sup> ed. Baltimore, MD: Sparky House Publishing.
- Mertl, A. (1976). Olfactory and visual cues in social interactions of *Lemur catta*. *Folia Primatologica* 26: 151-161.
- Morton, E. (1977). On the occurrence and significance of motivation-structural rules in some bird and mammal sounds. *American Naturalist* 111: 855-869.
- Moynihan, M. (1966). Communication in the titi monkey (*Callicebus*). *Journal of Zoology* 150: 77-127.
- Neville, M., Glander, K., Braza, F., and Rylands, A. (1988). The howling monkeys, genus *Alouatta*. In: Ecology and Behavior of Neotropical Primates, Vol. 2. Mittermeier, R., Rylands, A., Coimbra-Filho, A., and da Fonseca, G. (eds). Washington, D.C.: World Wildlife Fund, pp. 349-453.
- Oda, R. (1996). Effects of contextual and social variables on contact call production in free-ranging ringtailed lemurs (*Lemur catta*). *International Journal of Primatology* 17: 191-205.
- Oppenheim, A., Willsky, A., and Nawab, S. (1996). Signals and Systems 2<sup>nd</sup> ed. New York: Prentice Hall.
- Palagi, E., Telara, S., and Borgognini Tarli, S. (2003). Sniffing behavior in *Lemur catta*: seasonality, sex, and rank. *International Journal of Primatology* 24: 335-350.
- Parga, J. (2006a) Male mate choice in *Lemur catta*. *International Journal of Primatology* 27: 107-131.
- Parga, J. (2006b). Sexual selection in the ringtailed lemur (*Lemur catta*): female choice, male mating strategies, and male mating success in a female dominant primate. Ph.D. dissertation: University of Texas at Austin, Texas.
- Parga, J. (2010). Post-ejaculatory mounting in the ring-tailed lemur (*Lemur catta*): A behavior solicited by females? *Ethology* 116: 832-842.
- Pereira, M., and Kappeler, P. (1997). Divergent systems of agonistic behaviour in lemurid primates. *Behaviour* 134: 225-274.
- Pereira, M., and Weiss, M. (1991). Female mate choice, male migration, and the threat of infanticide in ringtailed lemurs. *Behavioral Ecology and Sociobiology* 28: 141-152.
- Peters, G. (2002). Purring and similar vocalizations in mammals. *Mammal Review* 32: 245-271.
- Petter, J., and Charles-Dominique, P. (1979). Vocal communication in prosimians. In: The study

- of prosimian behaviour. Doyle, G., and Martin, R. (eds.). New York: Academic Press, pp. 247-305.
- Pola, Y., and Snowdon, C. (1975). The vocalizations of pygmy marmosets (*Cebuella pygmaea*). *Animal Behaviour* 23: 826-842.
- Pomiankowski, A. (1987a). The costs of choice in sexual selection. *Journal of Theoretical Biology* 128: 195-218.
- Pomiankowski, A. (1987b). Sexual selection: the handicap principle does work - sometimes. *Proceedings of the Royal Society of London Series B, Biological Sciences* 231: 123-145.
- Pomiankowski, A., and Iwasa, Y. (1998). Handicap signaling: loud and true? The handicap principle: A missing piece of Darwin's puzzle. *Evolution* 52: 928-932.
- Pomiankowski, A., and Møller, A. (1995). A resolution of the lek paradox. *Proceedings of the Royal Society of London Series B, Biological Sciences* 260: 21-29.
- Pomiankowski A., Iwasa, Y., and Nee, S. (1991). The evolution of costly mate preference. I. Fisher and the biased mutation. *Evolution* 45: 1422-1430.
- Prestwich, K. (1994). The energetic of acoustic signaling in anurans and insects. *American Zoologist* 34: 625-643.
- Pride, R. (2005a). High faecal glucocorticoid levels predict mortality in ring-tailed lemurs (*Lemur catta*). *Biology Letters* 1: 60-63.
- Pride, R. (2005b). Optimal group size and seasonal stress in ring-tailed lemurs (*Lemur catta*). *Behavioral Ecology* 16: 550-560.
- Radesater, T., Jakobsson, S., Andbjør, N., Bylin, A., and Nystrom, K. (1987). Song rate and pair formation in the willow warbler. *Animal Behavior* 35: 1645-1651.
- Reby, D. and McComb, K. (2003). Anatomical constraints generate honesty: acoustic cues to age and weight in the roars of red deer stags. *Animal Behavior* 65: 519-530.
- Reid, J., Arcese, P., Cassidy, A., Hiebert, S., Smith, J., Stoddard, P., Marr, A. and Keller, L. (2004). Song repertoire size predicts initial mating success in male song sparrows, *Melospiza melodia*. *Animal Behavior* 68: 1055-1063.
- Remmers, J., and Gautier, H. (1972). Neural and mechanical mechanisms of feline purring. *Respiration Physiology* 16: 351-361.
- Rhine, R., and Linville, A. (1980). Properties of one-zero scores in observational studies of primate social behavior: The effect of assumptions on empirical analyses. *Primates* 21: 111-122.

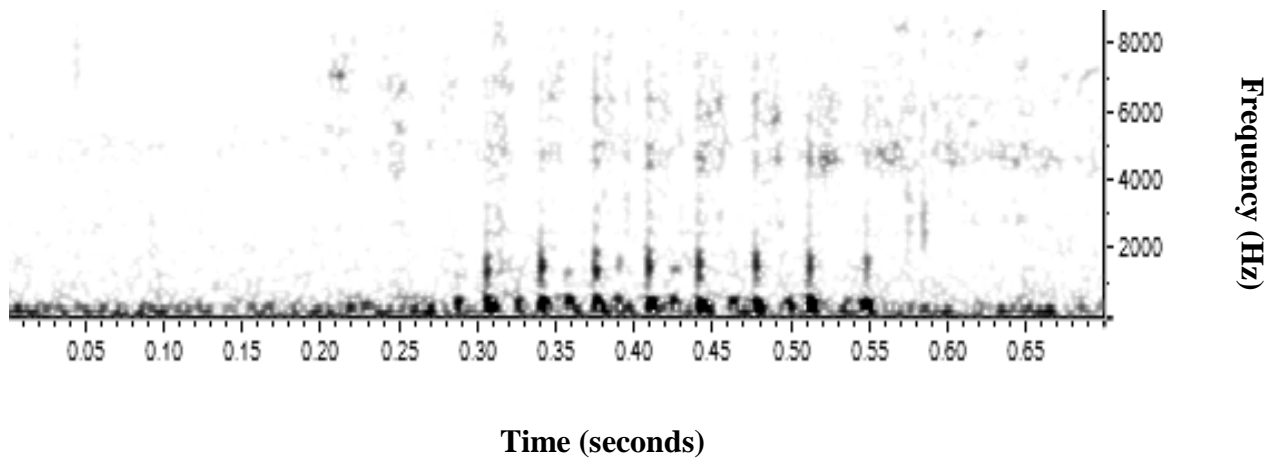
- Rowell, T., and R. Hinde (1962). Vocal communication by the rhesus monkey (*Macaca mulatta*). *Proceedings of the Zoological Society of London* 138: 279-294.
- Sarfaty, A., Margulis, S., and Atsalis, S. (2012). Effects of combination birth control on estrous behavior in captive western lowland gorillas, *Gorilla gorilla gorilla*. *Zoo Biology* 31: 350-361.
- Sauther, M. (1989). Antipredator behavior in troops of free-ranging *Lemur catta* at Beza Mahafaly Special Reserve, Madagascar. *International Journal of Primatology* 10: 595-606.
- Sauther, M. (1991). Reproductive behavior of free-ranging *Lemur catta* at Beza Mahafaly Special Reserve, Madagascar. *American Journal of Physical Anthropology* 84: 463-477.
- Sauther, M., and Cuzzo, F. (2008). Somatic variation in living, wild ring-tailed lemurs (*Lemur catta*). *Folia Primatologica* 79: 55-78.
- Sauther, M., and Cuzzo, F. (2009). The impact of fallback foods on wild ring-tailed lemur biology: A comparison of intact and anthropogenically disturbed habitat. *American Journal of Physical Anthropology* 140: 671-686.
- Sauther, M., Sussman, R., and Cuzzo, F. (2002). Dental and general health in a population of wild ring-tailed lemurs: a life history approach. *American Journal of Physical Anthropology* 117: 122-132.
- Schaller, G. (1963). *The mountain gorilla: Ecology and behavior*. Chicago, IL: Chicago University Press.
- Scheumann, M., Zimmermann, E., and Deichsel, G. (2007). Context-specific calls signal infants' needs in a strepsirrhine primate, the gray mouse lemur (*Microcebus murinus*). *Developmental Psychobiology* 49: 708-718.
- Schilling, A. (1974). A study of marking behavior in *Lemur catta*. In: *Prosimian biology*. Doyle, G., Martin, R., and Walker, A. (eds.). Pittsburg: University of Pittsburgh Press, pp. 347-362.
- Scordato, E., and Drea, C. (2007). Scents and sensibility: information content of olfactory signals in the ringtailed lemur (*Lemur catta*). *Animal Behaviour* 73: 301-314.
- Searcy, W., Anderson, R., and Nowicki, S. (2006). Bird song as a signal of aggressive intent. *Behavioral Ecology and Sociobiology* 60: 234-241.
- Snowdon, C. (2004). Sexual selection and communication. In: *Sexual selection in primates: new*

- and comparative perspectives. Kappeler, P., and van Schaik, C. (eds). Cambridge, UK: Cambridge University Press, pp. 57-70.
- Snowdon, C., and Hodun, A. (1981). Acoustic adaptations in pygmy marmoset contact calls: locational cues vary with distances between conspecifics. *Behavioral Ecology and Sociobiology* 9: 295-300.
- Sokal, R., and Rohlf, F. (1995). *Biometry: The principles and practice of statistics in biological research* 3<sup>rd</sup> ed. New York: W.H. Freeman and Company.
- Struhsaker, T. (1967) Auditory communication among vervet monkeys (*Cercopithecus aethiops*). In: *Social communication among primates*. Altmann, S. (ed). Chicago University Press, Chicago, IL, pp. 281-324.
- Suen, H., and Ary, D. (1984). Variables influencing one-zero and instantaneous time sampling outcomes. *Primates* 25: 89-94.
- Summers, C., and Winberg, S. (2006). Interactions between the neural regulation of stress and aggression. *Journal of Experimental Biology* 209: 4581-4589.
- Sussman, R. (1991). Demography and social organization of free-ranging *Lemur catta* in the Beza Mahafaly Reserve, Madagascar. *American Journal of Physical Anthropology* 84: 43-58.
- Sussman, R. (1992). Male life history and intergroup mobility among ringtailed lemurs (*Lemur catta*). *International Journal of Primatology* 13: 395-413.
- Sussman, R., and Ratsirarson, J. (2006). Beza Mahafaly Special Reserve: A research site in southwestern Madagascar. In: *Ringtailed lemur biology: Lemur catta in Madagascar*. Jolly, A., Sussman, R., Koyama, N., Rasamimanana, H. (eds.). New York: Springer, pp. 43-51.
- Sussman, R., Richard, A., Ratsirarson, J., Sauther, M., Brockman, D., Gould, L., Lawler, R., and Cuzzo, F. (2012). Beza Mahafaly Special Reserve: A research site in southwestern Madagascar. In: *Long Term Field Studies of Primates*. Kappeler, P., and Watts D. (eds.). New York: Springer, pp. 45-66.
- Suzuki, M., and Sugiura, H. (2011). Effects of proximity and activity on visual and auditory monitoring in wild Japanese macaques. *American Journal of Primatology* 73: 623-631.
- Taylor, L. (1986). Kinship, dominance, and social organization in a semi-free ranging group of ringtailed lemurs (*Lemur catta*). Ph.D. Dissertation: Washington University, Missouri.
- Taylor, L. and Sussman, R. (1985). A preliminary study of kinship and social organization in a

- semi-free-ranging group of *Lemur catta*. *International Journal of Primatology* 6: 601-614.
- Titus, R. (1998). Short-range and long-range songs: use of two acoustically distinct song classes by dark-eyed juncos. *The Auk* 115: 386-393.
- Van Horn, R., and Resko, J. (1977). The reproductive cycle of the ring-tailed lemur (*Lemur catta*), sex steroid levels and sexual receptivity under controlled photoperiods. *Endocrinology* 101: 1579-1586.
- Wiley, R. (1991). Lekking in birds and mammals: behavioral and evolutionary issues. *Advances in the Study of Behavior* 20: 201-291.
- Winter, P., Ploog, D., and Latta, J. (1966) Vocal repertoire of the squirrel monkey (*Saimiri sciureus*), its analysis and significance. *Experimental Brain Research* 1: 359-384.
- Wintle, B., Kavanagh, R., McCarthy, M., and Burgman, M. (2005). Estimating and dealing with detectability in occupancy surveys for forest owls and arboreal marsupials. *Journal of Wildlife Management* 69: 905-917.
- Zahavi, A. (1975). Male selection: a selection for a handicap. *Journal of Theoretical Biology* 53: 205-214.
- Zahavi, A., and Zahavi, A. (1997). The handicap principle: A missing piece of Darwin's puzzle. Oxford: Oxford University Press.
- Zimmermann, E., and Lerch, C. (1993). The complex acoustic design of an advertisement call in male mouse lemurs (*Microcebus murinus*) and sources of its variation. *Ethology* 93: 211-224.
- Zuberbühler, K., Jenny, D., and Bshary, R. (1999). The predator deterrence function of primate alarm calls. *Ethology* 105: 477-490.
- Zumpe, D., and Michael, R. (1986). Dominance index: A simple measure of relative dominance status in primates. *American Journal of Primatology* 10: 291-300.

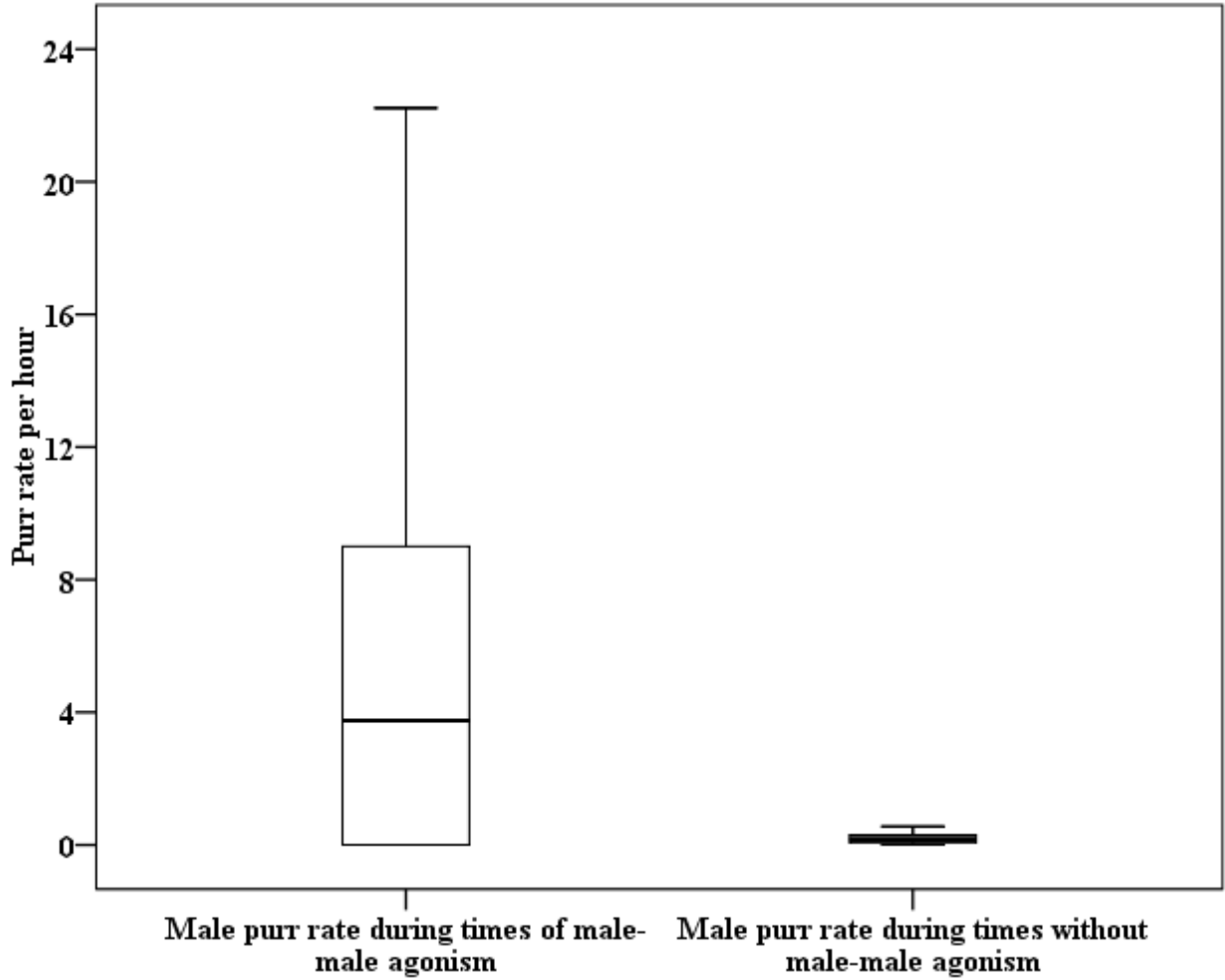
**Table 1. Male ring-tailed lemur study individuals at Beza Mahafaly Special Reserve,  
March-July 2010**

Troop	Individual name	Group membership status	Dominance index score in %	Known or approximate age in years
Green	Umm1g	Non-natal	91.9	≥4
Green	Umm2g	Non-natal	85	≥4
Green	175	Non-natal	71.9	≥8
Green	Umm3g	Non-natal	38.9	≥4
Green	203	Non-natal	36.4	≥8
Orange	263	Non-natal	98.2	≥7
Orange	259	Non-natal	83	7
Orange	Umm1o	Non-natal	49.1	≥4
Orange	291	Non-natal	45.7	≥7
Orange	318	Natal	37.8	3
Orange	226	Non-natal	12.6	≥12
Purple	Umm2p	Non-natal	100	≥4
Purple	Umm1p	Non-natal	76.5	≥4
Purple	Umm4p	Non-natal	69.9	≥4
Purple	323	Natal	46.4	3
Purple	322	Natal	41.7	3
Purple	Umm3p	Non-natal	36.1	≥4
Red	280	Non-natal	85	≥6
Red	273	Non-natal	72.7	≥6
Red	308	Natal	28.6	3
Red	307	Natal	13.7	3
Yellow	208	Non-natal	79.2	≥9
Yellow	Umm2y	Non-natal	75.2	≥4
Yellow	230	Non-natal	74.4	≥8
Yellow	Umm1y	Non-natal	46.2	≥4



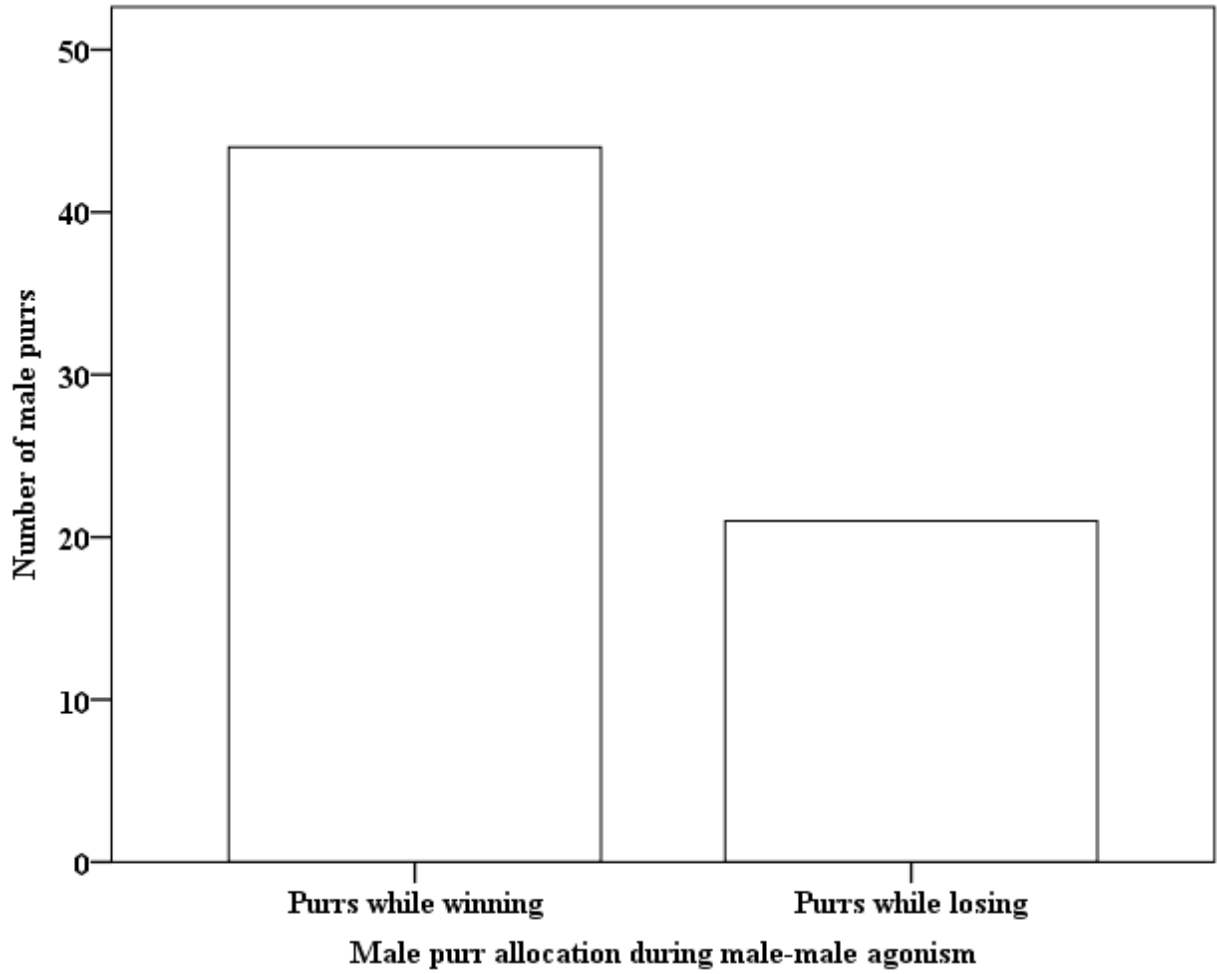
**Figure 1. Sound spectrogram of a male ring-tailed lemur purr, recorded with 44.1kHz sampling rate, 16-bit sample depth, and 64 kilobits/second MP3 compression, and with the spectrogram created using a Blackman window with 2048 frequency bins.**

This spectrogram shows pronounced purring activity from 0.3-0.55 seconds. Purring was composed of pulses observed at intervals of 0.033-0.04 seconds.

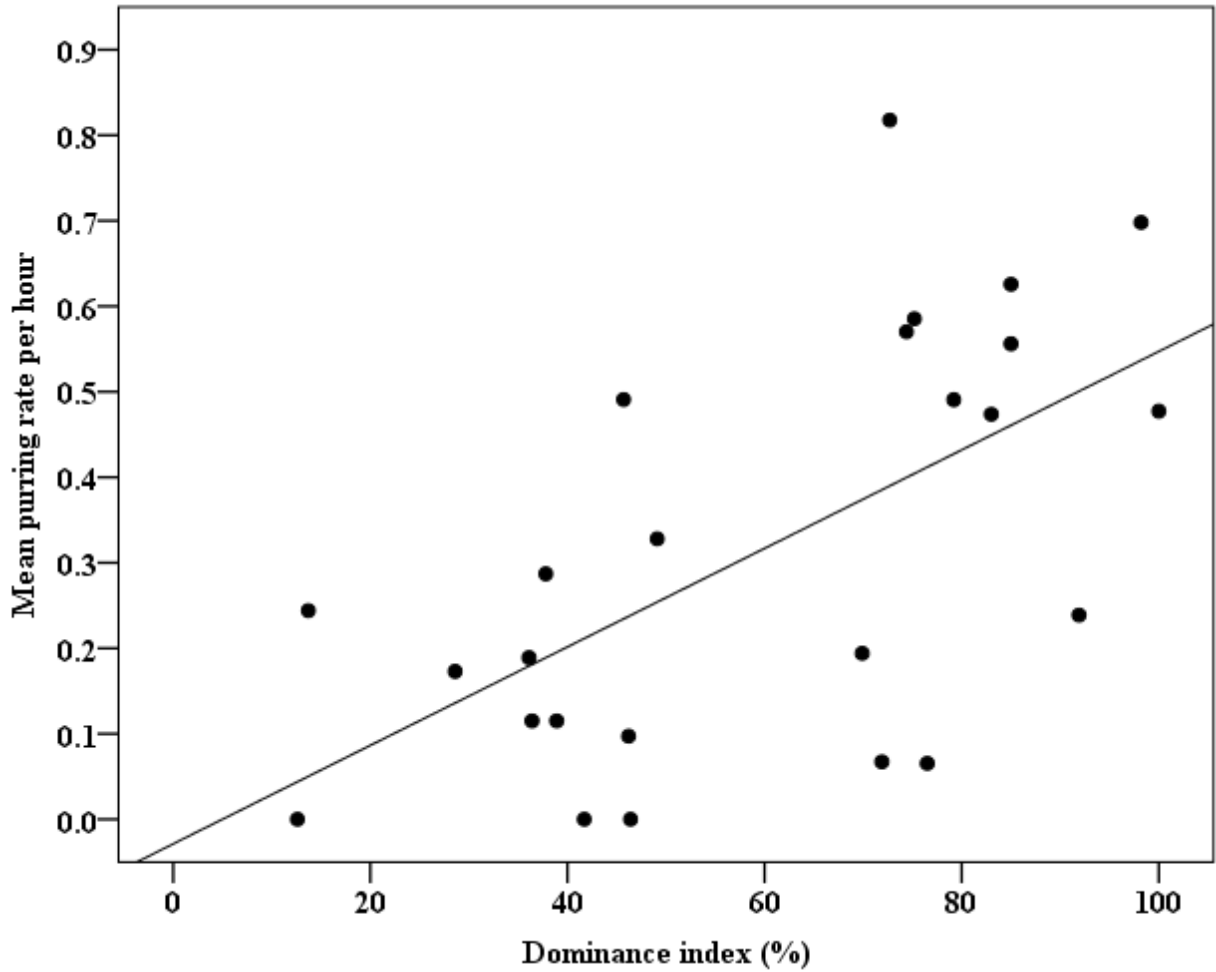


**Figure 2. Mean male ring-tailed lemur purring rate per hour during periods of male-male agonism versus male purring rate during times without agonism.**

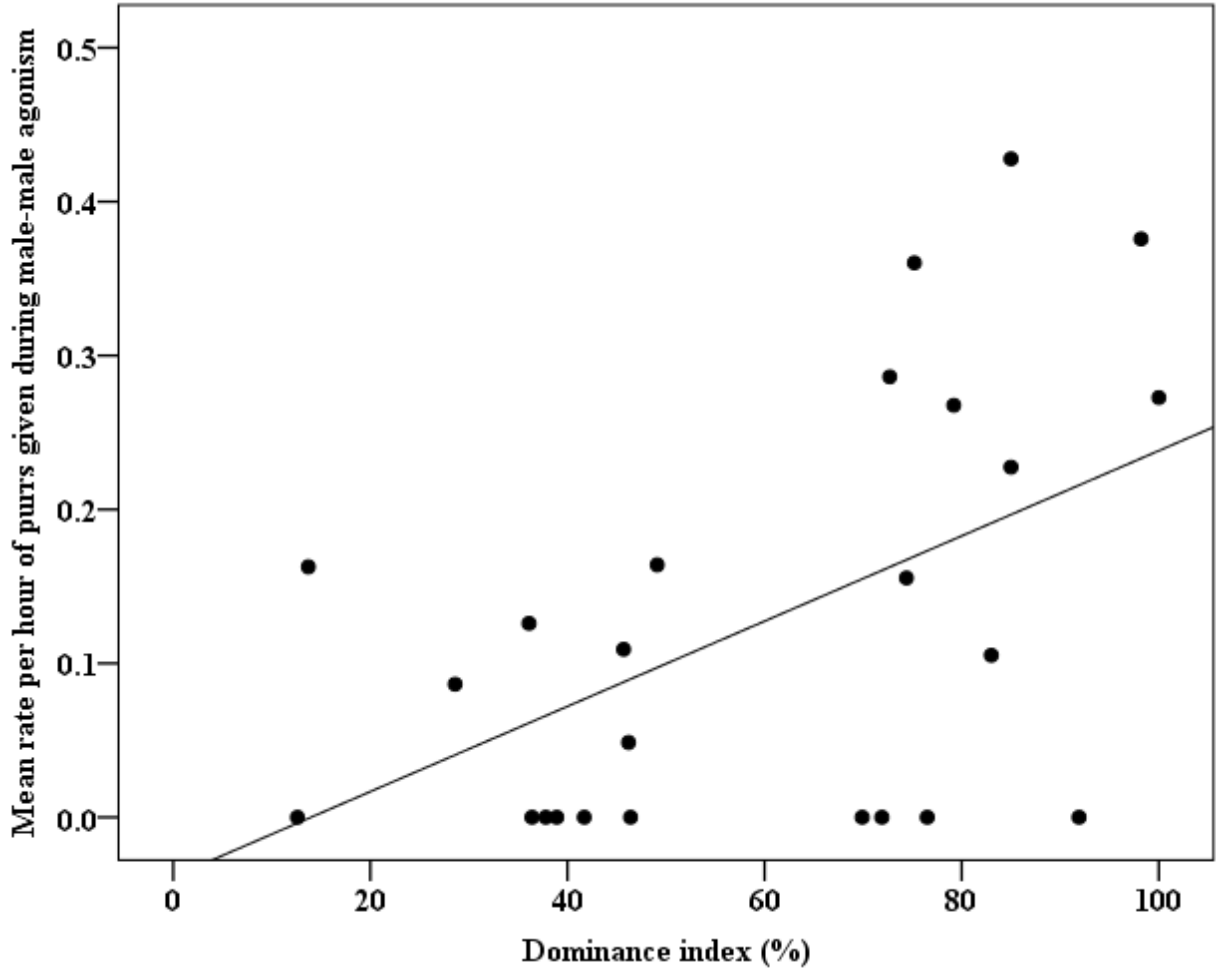
Boxes represent inter-quartile ranges, lines represent median values, and whiskers represent maximum and minimum values.



**Figure 3. Male ring-tailed lemur purr allocation during male-male agonism and outcome of the agonistic interaction.**



**Figure 4. Correlation between male ring-tailed lemur dominance index score and mean male purring rate, with linear regression. Individual points represent individual males.**



**Figure 5. Correlation between male ring-tailed lemur dominance index score and mean rate for purrs given during male-male agonism, with linear regression. Individual points represent individual males.**

## **Chapter 3. The function of howling in the ring-tailed lemur (*Lemur catta*)**

### **Abstract**

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

### **Introduction**

#### **Male long calls**

A variety of signals are used to mediate social relationships in group-living animals. While many signals are used by both sexes, vocal signals related to mate attraction and intra-sexual competition are often sex-specific (Bradbury and Vehrencamp, 1998; Searcy and Andersson, 1986). One of the best-researched types of sex-specific vocalization is the male long call or loud call, named for the long distance that such vocalizations carry. Male-specific long-

range calls are made by birds, amphibians, and mammals including non-human primates, and such calls carry for spans of greater than 1 kilometre in some species, such as Sumatran orangutans (*Pongo abelii*) (Delgado, 2006). Animals may have a variety of different vocalizations which carry for long distances, but the long call is typically the vocalization within a species' repertoire that carries for the longest distance, and is usually made only by males (Waser and Waser, 1977; Wich and Nunn, 2002).

Gautier and Gautier (1977) divided long calls given by adult male primates into two categories. Type 1 loud calls are stereotyped and discrete at individual or specific level, have high intensity, and small variability in form. In contrast, Type 2 loud calls are less stereotyped and more structurally variable calls, and are often used in anti-predator interaction. Male-specific long calls can be classified as type 1 loud calls, according to these criteria (Gautier and Gautier, 1977). When males hear a type 1 loud call, whether from a fellow group member or non-group male, they typically counter-call in response (Wich and Nunn, 2002). Male-specific long calls are found throughout a variety of amphibian, avian, and mammalian species, and they are typically repetitive, complex in form, individual- and species-specific, stereotyped, and seasonal (Bradbury and Vehrencamp, 1998; Delgado, 2006; Snowdon, 2004).

### **The handicap principle: Long calls honestly indicate male quality**

Male long calls are thought to be examples of handicap signals (Delgado, 2006; Wich and Nunn, 2002). The handicap hypothesis states that in order for a signal to remain honest over evolutionary time, it must be heritable as well as costly such that it "handicaps" the signaling individual's fitness (Zahavi, 1975). Further, the honest signal must have lower costs for high-quality individuals and higher costs for low-quality individuals (Grafen, 1990, 1991). Over generations, high-quality signalers will have higher fitness since they will be better able to bear the costs associated with the honest signal (Grafen, 1990; Zahavi and Zahavi, 1997).

In many animals, long calls include variations in spectral and temporal properties which honestly advertise individual male qualities (Andersson, 1982; Bradbury and Vehrencamp, 1998; Zimmermann, 1995a). Males who call compete with one another for the attention of mates, and this selects for variation in aspects of vocalizations which provide honest information about male competitive ability and condition (reviewed in Delgado, 2006). Sexual selection has the potential to act on the information about males provided by such variations. For example, in the red deer

(*Cervus elaphus*), long call rate indicates male body and energetic condition (Clutton-Brock and Albon, 1979; McComb, 1991), while in the gray tree frog (*Hyla versicolor*), call duration indicates genetic quality (Doty and Welch, 2001; Welch et al., 1998). Primates ranging from strepsirhines to anthropoids are known to have long calls which honestly indicate male characteristics (Delgado, 2006; Wich and Nunn, 2002). In Old World monkeys such as the chacma baboon (*Papio ursinus*), acoustic characteristics of male long calls correlate with male dominance rank, age, and calling bout length (Fischer et al., 2004). In chacma baboons, individual differences in long calls are linked to dominance level in males, such that high-ranking males make more frequent and longer loud calls at faster rates than low-ranking males (Kitchen et al., 2003a, 2003b, 2005). Long calling rate thus honestly indicates stamina and competitive ability in male chacma baboons (Kitchen et al., 2003b). Amongst New World monkeys, red howler monkeys (*Alouatta seniculus*) males are thought to assess one another based on duration and rate of howling bouts, allowing dominant males with higher competitive ability to monopolize females and discourage non-group males from approaching (Sekulic, 1982; Sekulic and Chivers, 1986).

### **Long calls are energetically expensive**

Evidence for the energetic expense of male-specific long calls exists for insects, anuran amphibians, and a variety of non-human primate species (review of insects and anurans: Prestwich, 1994; review of primates: Wich and Nunn, 2002). For gibbon species (*Hylobates* spp.), long calling rates decrease during seasons of low food abundance and with lower temperature and altitude, which is thought to be related to male condition (Cowlshaw, 1996). Cowlshaw (1996) suggests that such calls are therefore assessment signals, allowing conspecifics to assess the quality of a male gibbon through his long calling rate. Whitten (1982) found that Kloss gibbons (*Hylobates klossii*) give morning long calls at lower rates following nights with temperatures lower than 21.5°C, further suggesting the impact of low temperature on male body condition. Both Kloss gibbons and Thomas langurs (*Presbytis thomasi*) give morning long calls at lower rates following stormy nights, attesting to the negative effects of rain on male condition (gibbons: Whitten, 1982; langurs: Steenbeek et al., 1999). Wich and Nunn (2002) and Steenbeek et al. (1999) suggest that the lowered calling rate of male gibbons and langurs following rain evidences the energetic expense of long calls for these species.

## **Sexual selection and male long calls**

In general, increasing long call duration and repetition rate greatly augments the energetic costs of signaling for many species (Bradbury and Vehrencamp, 1998; Vehrencamp, 2000). Males with call qualities indicating good genes, good condition, or superior competitive ability are known to be preferred as mates by females (Bradbury and Vehrencamp, 1998; Delgado, 2006; Zahavi, 1975). Females are known to prefer high-quality mates who can afford to incur the costs associated with energetically costly vocalizations so that superior genes can be passed down to their offspring, while rival males are more likely to lose in fights to a superior competitor (reviewed in Wich and Nunn, 2002; Zahavi, 1975). Long-call vocal displays can thus be considered honest indicators of male fitness (Zahavi, 1975, 1982; Zahavi and Zahavi, 1997).

Snowdon (2004) established a set of guidelines to consult in determining whether signals such as vocalizations may be sexually selected. According to Snowdon's (2004) criteria, in order to be sexually selected, a signal must:

- 1) be sexually dimorphic
- 2) differ between same-sex individuals
- 3) be preferred or avoided in variant forms by conspecifics
- 4) be preferred or avoided by conspecifics in contexts related to reproduction
- 5) be linked to fitness and reproductive success.

Delgado (2006) felt that long calls in many primate species met Snowdon's (2004) criteria, and should therefore be further investigated with reference to sexual selection.

## **Hypotheses for male long calls in primates**

Across species, male-specific long calls typically have some role in attracting females or repelling rival males, and more generally serve as long-distance advertisements of a male's presence in a certain location (Bradbury and Vehrencamp, 1998; reviewed in Delgado, 2006). Further to these observations, several hypotheses have been proposed for the utility of male-specific primate long calls.

The leading hypothesis for male long calling in primates is the mate defense hypothesis, which states that males long call to mediate male-male competition for female mates (Wich and Nunn, 2002). According to the mate defense hypothesis, males make long calls in order to deter the approach of other males, both from within their group and from other groups, and to prevent these other males from mating with estrous females. Since males are known to compete with one another mainly for sexual access to females, this hypothesis is founded on intra-sexual selection theory (Emlen and Oring, 1977). The mate defense hypothesis has support from primates including the Thomas langur and the chacma baboon (langurs: van Schaik et al., 1992; baboons: Cheney and Seyfarth, 1977; Cowlshaw, 1995). During inter-troop encounters, male chacma baboons were more likely to long call and engage in aggression when estrous females were present, and dominant males called more frequently than low-ranking males (Kitchen et al., 2004a). In Thomas langurs, males advertised their presence in a group through long calling during inter-group encounters, and a high level of male-male agonism in inter-group encounters reflected mate defense rather than territoriality (van Schaik et al., 1992). These results provide support for the female defense hypothesis for both species (Kitchen et al., 2004a; van Schaik et al., 1992).

An alternative hypothesis for male long calling is the mate attraction hypothesis, which suggests that males make long calls as a courtship display, in order to entice estrous females to mate with them (Delgado, 2006; Wich and Nunn, 2002). According to this hypothesis, male long calls should attract estrous females and females should preferentially mate with calling males. This hypothesis has support from primates including gibbons and gray mouse lemurs (*Microcebus murinus*). In gibbon species, which are monogamous, unmated males consistently long call while mated males do not, and unmated males also produce the longest song bouts, suggesting a mate attraction function (Cowlshaw, 1992; Mitani, 1988; Raemaekers et al., 1984). In gray mouse lemurs, males produce trill calls at much higher rates when in the presence of an estrous female, and males who call at higher rates have greater reproductive success (Zimmermann, 1995b; Zimmermann and Lerch, 1993).

Much research exists relating these hypotheses to the long calling of primate species from diverse suborders, but Malagasy strepsirhines have been largely neglected in scholarship (reviewed in Delgado, 2006; reviewed in Wich and Nunn, 2002). To date, male-specific long calls have been studied in detail only in gray mouse lemurs, with support found for the mate

attraction hypothesis (Zimmermann, 1995a, 1995b; Zimmermann and Lerch, 1993; Zimmermann et al., 2000). My study will add to existing scholarship by evaluating how the mate defense and mate attraction hypotheses may be applied to the male long call of another Malagasy strepsirhine, the ring-tailed lemur (*Lemur catta*).

### **Background on the ring-tailed lemur**

The ring-tailed lemur is a female-dominant strepsirhine primate endemic to southern Madagascar (Jolly, 1966). It is a gregarious animal that lives in multi-male, multi-female groups of up to twenty-seven animals (Gould et al., 2003; Pride, 2005; Sussman, 1991). Males disperse from their natal group at 3-4 years of age and disperse to new groups approximately every three years, while females usually remain in their natal groups for their entire lives (Budnitz and Dainis, 1975; Jones, 1983; Sussman, 1992). Ring-tailed lemur groups are territorial, with females taking the primary role in group defense during inter-troop encounters (Jolly, 1966; Mertl-Milhollen, 2006).

Although females are dominant, males have their own dominance hierarchy, which is often linear (Budnitz and Dainis, 1975; Gould, 1994; Taylor, 1986). Dominance confers social advantages for high-ranking males, typically including first sexual access to group females when they are in estrus (Koyama, 1988; Parga, 2006b; Sauther, 1991). The ring-tailed lemur has an annual breeding season that begins in April/May in Madagascar, with females in asynchronous estrus (Jolly, 1966). Each female stays in estrus for 3.25 to 24 hours in total, and during this time females mate with multiple males (Jolly, 1966; Parga, 2006a; Sauther, 1991; Van Horn and Resko, 1977). Although resident males typically have mating priority, non-group males are also known to mate with females (Koyama, 1988; Sauther, 1991; Sussman, 1992). Mating opportunities are usually restricted to non-natal males, who are sexually mature and unrelated to group females (Parga, 2010; Sauther, 1991; Taylor and Sussman, 1985). The competition between non-natal males for mates leads to a high degree of male-male aggression during the breeding season, and can lead to severe injuries and even death (Gould and Ziegler, 2007; Jolly, 1966; Sauther 1991).

Male social behaviour is mediated by a number of vocalizations, which have been studied by a number of researchers (Andrew, 1963; Jolly, 1966; Macedonia, 1986, 1990, 1993; Oda, 1996; Petter and Charles-Dominique, 1979; Sauther, 1989). As a highly social strepsirhine, the

ring-tailed lemur has a large vocal repertoire comprised of 22 distinct vocalizations for adults (Macedonia, 1990). These consist of 8 calls used in affiliative interactions, 6 calls used in agonistic behaviour, and 8 anti-predator vocalizations (Macedonia, 1990). Of these 22 calls, several are long-range, two are male-specific, and some are known to be individually distinctive (Jolly, 1966; Macedonia, 1986, 1990, 1993). This study focuses on the howl vocalization, a male-specific long-distance call thought to be affiliative (Jolly, 1966; Macedonia, 1990).

### **Howling in the ring-tailed lemur**

In the ring-tailed lemur, the howl is known to be a male-specific call which carries for up to 1 km (Jolly, 1966; Macedonia, 1990; Petter and Charles-Dominique, 1979). The howl is thought to be individually distinctive in the ring-tailed lemur, with howler identity likely distinguishable by conspecifics (Koyama, 1988). The howl is tonal, song-like, and repetitive, with single howls lasting seconds combining into howling bouts which usually last for around 20-30 seconds (Andrew, 1963; Jolly, 1966). A howling bout may be composed of ten or more howls (Andrew, 1963). When represented spectrally, each ring-tailed lemur howl consists of 1-3 continuous simple tonal to complex units (Macedonia, 1990; **Figure 1**).

A single male may howl alone, or some or all of the males in his troop may join him in a howling bout (Andrew, 1963; Jolly, 1966; Macedonia, 1990). When males howl together, high-ranking males typically initiate howling bouts, with all group males joining him (Macedonia, 1990). When multiple males howl at the same time to create a howling chorus, each male howls at his own rate and no temporal coordination of howling occurs (Macedonia, 1990; **Figure 2**). Howling in the ring-tailed lemur is contagious, such that males often join a group male in howling, and also howl after hearing males from another group howl (Jolly, 1966; Macedonia, 1990). All ring-tailed lemur males who are past infancy howl (Macedonia, 1990), but females do not typically howl and have been observed howling only on rare occasions (Jolly, 1966; Sauther, 1991). Howling is thought to function as an inter-troop signal (Petter and Charles-Dominique, 1979) broadcasting the presence and location of the troop (Jolly, 1966; Macedonia, 1990).

Ring-tailed lemur males have been observed howling in a number of different social situations. Males howl due to changes of light and before sleeping (Jolly, 1966), as well as in response to other howls or recurring loud sounds (Andrew, 1963). A single high-ranking male typically howls throughout the year at dusk, when settling in night sleeping trees, with other

male group members often joining in (Jolly, 1966; Koyama, 1988; Macedonia, 1990). However, howling rate has been observed to increase both during the breeding season, when many males howl throughout the day and night (Jolly, 1966; Mertl-Milhollen et al., 1979), and at the end of the birthing season (Budnitz and Dainis, 1975). During the breeding season, Macedonia (1990) also observed males travelling a short distance from their troop, howling, and then awaiting a response from other lemurs.

### **My study: elucidating why male ring-tailed lemurs howl**

The goal of this study is to assess whether hypotheses for long calling that are related to sexual selection theory may be applicable for the ring-tailed lemur. This study will evaluate whether the mate defense and the mate attraction hypotheses for long-calling can be applied to the male-specific howl vocalization in the ring-tailed lemur. The mate defense hypothesis has relevance to intra-sexual selection both inside and outside social groups, and since the ring-tailed lemur is a polygynandrous species, male-male competition occurs between males in the same and different groups (Jolly, 1966; Sussman, 1992). For this reason, the mate defense hypothesis for male long calling will be addressed separately within and between groups.

### **H1: Intra-group function of the mate defense hypothesis**

I predict that higher ranking ring-tailed lemur males will have higher howling rates than lower ranking males. Anecdotal observations from other researchers indicate that high ranking males howl more often than do lower ranking males (Jolly, 1966; Koyama, 1988; Macedonia, 1990), but this idea has not been empirically tested. If male dominance rank is correlated with howling rate, then howling has the potential to indicate male agonistic ability. Howling may therefore be used in male-male agonism and as a form of self-advertisement to other males.

Further to this prediction, do high ranking ring-tailed lemur males produce howling bouts containing a greater number of howls (i.e. longer howling bouts) than do low-ranking males? If high ranking males produce longer howling bouts, then they would be repeating a stereotyped long call at a higher rate than lower ranking males. As would be consistent with the stereotyped, repetitive long calls of other male animals, if dominant males have longer howling bouts, this result would also provide support for the idea of the ring-tailed lemur male howl being an advertisement of male fighting ability and dominance rank.

Finally, do ring-tailed lemur males howl during male-male agonistic contexts, including immediately before or after an agonistic interaction? If males are more likely to howl before or after times of male-male agonism than at times without agonism, then this would provide support for the notion that howling is a behaviour associated with male-male competition. In some other primate species for which support has been found for the mate defense hypothesis, such as chacma baboons, males are known to howl while fighting (Kitchen et al., 2003b).

If none of these predictions are supported by the results of this study, then the null hypothesis, which states that the howl is not a display of individual male agonistic ability in the ring-tailed lemur, would be supported.

## **H2: Inter-group function of the mate defense hypothesis**

I predict that the howling rate of male ring-tailed lemur group members will be higher during inter-troop encounters or when male non-group members are present as opposed to contexts without non-group members present. If focal males howl at a higher rate when they are in contact with non-group members, this would suggest that males are howling to communicate with non-group ring-tailed lemurs as opposed to only group members. Resident males may howl to advertise their presence to non-group males, and to discourage extra-group males from approaching females, as has been hypothesized for other primate species (reviewed in Wich and Nunn, 2002). Although high-ranking males typically have mating priority and would therefore be the most likely to call in defense of females, due to the multi-male, multi-female mating system of the ring-tailed lemur, even low-ranking group males are likely to copulate with at least some females (Jolly, 1966; Koyama, 1988; Parga, 2006a; Sauther, 1991). As a result, discouraging extra-group males from approaching the ring-tailed lemur group would be beneficial for all male residents, regardless of their dominance ranking, and all would be expected to call.

Further to this hypothesis, do a greater number of resident males join in howling bouts given during inter-group encounters or when non-group members are present as opposed to contexts without non-group members? If a greater number of focal group males participate in howling bouts during inter-troop encounters, this would advertise the total number of males in the group. Such a result would provide support for howling being a form of male advertisement, indicating the number of males in a ring-tailed lemur troop, and thus discouraging new males from attempting to persist in the same area as the group. If these predictions are not met by the

results of this study, this would provide support for the null hypothesis that ring-tailed lemur male howling does not function in inter-group communication.

In other species where the mate defense hypothesis has been applied for male long calling, another common prediction is that males will take the primary role in group defense during inter-troop interactions (e.g. van Schaik et al., 1992). However, due to the female dominance of ring-tailed lemurs in conjunction with myriad prior study results indicating that ring-tailed lemur females take the primary role in group defense (Gould et al., 2003; Jolly, 1966), this prediction was not considered applicable.

### **H3: Mate attraction hypothesis**

I predict that male ring-tailed lemur howling rate will be higher on days of known estrus as opposed to days without estrus. If the male howl functions as a mate attraction signal or form of male advertisement to estrous females, then males should howl at higher rates at times when females are in estrus and males may have the opportunity to copulate.

Further to this hypothesis, do estrous females seek out or move towards males during or immediately after they are heard howling? If estrous ring-tailed lemur females are attracted to howling males, then this would provide support for the idea that the male howl functions as an advertisement of male presence and availability to potential mates.

If these predictions are not supported by the results of this study, then this indicates support for the null hypothesis, which states that howling is not a mate attraction signal for the ring-tailed lemur.

## **Methods**

### **Description of field site**

All data for this study were collected between March 1-July 1, 2010 at Beza Mahafaly Special Reserve, a protected governmental reserve in southwest Madagascar (23°30'S lat., 44°40'E long.) (Sussman and Ratsirarson, 2006; Sussman et al., 2012). This reserve was established in 1978 and has been protected since 1986 (Gould et al., 2003; Sussman et al., 2012). It consists of two non-contiguous forest types, dry forest in the western area of the reserve

(Parcel II, 500 ha) and riverine forest on the eastern side (Parcel I, 80 ha) (Sussman and Ratsirarson 2006). However, the two non-contiguous parcels have recently been connected in an expansion of the reserve to now nearly 4000ha (Sauther, pers comm.). A system of labeled trails roughly divided Parcel I into 100m<sup>2</sup> squares, making this forest easy to navigate. Beza Mahafaly was an optimal site for collecting high-quality behavioural data due to its secluded location away from major roads. The small number of motorized vehicles in the area limited environmental noise.

Approximately 225 free-ranging ring-tailed lemurs lived in 11 groups in Parcel I, and within these groups almost all adult lemurs were individually known (Gould and Ziegler 2007; Sauther and Cuozzo 2008). Most individuals were collared and labeled with visible numbers, an identification system dating to the late 1980s (Sussman 1991; Sauther et al., 2002; Cuozzo and Sauther 2006; Sauther and Cuozzo, 2009; Cuozzo et al., 2010). The only individuals left uncollared were infants, yearlings, and some adult males who had recently immigrated from groups outside of the reserve. I could easily identify any uncollared animals due to patches of black dye in different body areas, applied by another researcher in February, 2010. Five groups from Parcel I were the focus of this study.

### **Description of study animals**

Behavioural focal follows were performed six days per week from dawn until dusk on all males aged three and older from five ring-tailed lemur troops (green, orange, purple, red, and yellow troops). Only one group was followed per day. Each group was studied 1-2 days per week. Resident males were sampled using the focal animal sampling method on a randomized, rotational basis from dawn until dusk (Altmann 1974).

Focal data were collected from 25 sexually mature males in total (**Table 1**). Ages for most individuals are known from the decade-long work by Sauther and Cuozzo, who identify lemurs first as subadults (second year of age) when first captured, with age determined from a series of variables including dental development, sexual maturity (or lack thereof), body mass, and somatic development (Cuozzo and Sauther, 2006; Sauther and Cuozzo, 2008, 2009; Cuozzo et al., 2010). Thus collared lemurs aged two or greater are of known age. I estimated the age for all individuals with names beginning with “UMM” (unmarked male) as three or more. All “UMM” individuals were sexually mature males who were known to be new, non-natal members

to collared study groups in Parcel I within the last year (Beza Mahafaly Special Reserve unpublished data). Both natal and non-natal male group members were included in all statistical analyses because some natal males were observed mating with female group members (Bolt, unpublished data). At Beza Mahafaly Special Reserve, ring-tailed lemur study group size ranged from 9-20 individuals, with 4-8 males, 4-10 females, and 0-3 infants present per group.

### **Field methods**

During focal sampling, each male subject was followed for thirty minutes at a time, with data recorded every 2.5 minutes on a programmed palm pilot (Palm Z-22) using one-zero sampling (Martin and Bateson 2007) to document the actions that occurred during the previous time period, including the focal individual's behaviour (resting, vigilant, allogrooming, autogrooming, feeding, foraging, sunning, scent marking, tail waving, travelling, urinating/defecating, other, out of sight), and any agonistic interaction. During focal sampling, the following vocalization types were recorded: moan, wail, howl, hmm, huh, purr, chirp, yip, cackle, squeal, twitter, plosive bark, chatter, gulp, rasp, shriek, click, click series, yap (following Macedonia, 1990). Because male howling vocalizations occurred infrequently throughout the day and howls by any member of the focal group were easily audible, male howl vocalizations were collected via all-occurrences sampling (Altmann 1974) at all times of contact with the troop, with the time and identity of the caller noted. Animals were watched continuously during the focal period. The ethogram used in this study was based on those used by Jolly (1966), Gould (1994), Pereira and Kappeler (1997), and Parga (2006b).

Vocal recordings were made of all utterances by the focal animal during each focal follow when possible, using a Sennheiser ME66 directional microphone (Sennheiser Electronic GmbH and Company, KG) and digital Marantz PMD660 recorder (Marantz Corporation, New York, USA). Recordings were made with a 44.1kHz sampling rate, 16-bit sample depth, and 64 kilobits/second MP3 compression. The sampling rate refers to the number of digital sound samples taken in per second, while the 16-bit sample depth refers to 65 536 different levels of quantization recorded (Oppenheim et al., 1996). MP3 compression was necessary due to storage space limitations on the digital recorder. Sound spectrograms for howls were produced using Cool Edit Pro v.2.1 (Syntrillium Software, USA, 2003), with the spectrogram created using a Blackman window with 2048 frequency bins. A Blackman window is a mathematical function

used in spectral analysis and used to generate spectrograms, while the number of frequency bins refers to the frequency resolution of the spectrogram, with 2048 values in total of different frequencies that are measured and used to generate the spectrogram (Oppenheim et al., 1996). 2048 frequency bins allowed for optimal frequency and time resolution of the ring-tailed lemur howl vocalization, based on a visual inspection.

Additionally, inter-troop interactions (defined by another troop being in visible distance and within 20 metres of the focal troop) were noted, along with the presence of single non-group ring-tailed lemurs and their sexes and specific identities when known. The total time that all non-group members and other groups were in visible distance within 20m of the focal group was noted during focal follows.

Mating bouts were also observed opportunistically during the mating season. When a mating bout occurred, ongoing focal sampling was suspended in order to perform *ad libitum* sampling regarding the bout (Altmann 1974). I identified female estrus as a period of time when a female ring-tailed lemur copulated and made proceptive sexual presentations towards males (Beach 1976).

In my study, an agonistic interaction is defined as any behaviour involving contest competition between two individuals. This could consist of low-arousal behaviour (e.g. a displacement or lunge-withdraw) or higher-arousal behaviour (e.g. cuff, bite, or jump fight). An agonistic interaction involves one or more acts of avoidance, aggression, or defense between two individuals. A period without male-male agonism is defined as a time without contest competition between individuals.

### **Calculating male rank**

The male dominance hierarchy in a ring-tailed lemur troop is often linear, but is sometimes non-linear (Budnitz and Dainis, 1975; Gould, 1994; Jolly, 1966). In my study, dominance was determined from focal data using dominance index calculations, which take all decided agonistic and submissive interactions into account before assigning each male an individual dominance percentage within its troop (Zumpe and Michael, 1986). In my study, dominance index was calculated using the following equation:

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

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

In calculating dominance indices, all agonistic behaviours (e.g. chase, lunge-withdraw, cuff) were treated equally (following Gould, 1994). Dominance indices were calculated separately for males in each group. Males with higher dominance percentages won more fights and had a higher ranking within their troops. Dominance index calculations for all males in each troop are presented in **Table 1**.

### **Data analysis**

For each data set used in my study, data were not normally distributed, requiring the use of non-parametric tests. In addition, the sample size was small ( $n=25$  males), which meant that non-parametric tests were appropriate. For this reason, analyses in my study were performed using non-parametric statistics, such as Spearman rank correlations, one-sample binomial tests, and Wilcoxon signed-rank tests.

In my study, the Spearman rank correlation test was used to evaluate the prediction from my Hypothesis 1, that high-ranking males will have higher howling rates. The Spearman rank

correlation test is used when there are two measurement variables (e.g. howling rate and dominance index) and one nominal variable (e.g. individual) which groups measurement variables into pairs (McDonald, 2009; Sokal and Rohlf, 1995). The test determines if the ranks of each variable co-vary (e.g. if one value increases when the other decreases, or if one increases as the other increases) (McDonald, 2009; Sokal and Rohlf, 1995). The null hypothesis for the Spearman rank test states that the ranks of one measurement variable do not co-vary with the ranks of the other measurement variable (i.e. as one variable increases, the other is not more likely to increase or decrease) (McDonald, 2009; Sokal and Rohlf, 1995). For this test, the two variables were male ring-tailed lemur howling rate and dominance index. I also used this test to evaluate a further prediction associated with this hypothesis, that high-ranking males will have howling bouts containing a greater number of howls. For this test, the two variables were mean number of howls contained in a howling bout and dominance index. When the Spearman rank test was performed, polynomial regression was also performed in order to visually summarize the relationship between the variables (McDonald, 2009).

In my study, the one-sample binomial test was used to evaluate various questions associated with my hypotheses. The one-sample binomial test allows for the testing of whether the proportion of successes on a two-level categorical dependent variable (e.g. agonistic wins while howling versus agonistic losses while howling) significantly differs from a hypothesized, predicted value (McDonald, 2009; Sokal and Rohlf, 1995). For the binomial test, the statistical null hypothesis states that categorical values should be equally represented, or do not differ significantly from 50% (McDonald, 2009; Sokal and Rohlf, 1995). For Hypothesis 1, I determined whether howling occurred immediately before or after times of male-male agonism. For this binomial test, the two-level categorical dependent variables for male howling were agonism versus no agonism. The binomial test was also used in evaluating Hypothesis 2. For Hypothesis 2, I used the binomial test to determine whether howling bouts involving two or more group members were given during inter-troop encounters. For this test, the two-level categorical dependent variables for two or more males howling were inter-troop encounter versus no inter-troop encounter. I also used the binomial test to assess a question related to Hypothesis 3, to evaluate whether howling attracted estrous females. For this test, the two-level categorical dependent variables for male howling on days of known estrus were female approach after howling versus female lack of approach.

In my study, the Wilcoxon signed-rank test was used to evaluate several predictions and related questions stemming from Hypotheses 2 and 3. The Wilcoxon signed-rank test allows for the testing of differences between two nominal variables (e.g. individual and estrus day versus non-estrus day) and a measurement variable (e.g. howling rate) (McDonald, 2009; Sokal and Rohlf, 1995). The null hypothesis for the Wilcoxon signed-rank test states that the median difference between pairs of observation is zero (McDonald, 2009; Sokal and Rohlf, 1995). Under the null hypothesis, smaller values of  $z$  are less likely (McDonald, 2009; Sokal and Rohlf, 1995). In my study, the Wilcoxon signed-rank test was used to evaluate the prediction from my Hypothesis 2, that howling rate will be higher during inter-troop encounters. The dependent variable was ring-tailed lemur howling rate, and the independent variable was encounter context (i.e. during an inter-troop encounter versus not during an inter-troop encounter). Further to this prediction from Hypothesis 2, I used the Wilcoxon test to evaluate whether a greater number of ring-tailed lemur males participated in a howling bout when non-group members were present. The dependent variable was the number of ring-tailed lemur group males who joined in the howling bout, and the independent variable was encounter context (i.e. during an inter-troop encounter versus not during an inter-troop encounter). The Wilcoxon test was also used to evaluate the prediction from my Hypothesis 3, that male howling rate will be higher on days of known estrus. For this test, the dependent variable was howling rate, and the independent variable was estrus status (i.e. on a day of known estrus versus on a day without known estrus).

In my study, since howling was an infrequent behaviour and was noted using all-occurrences sampling, howling rates for each male were calculated using total focal time for each ring-tailed lemur troop, rather than the focal time of individual males. When determining results for questions related to male howling rates and lengths on estrus days versus non-estrus days, males were excluded from analysis if estrus was not observed in their group ( $n=6$  males excluded, from 1 group). When determining results for differences in howling bout length, males were excluded from analysis if they were not heard howling ( $n=12$  males excluded) and if their average howling bout length was not accurately recorded ( $n=1$  male excluded). All tests were two-tailed, and means were reported with standard deviations (SD). For all tests, the alpha level was set to 0.05. All statistical tests were performed using SPSS version 20 (IBM SPSS Statistics, IBM Corporation, Armonk, NY, USA, 2011).

## **Results**

### **Howling rate was not significantly associated with dominance index**

Male howling rate was not correlated with male dominance index, such that males with higher overall howling rates did not have higher dominance status (Spearman rank correlation:  $r_s = -0.04$ ,  $n = 25$  males,  $p = 0.842$ , NS; polynomial regression:  $r^2 = 0.055$ ,  $df = 21$ ,  $p = 0.75$ , NS; **Figure 3**). In addition, the mean number of howls in a male howling bout was not correlated with male dominance index, such that males with howling bouts containing a greater mean number of howls per bout did not have higher or lower dominance status (Spearman rank correlation:  $r_s = -0.16$ ,  $n = 12$  males,  $p = 0.614$ , NS; polynomial regression:  $r^2 = 0.305$ ,  $df = 8$ ,  $p = 0.38$ , NS; **Figure 4**).

Further, howling was not likely to occur immediately before or after times of male-male agonism. Of total howls heard by identified males during the study period ( $n=30$  howling bouts by focal males), 10% (3/30) of howls were given by males after they lost an agonistic interaction with another male, while 90% (27/30) of howls were given by males during non-agonistic contexts. Howling was not directly related to male-male agonism (binomial test:  $z = -4.38$ ,  $n = 30$  howls,  $x = 27$  howls,  $p < 0.0001$ ).

### **Males howl more during inter-group encounters**

There was a significant difference in male howling rate during inter-group encounters or at times when male non-group members were present when compared to periods without non-group members present (Wilcoxon signed rank test:  $z = -2.77$ ,  $n = 25$  males,  $p = 0.006$ ; **Figure 5**). Mean male howling rate was higher when non-group members were present (0.06 howls per hour  $\pm$  0.09,  $n = 25$  males) than mean male howling rate at times without non-group members (0.004 howls per hour  $\pm$  0.01,  $n = 25$  males). When tests were re-done with outliers excluded ( $n = 4$  male outliers excluded in total; 3 outliers for howling rate per hour with non-group members present [0.28 howls per hour for males 273, 307 and 308] and 1 outlier for howling rate per hour with no non-group members present [0.02 howls per hour for male 203]) results remained statistically significant (Wilcoxon test:  $z = -2.32$ ,  $n = 21$  males,  $p = 0.02$ ). See **Appendix II** for data on individual male howling rates, which were quite variable.

There was a significant difference in number of group males participating in a howling bout when non-group members were present when compared to the number of males

participating in a howling bout when only group residents were present (Wilcoxon test:  $z = -2.17$ ,  $n = 25$  males,  $p = 0.03$ ). A greater mean number of resident males participated in howling bouts when non-group members were present ( $0.81$  males  $\pm 1.24$ ,  $n = 25$  males) when compared to the number of resident males that participated in howling bouts when no non-group members were present ( $0.24 \pm 0.44$ ,  $n = 25$  males). When tests were re-done with outliers excluded ( $n = 9$  male outliers excluded in total; 5 outliers for average number of group males in howling bouts when non-group members present [values of 4, 3, and 2.67 for males Umm3p, 308, 280, 307, and 273] and 6 outliers for average number of group males in howling bouts when no non-group members present [value of 1 for males 203, Umm2g, 263, 273, 308, 208]), results remained statistically significant (Wilcoxon test:  $z = -2$ ,  $n = 16$  males,  $p = 0.046$ ).

All observed howling bouts involving two or more male group members (100% of  $n=11$  howling bouts with multiple howlers from the same group) were given when non-group members were present. The participation of multiple group members in a howling bout was related to the presence of non-group members (binomial test:  $z = 5.2$ ,  $n = 11$  howling choruses,  $x = 11$  howling choruses,  $p = 0.001$ ).

### **Howling rate was not significantly associated with female estrus**

There was no significant difference in mean male howling rate on days of known estrus when compared with non-estrus days (Wilcoxon test:  $z = -0.86$ ,  $n = 19$  males,  $p = 0.388$ , NS; **Figure 6**). Although mean male howling rate was higher on known estrus days ( $0.04$  howls per hour  $\pm 0.06$ ,  $n = 19$  males) when compared with mean male howling rate on non-estrus days ( $0.01$  howls per hour  $\pm 0.02$ ,  $n = 19$  males), this difference was not significant. When tests were re-done with outliers excluded ( $n = 2$  male outliers excluded in total for howling rate on days without known estrus [0.4274 howls per hour for male 273 and 0.53429 howls per hour for male 208]), results remained statistically non-significant (Wilcoxon test:  $z = -1.28$ ,  $n = 17$  males,  $p = 0.202$ , NS).

Further, male howling did not attract estrous females. Of total howls heard by identified focal males on days of known estrus, only 20% of howls ( $n = 1$  howl of  $n = 5$  howls total) had females move towards howling males within 1 minute. Howling males were not more or less likely to have estrous females approach them after howling (binomial test:  $z = -1.34$ ,  $n = 5$  howls  $x = 1$  howl,  $p = 0.375$ , NS).

## Discussion

### **Howling rate increases during inter-group encounters and honestly indicates minimum number of males in a group**

Results from my study showed no support for the intra-group function of the mate defense hypothesis. Contrary to reports that high-ranking ring-tailed lemur males howl more often than low-ranking males (Jolly, 1966; Koyama, 1988; Macedonia, 1990), howling had no observable relationship with individual male dominance index. Male dominance rank was not related to howling rate or number of howls in a bout, indicating that these aspects of howling did not play a role in male-male relations between individuals. In addition, male ring-tailed lemurs did not howl immediately before or after male-male agonistic interactions, suggesting a further lack of support for howling playing a role in male-male agonistic contexts. There is no evidence suggesting that male group members howled as a means of competing as individuals, or advertising any of their characteristics, to one another. The intra-group function of the mate defense hypothesis is therefore unsupported.

In contrast, the howling rate of ring-tailed lemur males increased during inter-troop encounters and when non-group members were present. Significantly more males participated in howling bouts when non-group ring-tailed lemurs were within 20m and in visual range. These results support the inter-group function of the mate defense hypothesis, suggesting that males howl to advertise their presence to ring-tailed lemurs from other groups, as opposed to male or female members of their own troop. However, my results should be interpreted with a degree of caution in that many howls (37% of howls given by focal males) occurred when no other troops were within visual range. Since the howl is a long-distance vocalization which can carry up to 1 km through riverine forest (Jolly, 1966), other troops out of visual range but within 1 km would be able to hear howl vocalizations, but it is unknown how this may influence troop movements and whether hearing howling would discourage other troops from approaching the area of a troop containing howling males.

Although ring-tailed lemur howling rate and bout length were not related to individual male dominance rank, and therefore did not seem to convey detailed information about the fighting ability of individuals, howling did indicate male presence and a minimum number of

males resident in a group. The result that larger numbers of focal group males joined in howling bouts during inter-troop encounters indicates that ring-tailed lemur troops may have been advertising the total number of males in their troop when they howled. Because individual voices are staggered within a ring-tailed lemur howling chorus (Macedonia, 1990; Bolt, this study), neighbouring troops would hear the number of howlers participating in a bout, and be made aware of a minimum number of males already present in a ring-tailed lemur group. This notion has also been proposed for other species with offset long calls comprising group-wide choruses, such as lions (*Leo* spp.), red howler monkeys (*Alouatta seniculus*), and black howler monkeys (*Alouatta caraya*) (lions: McComb et al., 1994; red howler monkeys: Sekulic, 1982; black howler monkeys: Kitchen, 2004; Kitchen et al., 2004b). Results from my study therefore provide some support for the idea proposed by Jolly (1966), that ring-tailed lemur howling functions as a self-advertisement and group-advertisement, with males howling to notify non-group members of their residence in a social group. However, it is unknown how non-group males may use and respond to this information. In other primate species such as grey-cheeked mangabeys (*Lophocebus albigena*), social groups use long calls as a means of spacing themselves by avoiding other calling groups and individual males (Waser, 1975).

Finally, there was no support for the mate attraction hypothesis. Contrary to observations by past researchers that ring-tailed lemur howling rate increases during the mating season (Jolly, 1966; Mertl-Milhollen et al., 1979), results from my study indicated that howling rate did not have a significant relationship with female estrus or whether females approached males. Although howling rate was higher on known estrus days when compared with non-estrus days, this trend was not significant. This result indicates a lack of support for the mate attraction hypothesis.

### **Comparing study results to previous research on ring-tailed lemur howling function and primate long call function**

My study provides support for the male howl as an indicator of a group's presence and location (Macedonia, 1990). Because each male ring-tailed lemur howls at his own rate without entrainment, regardless of the number of males howling at the same time, the number of males in a group is honestly advertised to all groups within auditory range.

As Kitchen (2004, 2006) observed, primate group-level fighting ability likely depends on the number of participants in the fight, and groups with more competitors have a greater chance of winning in an agonistic interaction. In mammals including lions, common chimpanzees (*Pan troglodytes*), and black howler monkeys (lions: Grinnell et al., 1995; chimpanzees: Wilson et al., 2001; black howler monkeys: Kitchen, 2004), group members are known to be aware of the relative number of competitors in two different groups, or their “numeric odds” through assessing long calls (Kitchen, 2006, p.74). For black howler monkeys, males are known to assess the fighting ability of other groups based on numerical odds provided by these group-wide long call choruses (Kitchen, 2004). As Kitchen et al. (2004b) note, howling choruses in primates are honest indicators of the minimum number of males in a social group. Males participate in a long call chorus call at staggered intervals, meaning that a single howling male cannot deceive a listener or be mistaken for multiple calling males (Kitchen et al., 2004b). Group long calling displays are therefore reliable signals of the minimum number of group males. According to the predictions of game theory, which suggests that individuals and groups should avoid fights that they will likely lose (Maynard Smith, 1982), Kitchen et al. (2004b) proposed that groups of black howler monkeys use howling displays to gauge relative combat ability at group-level and can therefore withdraw from fights they would be unlikely to win.

As in black howler monkeys, individual male ring-tailed lemur howls are offset within a multi-male howl chorus. Howling choruses therefore honestly indicate a minimum number of males in a group, and by extension, the minimum number of males that could participate in a fight if challenged. Other ring-tailed lemur groups have the potential to assess the likelihood of winning in group-wide competition based on information received from the multi-male howling bout of a challenging group. However, it is unknown whether or how this information is used by other ring-tailed lemur groups.

Because ring-tailed lemur females typically take the primary role in resource and group defense in this female-dominant species (Gould et al., 2003), male howling would be unlikely to dissuade non-group females from stealing food or spatial resources that the males themselves possess, or from otherwise attacking resident males. Instead, howling is more likely to function as an assertion of male presence to the males from the other group. Resident males may howl to discourage non-group males from approaching and gaining sexual access to group females, as the mate defense hypothesis predicts (Wich and Nunn, 2002). This notion is further supported by

the increased level of male-male agonism during inter-group encounters (Bolt, unpublished data), which suggests that ring-tailed lemur resident males wish to discourage non-group males from remaining in the area.

Ring-tailed lemur howling choruses also have the potential to mediate male migration. Ring-tailed lemur males who are dispersing from their present group are more likely to choose the new group with fewest mature males for membership (Parga and Lessnau, 2008). Dispersing males may be made aware of a minimum number of males resident in a ring-tailed lemur group through staggered howling choruses. Ring-tailed lemur males would be discouraged from trying to join a group that already has a large number of mature males (Parga and Lessnau, 2008), while they would be encouraged to join a group with few or no howling males. Non-group males who visit or engage in an inter-troop encounter with a focal ring-tailed lemur troop may be discouraged from continuing to remain with the new group or staying in the area if males from the focal troop howl to assert their presence and numbers. In sympatric lemur species such as Verreaux's sifaka (*Propithecus verreauxi*), resident males are known to form coalitions to forcibly keep extra-group males out of a social group in order to prevent them from mating with estrous females (Lewis and van Schaik, 2007). The group-wide howling bouts of ring-tailed lemurs may be a form of acoustic coalition which accomplishes the same mate-defense purpose.

Within the polygynandrous mating system of the ring-tailed lemur, most non-natal males in a social group have the opportunity to mate with at least some estrous females, regardless of their rank (Gould, 1994; Parga, 2006a; Sauther, 1991; Sussman, 1992). Even sexually mature natal males were observed mating with a resident female in the present study (Bolt, unpublished data). In addition, non-group males are known to mate with estrous females (Bolt, unpublished data; Koyama, 1988; Sauther, 1991; Sussman, 1992). There are therefore potentially fitness consequences for resident males if extra-group males are allowed to persist in the area where resident females may be in estrous. Accordingly, repelling non-group male competitors is beneficial for all resident males, as Kitchen et al. (2003b) suggest for chacma baboons. It is an advantageous behaviour for each individual male in a ring-tailed lemur troop, as well as a beneficial behaviour group-wide.

### **Contextualizing study results in sexual selection theory**

Although the ring-tailed lemur male howl meets some of the predictions established by Snowdon (2004) for being a sexually selected signal, my study does not support many of these predictions. Although the howl is male-specific (Prediction #1), and likely individually distinctive (Prediction #2), two of Snowdon's (2004) criteria were not met and one was not assessed. Howling rate did not increase on days or at times of mating (Prediction #4), and was not linked to agonistic ability (Prediction #5), although reproductive success was not measured. Whether howls were preferred with specific spectral traits by conspecifics as opposed to forms with various spectral traits (Prediction #3) was not assessed (Snowdon, 2004). Results from my study were therefore mixed, and provided a limited amount of support for sexual selection and ring-tailed lemur howling rate. The findings of my study indicate that some aspects of intra-sexual selection theory, namely intra-sexual competition between males from different groups, have potential to be applicable to ring-tailed lemur howling function. However, many predictions for how howling would relate to both intra- and inter-sexual selection were not met. There was no observed link between howling rate and male dominance rank. Howling rate did not increase at times of estrus or mating, nor did estrous females move toward or demonstrate any type of preference for howling males.

In light of the limited support for sexual selection theory applying to ring-tailed lemur howling, other explanations for male-specific long calling may also be relevant to the ring-tailed lemur. Although the inter-group function for the mate defense hypothesis has some support from the ring-tailed lemur, alternate hypotheses for male long calling, such as the resource defense hypothesis, which suggests that males howl to defend food resources or a territory (e.g. Fashing, 2001), should also be investigated in future study.

It is also possible that aspects of howls not investigated in this study, such as spectral characteristics like howl fundamental frequencies and formant dispersions, and temporal characteristics like the length of individual howls within a bout, are linked to the traits of individual males, as has been found in chacma baboons (Fischer et al., 2004). Ring-tailed lemur male dominance rank and agonistic ability may be indicated by howl spectral and temporal qualities, rather than howling occurrence and rate. Further study involving the spectrographic analysis of recorded howls should investigate whether howl components may indicate male qualities.

## **Conclusions**

In the ring-tailed lemur, male howling rate increased during inter-group encounters, but had no observed relationship with female attraction or individual male dominance rank. Howling appeared to advertise male presence and was a signal directed towards non-group conspecifics, as opposed to males or females within a social group. Multi-male howling choruses were strongly associated with inter-troop encounters, and honestly indicated the minimum number of resident males in a ring-tailed lemur group. Results from this study provided support for the inter-group function of the mate defense hypothesis, but no support for the mate attraction hypothesis or the intra-group function of the mate defense hypothesis.

## References

- Altmann, J. (1974). Observational study of behavior: sampling methods. *Behaviour* 49: 227-265.
- Andersson, M. (1982). Sexual selection, natural selection and quality advertisement. *Biological Journal of the Linnean Society* 17: 375–393.
- Andrew, R. (1963). The origins and evolution of calls and facial expressions of the primates. *Behaviour* 20: 1-109.
- Bradbury, J., and Vehrencamp, S. (1998). Principles of animal communication. Sunderland, MA: Sinauer Associates.
- Budnitz, N. and Dainis, K. (1975). *Lemur catta*: Ecology and behavior. In: Lemur biology. Tattersall, I., and Sussman, R. (eds.). New York: Plenum Press, pp. 219-235.
- Cheney, D., and Seyfarth, R. (1977). Behavior of adult and immature male baboons during intergroup encounters. *Nature* 269: 404-406.
- Clutton-Brock, T., and Albon, S. (1979). The roaring of red deer and the evolution of honest advertisement. *Behaviour* 69: 145–169.
- Cowlshaw, G. (1992). Song function in gibbons. *Behaviour* 121: 131–153.
- Cowlshaw, G. (1995). Behavioural patterns in baboon group encounters: The role of resource competition and male reproductive tactics. *Behaviour* 132: 75-86.
- Cowlshaw, G. (1996). Sexual selection and information content in gibbon song bouts. *Ethology* 102: 272–284.
- Delgado, R. (2006). Sexual selection in the loud calls of male primates: signal content and function. *International Journal of Primatology* 27: 5-25.
- Doty, G., and Welch, A. (2001). Advertisement call duration indicates good genes for offspring feeding rate in gray tree frogs (*Hyla versicolor*). *Behavioral Ecology and Sociobiology* 49: 150-156.
- Emlen, S., and Oring, L. (1977). Ecology, sexual selection, and the evolution of mating systems. *Science* 197: 215-223.
- Fashing, P. (2001). Male and female strategies during intergroup encounters in guerezas (*Colobus guereza*): evidence for resource defense mediated through males and a comparison with other primates. *Behavioral Ecology and Sociobiology* 50:219–230.
- Fischer, J., Kitchen, D., Seyfarth, R., and Cheney, D. (2004). Baboon loud calls advertise male

- quality: acoustic features and their relation to rank, age, and exhaustion. *Behavioral Ecology and Sociobiology* 56: 140-148.
- Gautier, J., and Gautier, A. (1977). Communication in old world monkeys. In: How animals communicate. Sebeok, T. (ed.). Bloomington, ID: Indiana University Press, pp. 890–964.
- Gould, L. (1994). Patterns of affiliative behavior in adult male ringtailed lemurs (*Lemur catta*) at the Beza-Mahafaly reserve, Madagascar. Ph.D. dissertation: Washington University, Missouri.
- Gould, L., Sussman, R., and Sauther, M. (2003). Demographic and life-history patterns in a population of ring-tailed lemurs (*Lemur catta*) at Beza Mahafaly Reserve, Madagascar: A 15-year perspective. *American Journal of Physical Anthropology* 120: 182-194.
- Gould, L., and Zeigler, T. (2007). Variation in fecal testosterone levels, inter-male aggression, dominance rank and age during mating and post-mating periods in wild adult male ring-tailed lemurs (*Lemur catta*). *American Journal of Primatology* 69: 1325-1339.
- Grafen, A. (1990). Biological signals as handicaps. *Journal of Theoretical Biology* 144: 475-546.
- Grafen, A. (1991). Modelling in behavioural ecology. In: Behavioural ecology: an evolutionary approach, 3<sup>rd</sup> edition. Krebs, J., and Davies, N. (eds.). Oxford: Blackwell, pp. 5-31.
- Grinnell, J., Packer, C., and Pusey, A. (1995). Cooperation in male lions: kinship, reciprocity or mutualism? *Animal Behavior* 49: 95-105.
- Jolly, A. (1966). Lemur behavior: A Madagascar field study. London: University of Chicago Press.
- Jones, K. (1983). Inter-troop transfer of *Lemur catta* males at Berenty, Madagascar. *Folia Primatologica* 40: 145-160.
- Kitchen, D. (2004). Alpha male black howler monkey responses to loud calls: Effect of numeric odds, male companion behaviour and reproductive investment. *Animal Behavior* 67: 125–139.
- Kitchen, D. (2006). Experimental test of female black howler monkey (*Alouatta pigra*) responses to loud calls from potentially infanticidal males: effects of numeric odds, vulnerable offspring and companion behavior. *American Journal of Physical Anthropology* 131: 73-83.
- Kitchen, D., Cheney, D., and Seyfarth, R. (2003a). Female baboons' responses to male loud calls. *Ethology* 109: 401-412.
- Kitchen, D., Seyfarth, R., Fischer, J., and Cheney, D. (2003b). Loud calls as indicators of

- dominance in male baboons (*Papio cynocephalus ursinus*). *Behavioral Ecology and Sociobiology* 53: 374-384.
- Kitchen, D., Cheney, D., and Seyfarth, R. (2004a). Factors mediating inter-group encounters in chacma baboons (*Papio cynocephalus ursinus*). *Behaviour* 141: 197-218.
- Kitchen, D., Horwich, R., and James, R. (2004b). Subordinate male black howler monkey (*Alouatta pigra*) responses to loud calls: experimental evidence for the effects of intra-group male relationships and age. *Behaviour* 141: 703-723.
- Kitchen, D., Cheney, D., and Seyfarth, R. (2005). Male chacma baboons (*Papio hamadryas ursinus*) discriminate loud call contests between rivals of different relative ranks. *Animal Cognition* 8:1-6.
- Koyama, N. (1988). Mating behavior of ring-tailed lemurs (*Lemur catta*) at Berenty, Madagascar. *Primates* 29: 163-175.
- Lewis, R., van Schaik, C. (2007). Bimorphism in male Verreaux's sifaka in the Kirindy forest of Madagascar. *International Journal of Primatology* 28: 159–182.
- Macedonia, J. (1986). Individuality in a contact call of the ringtailed lemur. *American Journal of Primatology* 11: 163-179.
- Macedonia, J. (1990). Vocal communication and antipredator behavior in the ringtailed lemur (*Lemur catta*). Ph.D. dissertation: Duke University, North Carolina.
- Macedonia, J. (1993). The vocal repertoire of the ringtailed lemur (*Lemur catta*). *Folia Primatologica* 61:186-217.
- Martin, P., and Bateson, P. (2007). *Measuring Behavior: An Introductory Guide*. 3rd ed. Cambridge, UK: Cambridge University Press.
- Maynard Smith, J. (1982). *Evolution and the theory of games*. Oxford: Oxford University Press.
- McComb, K. (1991). Female choice for high roaring rates in red deer, *Cervus elaphus*. *Animal Behavior* 41: 79–88.
- McComb, K., Packer, C., and Pusey, A. (1994). Roaring and numerical assessment in contests between groups of female lions, *Panthera leo*. *Animal Behavior* 47: 379-387.
- McDonald, J. (2009). *Handbook of biological statistics* 2<sup>nd</sup> ed. Baltimore, MD: Sparky House Publishing.
- Mertl-Milhollen, A. (2006). Scent marking as resource defense by female *Lemur catta*. *American Journal of Primatology* 68: 605-621.

- Mertl-Milhollen, A., Gustafson, H., Budnitz, N., Dainis, K., and Jolly, A. (1979). Population and territory stability of the *Lemur catta* at Berenty, Madagascar. *Folia Primatologica* 31: 106-122.
- Mitani, J. (1988). Male gibbon (*Hylobates agilis*) singing behavior: natural history, song variations and function. *Ethology* 79: 177-194.
- Oda, R. (1996). Effects of contextual and social variables on contact call production in free-ranging ringtailed lemurs (*Lemur catta*). *International Journal of Primatology* 17: 191-205.
- Oppenheim, A., Willsky, A., and Nawab, S. (1996). *Signals and Systems* 2<sup>nd</sup> ed. New York: Prentice Hall.
- Parga, J. (2006a) Male mate choice in *Lemur catta*. *International Journal of Primatology* 27: 107-131.
- Parga, J. (2006b). Sexual selection in the ringtailed lemur (*Lemur catta*): female choice, male mating strategies, and male mating success in a female dominant primate. Ph.D. dissertation: University of Texas at Austin, Texas.
- Parga, J. (2010). Evaluation of male inter-troop transfer as a mating strategy in ring-tailed lemurs on St. Catherines Island, USA. *Folia Primatologica* 81: 146-162.
- Parga, J., and Lessnau, R. (2008). Dispersal among male ring-tailed lemurs (*Lemur catta*) on St. Catherines Island. *American Journal of Primatology* 70: 650-660.
- Pereira, M., and Kappeler, P. (1997). Divergent systems of agonistic behaviour in lemurid primates. *Behaviour* 134: 225-274.
- Petter, J., and Charles-Dominique, P. (1979). Vocal communication in prosimians. In: *The study of prosimian behaviour*. Doyle, G., and Martin, R. (eds.). New York: Academic Press, pp. 247-305.
- Prestwich, K. (1994). The energetic of acoustic signaling in anurans and insects. *American Zoologist* 34: 625-643.
- Pride, R. (2005). Optimal group size and seasonal stress in ring-tailed lemurs (*Lemur catta*). *Behavioral Ecology* 16: 550-560.
- Raemaekers, J., Raemaekers, P., and Haimoff, E. (1984). Loud calls of the gibbon (*Hylobates lar*): Repertoire, organisation and context. *Behaviour* 91: 146-189.
- Sauther, M. (1989). Antipredator behavior in troops of free-ranging *Lemur catta* at Beza

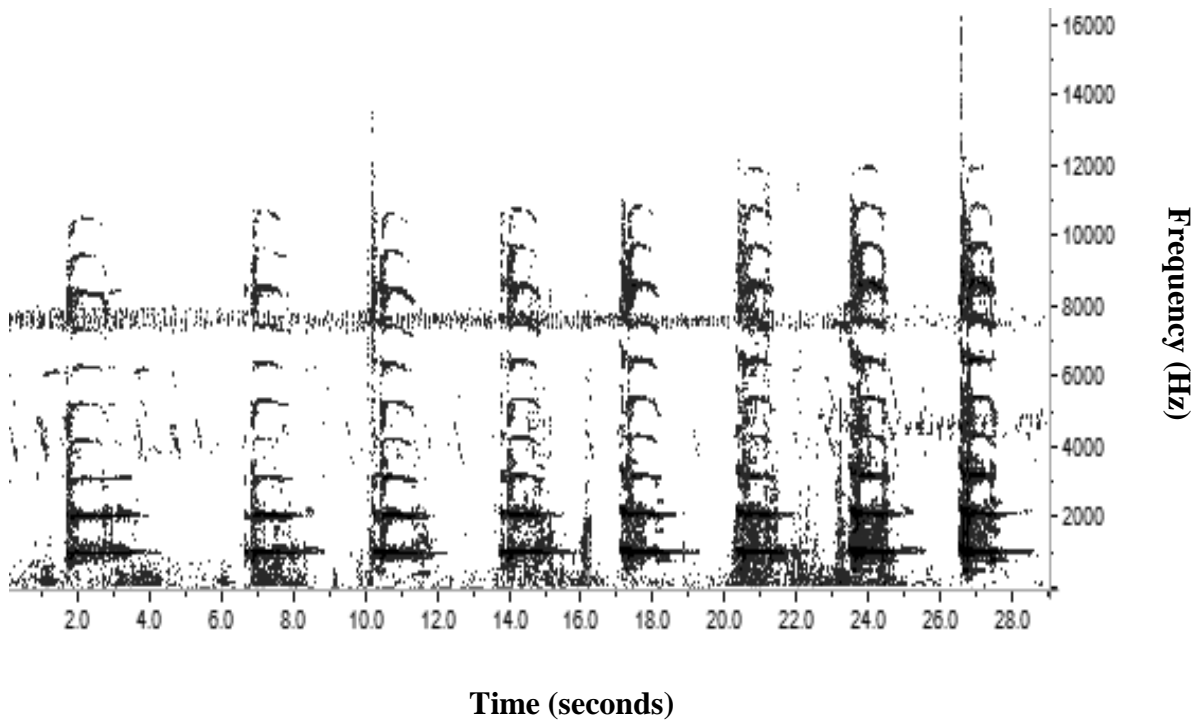
- Mahafaly Special Reserve, Madagascar. *International Journal of Primatology* 10: 595-606.
- Sauther, M. (1991). Reproductive behavior of free-ranging *Lemur catta* at Beza Mahafaly Special Reserve, Madagascar. *American Journal of Physical Anthropology* 84: 463-477.
- Searcy, W., and Andersson, M. (1986). Sexual selection and the evolution of song. *Annual Review of Ecology, Evolution and Systematics* 17: 507-533.
- Sekulic, R. (1982). The function of howling in red howler monkeys (*Alouatta seniculus*). *Behaviour* 81:38-54.
- Sekulic, R., and Chivers, D. (1986). The significance of call duration in howler monkeys. *International Journal of Primatology* 7: 183-190.
- Snowdon, C. (2004). Sexual selection and communication. In: Sexual selection in primates: New and comparative perspectives. Kappeler, P., and van Schaik, C. (eds.). Cambridge: Cambridge University Press, pp. 57-70.
- Sokal, R., and Rohlf, F. (1995). Biometry: The principles and practice of statistics in biological research 3<sup>rd</sup> ed. New York: W.H. Freeman and Company.
- Steenbeek, R., Assink, P., and Wich, S. (1999). Tenure related changes in the wild Thomas's langurs II: Loud calls. *Behaviour* 136: 627-650.
- Sussman, R. (1991). Demography and social organization of freeranging *Lemur catta* in the Beza Mahafaly Reserve, Madagascar. *American Journal of Physical Anthropology* 84: 43-58.
- Sussman, R. (1992). Male life history and intergroup mobility among ringtailed lemurs (*Lemur catta*). *International Journal of Primatology* 13: 395-413.
- Sussman, R., and Ratsirarson, J. (2006). Beza Mahafaly special reserve: A research site in southwestern Madagascar. In: Ringtailed lemur biology: *Lemur catta* in Madagascar. Jolly, A., Sussman, R., Koyama, N., Rasamimanana, H. (eds.). New York: Springer, pp. 43-51.
- Taylor, L. (1986). Kinship, dominance, and social organization in a semi-free ranging group of ringtailed lemurs (*Lemur catta*). Ph.D. Dissertation: Washington University, Missouri.
- Taylor, L. and Sussman, R. (1985). A preliminary study of kinship and social organization in a semi-free-ranging group of *Lemur catta*. *International Journal of Primatology* 6: 601-614.
- Van Horn, R., and Resko, J. (1977). Reproductive cycle of the ringtailed lemur (*Lemur catta*):

- sex steroid levels and sexual receptivity under controlled photoperiods. *Endocrinology* 101:1579.
- Van Schaik C., Assink P., and Salafsky, N. (1992). Territorial behavior in southeast Asian langurs: resource defense or mate defense? *American Journal of Primatology* 26: 233-242.
- Vehrencamp, S. (2000). Handicap, index, and conventional signal elements of bird song. In: *Animal signals: Signalling and signal design in animal communication*. Espmark, Y., Amundsen, T., and Rosenqvist, G. (eds.). Trondheim, Norway: Tapir Academic Press, pp. 277-300.
- Waser, P. (1975). Experimental playbacks show vocal mediation of intergroup avoidance in a forest monkey. *Nature* 255: 56–58.
- Waser, P., and Waser, M. (1977). Experimental studies of primate vocalization: Specializations for long-distance propagation. *Zeitschrift für Tierpsychologie* 43: 239–263.
- Welch, A., Semlitsch, R., and Gerhardt, H. (1998). Call duration as an indicator of genetic quality in male gray tree frogs. *Science* 280: 1928–1930.
- Whitten, A. (1982). The ecology of singing in Kloss gibbons (*Hylobates klossi*) on Siberut Island, Indonesia. *International Journal of Primatology* 3: 33-51.
- Wich, S., and Nunn, C. (2002). Do male “long-distance calls” function in mate defense? A comparative study of long-distance calls in primates. *Behavioral Ecology and Sociobiology* 52: 474-484.
- Wilson, M., Hauser, M., and Wrangham, R. (2001). Does participation in intergroup conflict depend on numerical assessment, range location or rank for wild chimpanzees? *Animal Behavior* 61: 1203-1216.
- Zahavi, A. (1975). Mate selection: A selection for a handicap. *Journal of Theoretical Biology* 53: 204–214.
- Zahavi, A. (1982). The pattern of vocal signals and the information they convey. *Behaviour* 80: 1–8.
- Zahavi, A., and Zahavi, A. (1997). *The handicap principle: A missing piece of Darwin’s puzzle*. Oxford: Oxford University Press.
- Zimmermann, E. (1995a). Acoustic communication in nocturnal prosimians. In: *Creatures of the dark: Biology of nocturnal prosimians*. Alterman, L., Doyle, G., and Izard, M. (eds.). New York: Plenum Press, pp. 311-330.

- Zimmermann, E. (1995b). Loud calls in nocturnal prosimians: Structure, evolution, and ontogeny. In: Current topics in primate vocal communication. Zimmermann, E., Newman, J., and Jurgens, U. (eds.). New York: Plenum Press, pp. 47–72.
- Zimmermann, E., and Lerch, C. (1993). The complex acoustic design of an advertisement call in male mouse lemurs (*Microcebus murinus*, Prosimii, Primates) and sources of its variation. *Ethology* 93: 211–224.
- Zimmermann, E., Vorobieva, E., Wrogemann, D., and Hafen, T. (2000). Use of vocal fingerprinting for specific discrimination of gray (*Microcebus murinus*) and rufous mouse lemurs (*Microcebus rufus*). *International Journal of Primatology* 21: 837-852.
- Zumpe, D., and Michael, R. (1986). Dominance index: A simple measure of relative dominance status in primates. *American Journal of Primatology* 10: 291-300.

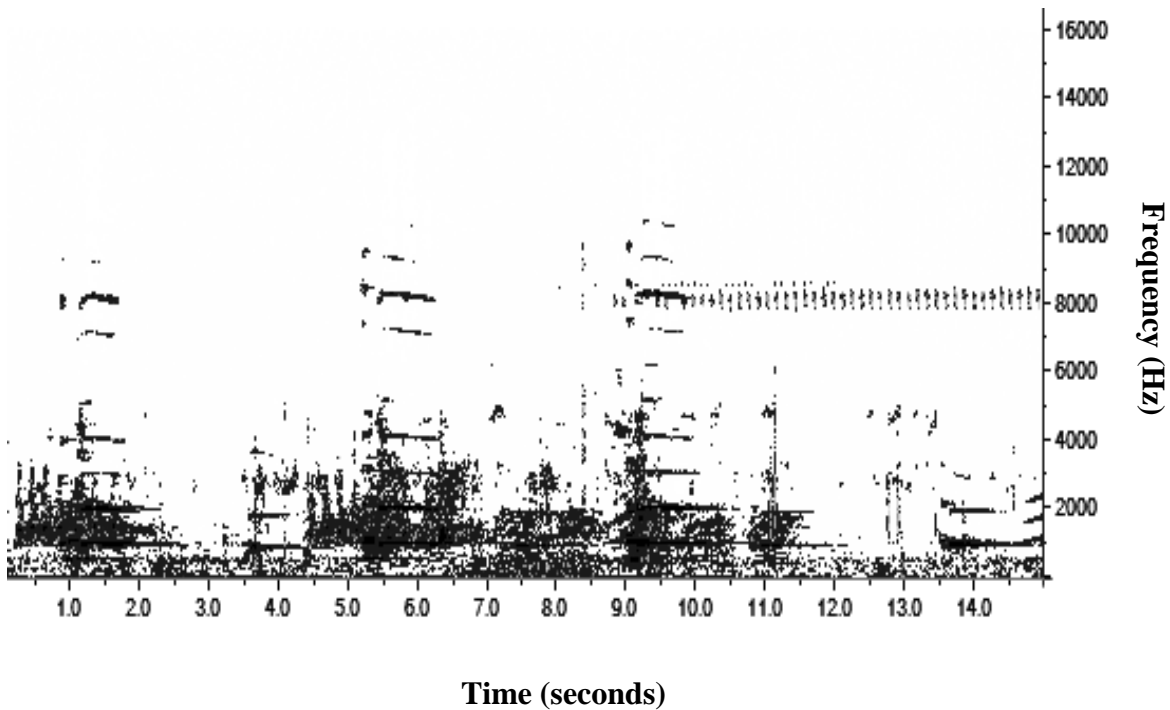
**Table 1. Male ring-tailed lemur study individuals at Beza Mahafaly Special Reserve,  
March-July 2010**

Troop	Individual name	Group membership status	Dominance index score in %	Known or approximate age in years
Green	Umm1g	Non-natal	91.9	≥4
Green	Umm2g	Non-natal	85	≥4
Green	175	Non-natal	71.9	≥8
Green	Umm3g	Non-natal	38.9	≥4
Green	203	Non-natal	36.4	≥8
Orange	263	Non-natal	98.2	≥7
Orange	259	Non-natal	83	7
Orange	Umm1o	Non-natal	49.1	≥4
Orange	291	Non-natal	45.7	≥7
Orange	318	Natal	37.8	3
Orange	226	Non-natal	12.6	≥12
Purple	Umm2p	Non-natal	100	≥4
Purple	Umm1p	Non-natal	76.5	≥4
Purple	Umm4p	Non-natal	69.9	≥4
Purple	323	Natal	46.4	3
Purple	322	Natal	41.7	3
Purple	Umm3p	Non-natal	36.1	≥4
Red	280	Non-natal	85	≥6
Red	273	Non-natal	72.7	≥6
Red	308	Natal	28.6	3
Red	307	Natal	13.7	3
Yellow	208	Non-natal	79.2	≥9
Yellow	Umm2y	Non-natal	75.2	≥4
Yellow	230	Non-natal	74.4	≥8
Yellow	Umm1y	Non-natal	46.2	≥4



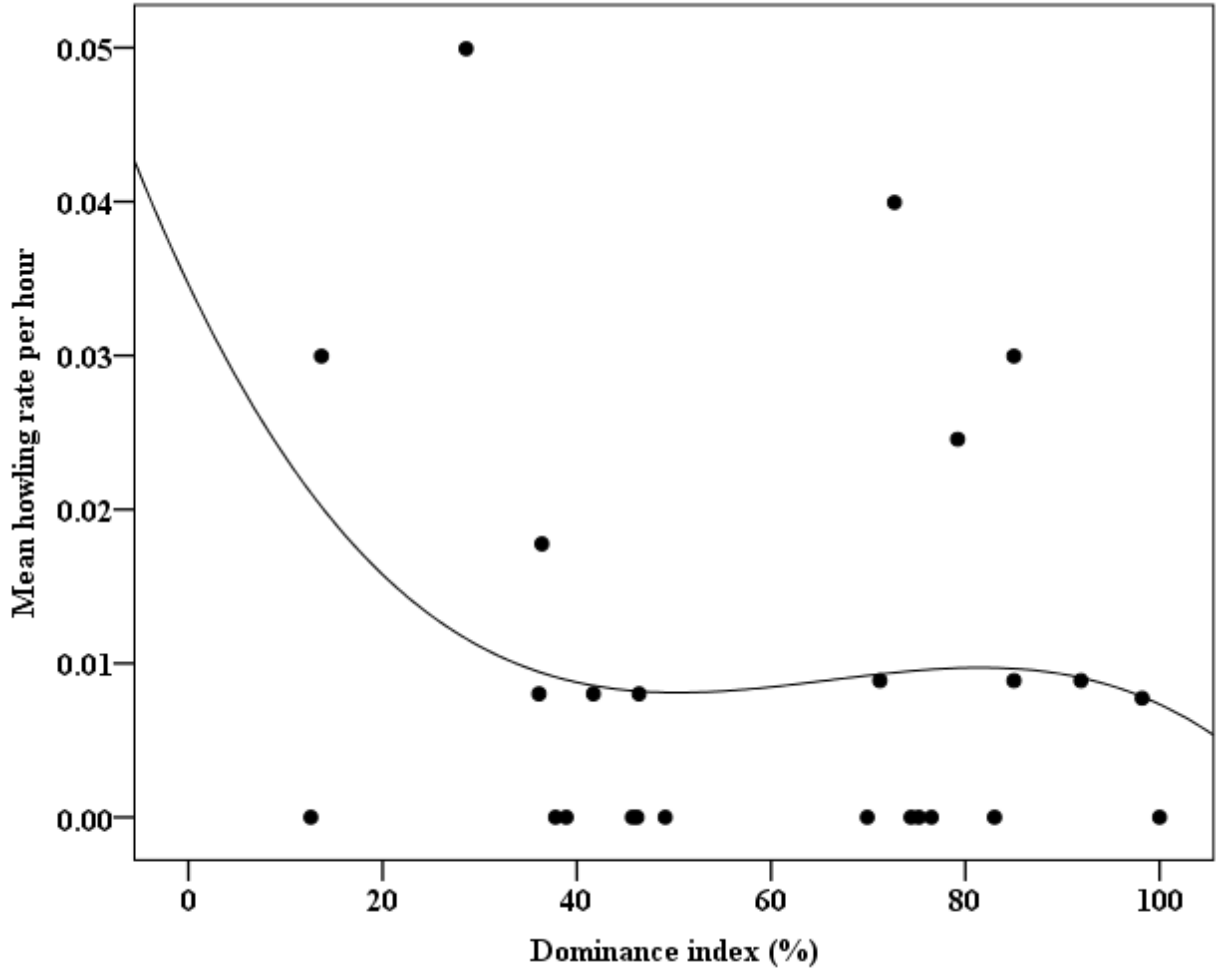
**Figure 1. Sound spectrogram of a male ring-tailed lemur howl bout, recorded with 44.1kHz sampling rate, 16-bit sample depth, and 64 kilobits/second MP3 compression, and with the spectrogram created using a Blackman window with 2048 frequency bins.**

This spectrogram shows a howling bout by male 273 comprised of 8 howls visible as spectral peaks, with the first peak occurring at 1.7-3.5 seconds and subsequent howls occurring every 1.8-3.2 seconds.

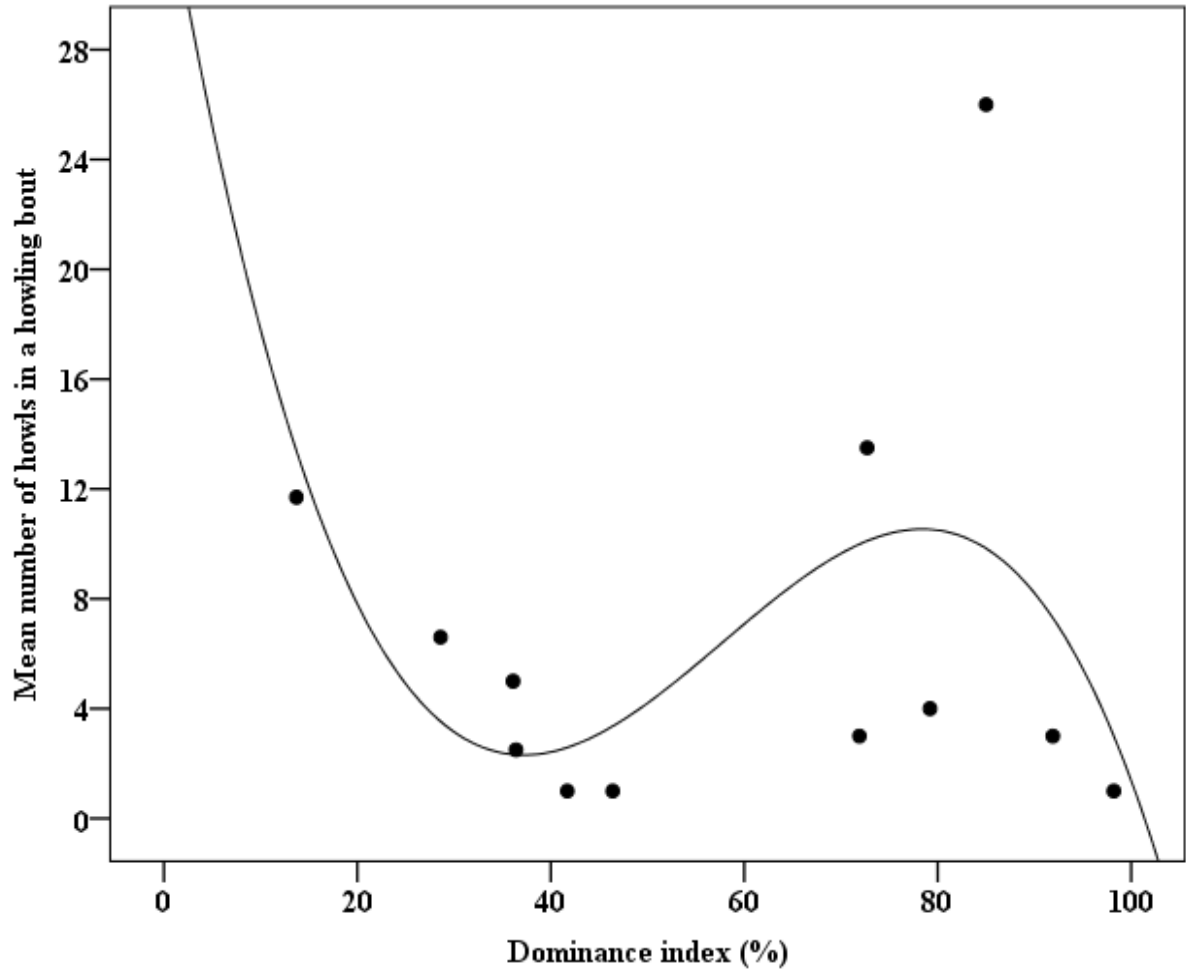


**Figure 2. Sound spectrogram of a ring-tailed lemur howling chorus, with howls from two males, recorded with 44.1kHz sampling rate, 16-bit sample depth, and 64 kilobits/second MP3 compression, and with the spectrogram created using a Blackman window with 2048 frequency bins.**

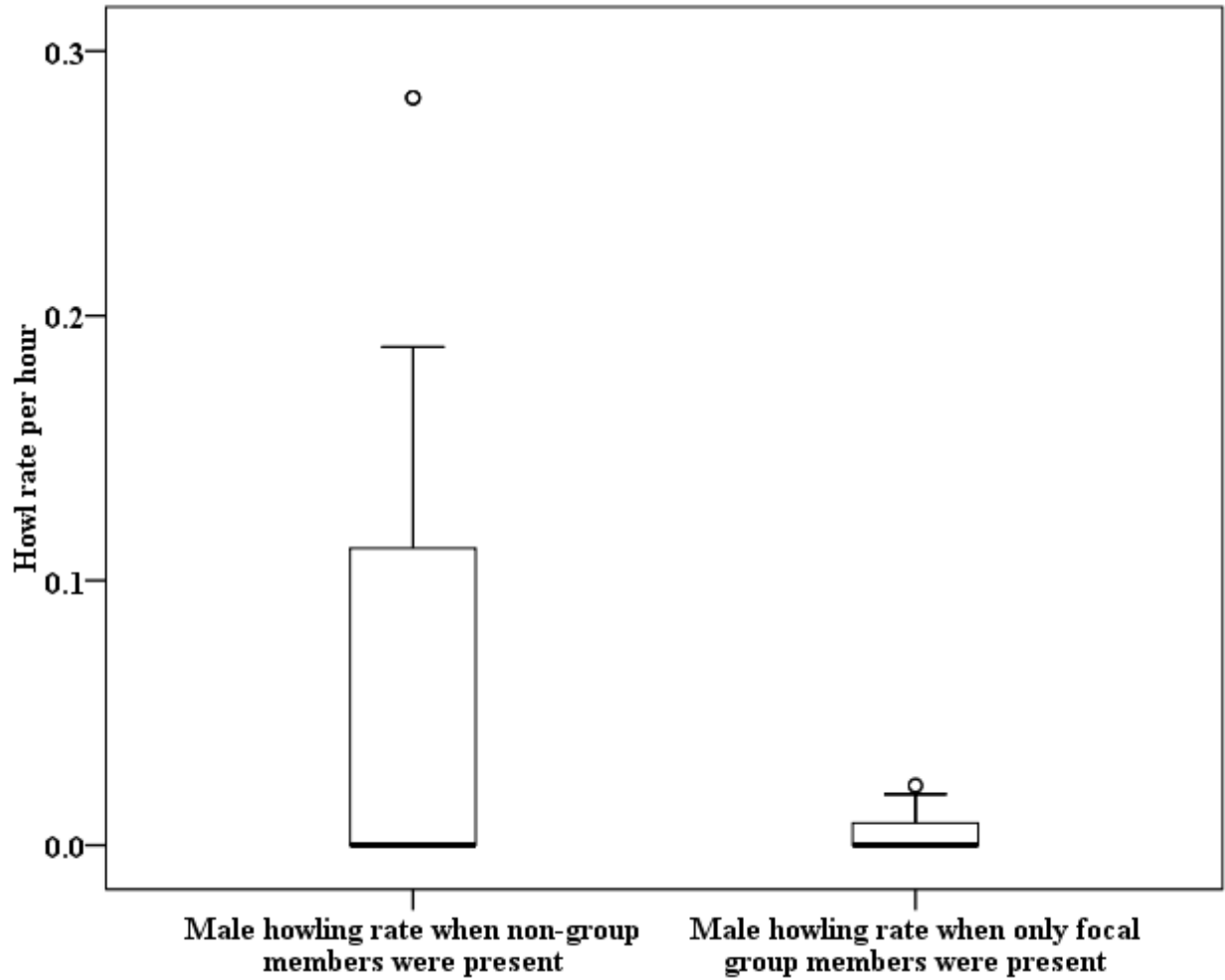
This spectrogram shows an offset howling bout showing howls from two different males, 3 howls from male 1 and 4 howls from male 2. Howls from male 1 are visible as peaks at 1-2 secs, 5.2-6.5 secs, and 9-10.2 secs, while howls from male 2 are visible as peaks at 3.5-4 secs, 7.4-7.9 secs, 10.9-11.4 secs, and 13.5-14.3 secs. Yapping vocalizations from other ring-tailed lemurs are visible at 0-1 secs and 4.4-5.2 secs.



**Figure 3. Correlation between male ring-tailed lemur dominance index score and mean male howling rate, with polynomial regression. Individual points represent individual males.**

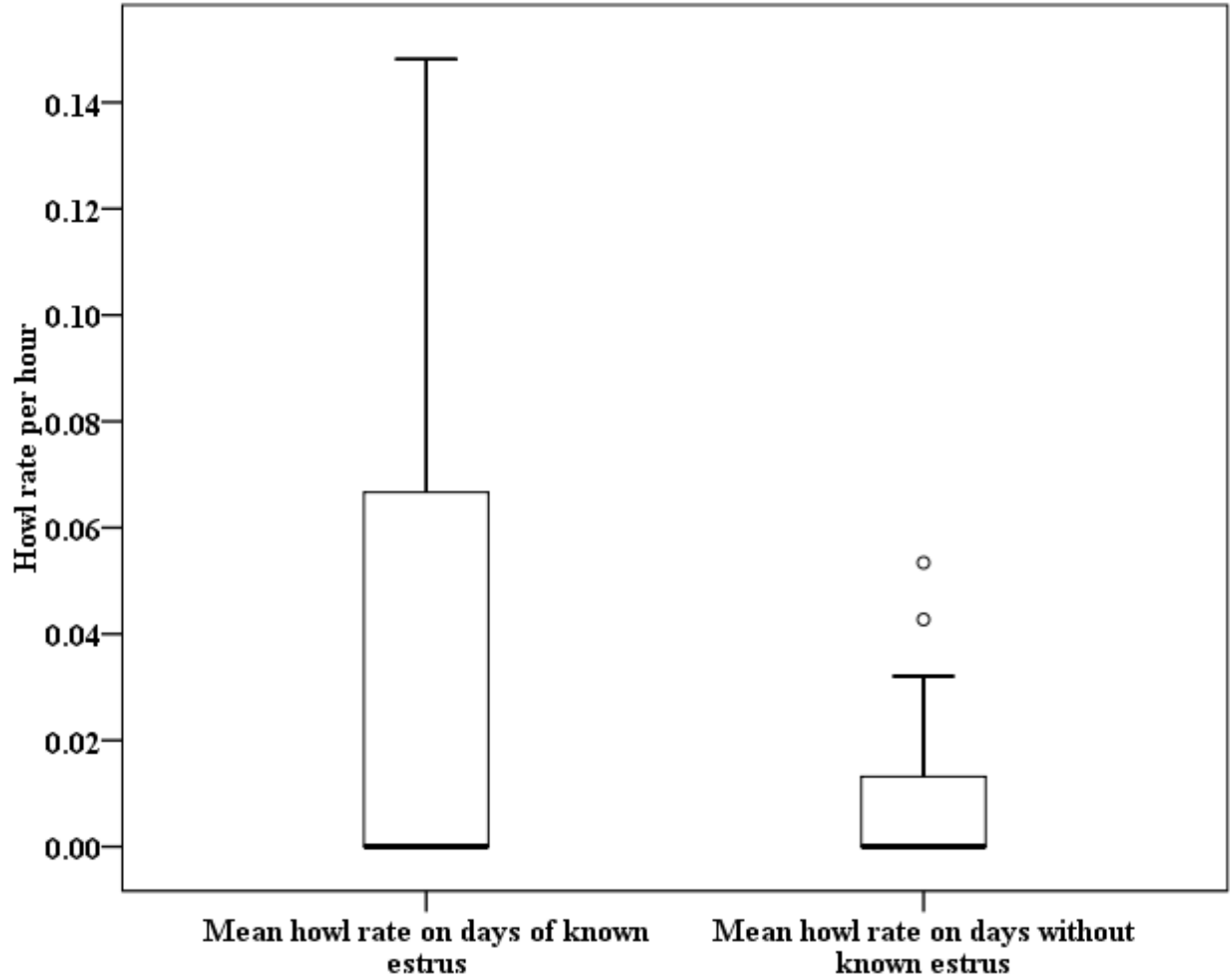


**Figure 4. Correlation between male ring-tailed lemur dominance index score and mean number of howls in a howling bout, with polynomial regression. Individual points represent individual males.**



**Figure 5. Male howling rate per hour during periods when non-group ring-tailed lemurs were present versus male howling rate when no non-group members were present.**

Boxes represent inter-quartile ranges, lines represent median values, whiskers represent maximum and minimum values, and dots represent outliers.



**Figure 6. Mean male ring-tailed lemur howling rate on days of known female estrus versus mean howling rate on days without known estrus.**

Boxes represent inter-quartile ranges, lines represent median values, whiskers represent maximum and minimum values, and dots represent outliers.

## **Chapter 4: Squealing rate indicates dominance rank in the ring-tailed lemur (*Lemur catta*)**

### **Abstract**

Squeals are sharp and forceful short-range vocalizations used as aggressive and submissive agonistic signals by many mammalian species. The ring-tailed lemur (*Lemur catta*), a female-dominant strepsirhine primate, has a male-specific squeal call with proposed male-male agonistic functions that have never been empirically tested. The goal of my study is to clarify why ring-tailed lemur males squeal at other males, and to elucidate how the rate of a male-specific call relates to male-male behaviour in a Malagasy strepsirhine. To test whether males squeal towards other males to assert dominance, I predict that male squealing rate is positively correlated with dominance rank. I further predict that male ring-tailed lemurs squeal at other males while engaged in agonistic interactions, and that squealing during an interaction is positively correlated with winning that encounter. From March-July 2010, 480 hours of focal data were collected on 25 males aged three and older at Beza Mahafaly Special Reserve, Madagascar. I continuously observed each male for 30 minutes at a time and recorded all behaviour, agonistic interactions, and squeal vocalizations using one-zero sampling at 2.5 minute intervals. Squealing rate was higher during times of male-male agonism when compared to times without male-male agonism, and males with higher dominance ranks had higher squealing rates. My results suggest that the male squeal is an agonistic signal when used in male-male interaction in ring-tailed lemurs, indicating both aggression and submission.

### **Introduction**

#### **Male-specific vocalizations as handicap signals**

Sex-specific vocalizations characterize a wide variety of animals. In species where such vocalizations are male-specific, the purpose and function of these vocalizations usually relates to sexual selection (Andersson, 1994; Darwin, 1871). Sexual selection is a form of natural selection which operates between individuals of the same sex as they compete against rivals, and between members of the opposite sex as they compete to attract mates (Darwin, 1871). Males are thought to vocalize with sex-specific calls to other males as a way of competing for resources such as

food, mates, and dominance status, while males vocalize to females as a means of gaining sexual access (Andersson, 1994; Snowdon, 2004). Sexual selection theory predicts that those males who are the most successful in driving away rivals and in gaining sexual access to females produce more viable offspring and have more of their genes passed along to subsequent generations, and therefore have greater fitness (Bradbury and Vehrencamp, 1998; Darwin, 1871).

In order to attain this fitness, males of many species have developed elaborate ornaments, such as elongated and colourful tails in birds (e.g. the barn swallow, *Hirundo rustica*; Møller, 1988) and in fish (e.g. the guppy, *Poecilia reticulata*; Brooks and Endler, 2001). Such traits serve to intimidate male rivals and attract female mates while providing some cost to the animal with the trait itself (Zahavi, 1975; Zahavi and Zahavi, 1997). This cost may be increased predation pressure, in that a male with a highly visible physical trait like a coloured tail would be easier for a predator to target than a male without such visible attributes, or energetic, in that there may be significant physiological costs to developing and maintaining larger physical structures such as elongated tails (Andersson, 1994; Zahavi, 1975). Empirical studies, though few, confirm the fitness costs for such traits (Godin and McDonough, 2003; Møller and de Lope, 1994). Barn swallows with artificially elongated tail feathers are known to have reduced survival, while those with naturally long tails are better able to bear the cost of plumage maintenance (Møller and de Lope, 1994). Further, more brightly-coloured guppies are preferentially targeted by predators and have lower viability as a result of predation (Godin and McDonough, 2003).

Costly, fitness-related ornaments can also take the form of displays, in which males participate in a repeated, ritualized behaviour which serves to attract females as well as to intimidate other males (Darwin, 1871; Zahavi and Zahavi, 1997). Such displays are known in a variety of animal species, and like ornaments, they are thought to have proximate costs and to impair a male's chances of survival for the ultimate advantage of increased evolutionary fitness (Zahavi, 1975). For example, in the male sage grouse (*Centrocercus urophasianus*), males making sexual displays to females showed individual differences in display rate and energetic expenditure, with all displaying males showing significant increases in metabolic rate (Vehrencamp et al., 1989). Costly displays often contain or take the form of repeated vocalizations or acoustic utterances (Bradbury and Vehrencamp, 1998). For example, the male wolf spider (*Hygrolycosa rubrofasciata*) performs a drumming display at a high rate which attracts mates (Kotiaho, 2000). Male wolf spiders manipulated to be in good condition were

found to better survive displaying at a high rate when compared with males in poor condition, attesting to the expense of this signal (Kotiaho, 2000). Repeated acoustic signals and vocalizations are considered costly because increasing repetition rate is thought to increase the energetic cost of signaling (Vehrencamp, 2000). Additionally, males who repeat an acoustic signal at a high rate incur costs in that they receive more attention from every other animal in the area, and therefore put themselves at higher risk for predation and for violence from other males (Andersson, 1982, 1994). In species where repeated vocalization displays occur, such as red deer (*Cervus elaphus*), chacma baboons (*Papio ursinus*), and common toads (*Bufo bufo*), there is also evidence that higher display frequency is related to quality, such that males with high call repetition rates have higher dominance rank and better fighting ability (red deer: Clutton-Brock and Albon, 1979; common toad: Davies and Halliday, 1978; chacma baboon: Kitchen et al., 2003). Males of these animal species are known to repeat the same sex-specific vocalization at times of female estrus and male-male competition, and this advertises their fitness, as a rival and mate (Bradbury and Vehrencamp, 1998). These costly, repeated vocalizations can be termed quality handicap signals (Zahavi, 1975; Zahavi and Zahavi, 1997).

Handicap signals, as male-specific utterances used in both courtship and male-male competition, are likely to be honest as well as costly (Zahavi, 1975). Deception is not thought to be present in handicap signals (Zahavi and Zahavi, 1997). Deceptive signals are only selected for in a species when the benefits to the dishonest signaler outweigh the costs of producing a dishonest signal, therefore allowing such signals to persist through generations (Maynard Smith and Harper, 1995; Vehrencamp, 2000). When considering whether the repetition level of a vocalization honestly indicates male quality, the myriad costs of signals are thought to keep repetition rate honest (Maynard Smith and Harper, 1995, 2003; Vehrencamp, 2000; Zahavi, 1975). Only males who can spare the energetic and physiological costs necessary to engage in repeated vocal displays will do so, making these displays accurate indicators of male fitness. Repeated vocalizations cause a male to incur costs (thus “handicapping” him), and the sum of the costs that he is able to bear honestly indicates his quality. Over generations, high-quality signalers will have higher fitness since they will be better able to bear the costs associated with the honest signal (Grafen, 1990, 1991; Zahavi, 1975). Females are known to preferentially select such males as mates so that his high-quality genes will be inherited by their offspring, while rival

males are more likely to be ousted in competition by this superior fighter (Andersson, 1982, 1994; Snowdon, 2004).

### **Game theory and agonistic vocalization rate in males**

When a male-specific, repeated vocalization is thought to be a handicap signal, the predictions of game theory can also be applied to the use of this vocalization (Maynard Smith, 1982, 1994). Game theory is a model which, in evolutionary biology, predicts the success of one animal at obtaining a finite, indivisible resource, such as a mate or food source, based on the actions and choices of another animal (Bishop et al., 1978; Maynard Smith, 1982, 1994; Maynard Smith and Price, 1973; Maynard Smith and Parker, 1976). Contest competitions between animals usually start with a low level of aggression and then gradually escalate, as each competitor matches his own aggression level to the aggression level of his opponent (Maynard Smith, 1982). Most instances of aggression between animals are mediated by communication, such that the signals given by one animal influences the actions of its opponent (Maynard Smith, 1982, 1994; Enquist and Leimar, 1983; Hurd and Enquist, 1998). During fights, animals are thought to use communicatory signals to assess the fighting ability of their competitors (Huntingford et al., 2000). Game theory predicts that since all individuals want to be successful in “winning” the interaction (i.e. obtaining the resource in question, which may be a food item, copulation, or other item), they will avoid unnecessary costs to themselves whenever possible (Maynard Smith, 1982; Maynard Smith and Price, 1973; Maynard Smith and Parker, 1976). Animals will therefore avoid escalation to full-scale physical fighting whenever they can, and preferentially settle a contest competition using non-violent means such as ritual display and reciprocal communication (Huntingford et al., 2000; Maynard Smith, 1982; Maynard Smith and Price, 1973; Maynard Smith and Parker, 1976). One of these non-violent means of reciprocal communication is vocalization use (Bradbury and Vehrencamp, 1998).

Game theory predicts that one of the ways in which individuals assess an opponent’s fighting ability is based on the rate of their vocal displays (Maynard Smith, 1982). Animal species from toads to red deer to chacma baboons are known to vocalize threat signals to exhibit their quality to potential opponents, thus allowing the opponents to assess the quality of the displayer and to determine who would win in a fight without actually fighting (Clutton-Brock and Albon, 1979; Davies and Halliday, 1978; Kitchen et al., 2003, 2005a). An agonistic

interaction is most likely to be won by the stronger, healthier, and more motivated individual, and honest vocalization signals provide reliable information about these traits in competitors (Maynard Smith, 1982; Zahavi, 1975). According to the predictions of game theory, contests between individuals of very different competitive abilities will end quickly, when one individual realizes that it would lose in combat if the interaction escalated (Bradbury and Vehrencamp, 1998; Maynard Smith and Parker, 1976). In contrast, contests between more evenly matched individuals will last for a longer duration, be more intense, and be more likely to escalate to potentially harmful physical agonism (Bishop et al., 1978; Enquist and Leimar, 1983, 1990; Maynard Smith and Parker, 1976). In these persistent contests, individuals are thought to be unable to find a difference between their own and their opponent's agonistic ability, and/or to be unwilling to stop aggressive behaviour (Bishop et al., 1978; Maynard Smith, 1982). Such evenly matched individuals continue displaying to one another until one competitor either becomes exhausted and stops displaying, or escalates the contest to physical violence, allowing actual fighting to determine which individual is the winner (Bishop et al., 1978; Maynard Smith, 1982). In such situations, repeated vocalizations therefore function as assessment signals, allowing competitors to reliably gauge the quality of opponents and to stop calling when it becomes clear that they would be unable to win in an escalated fight (Zahavi, 1975, 1977).

The predictions for how game theory relates to vocalization rate have been strongly supported in several different animal species (Clutton-Brock and Albon, 1979; Davies and Halliday, 1978; Kitchen et al., 2003, 2005a). In common toads, males are known to use vocalization characteristics including the vocalization rate of an opponent to decide whether or not to attack, or to continue in an agonistic interaction that is already underway (Davies and Halliday, 1978). In red deer, males engage in ritualized roaring contests before escalating to fighting, and higher roaring rate is linked to better fighting ability. Roaring rate therefore functions as an assessment signal, an honest proxy for ability in combat. In addition, both roaring and fights occur most frequently between deer of similar dominance rank, as predicted by game theory (Clutton-Brock and Albon, 1979). This trend is also found in chacma baboons, with competing males of similar dominance ranks exchanging sex-specific agonistic vocalizations at higher rates and for longer durations (Kitchen et al., 2003). Males are thought to observe the dominance level of their rivals and to adjust their own signaling behaviour accordingly (Kitchen, 2004; Kitchen et al., 2005b). Fights between male baboons also echoed this pattern, such that

males were more likely to fight with individuals of similar rather than disparate rank, and that fights between fairly equally matched males lasted for longer durations (Kitchen et al., 2005a).

Although the predictions of both game theory and the handicap hypothesis are known to apply to the sex-specific agonistic vocalization rates of the chacma baboon, they have not been examined with reference to the male-specific agonistic vocalizations in other primates. My study will examine how the handicap hypothesis and game theory may relate to the male-specific, agonistic squeal vocalization of a Malagasy strepsirhine, the ring-tailed lemur (*Lemur catta*).

### **Background on the ring-tailed lemur**

The ring-tailed lemur is a female-dominant strepsirhine primate endemic to southern Madagascar (Jolly, 1966). It is a gregarious animal that lives in multi-male, multi-female groups of up to twenty-seven animals (Gould et al., 2003; Pride, 2005; Sussman, 1991). Males disperse from their natal group at 3-4 years of age and disperse to new groups approximately every three years, while females usually remain in their natal groups for their entire lives (Budnitz and Dainis, 1975; Jones, 1983; Sussman, 1992).

Ring-tailed lemurs have an annual breeding season that begins in April/May in Madagascar, with females in asynchronous estrus (Jolly, 1966). Each female stays in estrus for 3.25 to 24 hours in total, and during this time usually mates with multiple males (Jolly, 1966; Parga, 2006a; Sauther, 1991; Van Horn and Resko, 1977). Mating opportunities are usually restricted to non-natal males, who are sexually mature and unrelated to group females (Parga, 2010; Sauther, 1991; Taylor and Sussman, 1985). The competition between non-natal males for mates leads to a high degree of male-male aggression during the breeding season, and can lead to severe injuries and even death (Gould and Ziegler, 2007; Jolly, 1966; Sauther 1991). Although females are dominant, males have their own dominance hierarchy, which is often linear (Budnitz and Dainis, 1975; Gould, 1994; Taylor, 1986). Dominance confers social advantages for high-ranking males, typically including first sexual access to group females when they are in estrus (Koyama, 1988; Parga, 2006b; Sauther, 1991; but see Gould, 1994). Being an earlier-mating male during female estrus may also provide a fertilization advantage (Pereira and Weiss, 1991). Dominance is therefore an extremely desirable characteristic for ring-tailed lemur males.

Males maintain their dominance hierarchy through physical combat as well as through ritualized scent marking and tail waving displays (Gould, 1994; Gould and Ziegler, 2007; Palagi et al., 2003; Scordato and Drea, 2007). When a male tail waves, he rubs his high-contrast ringed tail across scent glands located on his wrists and shoulders, then lifts his tail over his head and waves his tail repeatedly to wafts his scent towards a rival male, who is 1-3 metres away (Gould, 1994; Jolly, 1966; Mertl, 1976). The rival male may retreat, reciprocate, or attack in response (Jolly, 1966). Tail waving can also escalate into a more involved reciprocal display called “stink fighting”, where two males standing 3-10 metres scent mark and tail-wave at one another at the same time, and may do so repeatedly (Jolly, 1966; Sauther et al., 1999).

In addition to tail-waving and scent marking, vocalizations mediate male ring-tailed lemur behaviour, and have been studied by a number of researchers (Andrew, 1963; Jolly, 1966; Macedonia, 1986, 1990, 1993; Oda, 1996; Petter and Charles-Dominique, 1979; Sauther, 1989). As a highly social strepsirhine, the ring-tailed lemur has a large vocal repertoire comprised of 22 distinct vocalizations for adults (Macedonia, 1990). These consist of 8 calls used in affiliative interactions, 6 calls used in agonistic behaviour, and 8 anti-predator vocalizations (Macedonia, 1990). Of these 22 calls, several are long-range, two are male-specific, and some are known to be individually distinctive (Jolly, 1966; Macedonia, 1986, 1990, 1993). My study focuses on the squeal vocalization, a male-specific agonistic call that often occurs in concert with tail-waving displays (Andrew, 1963; Jolly, 1966; Macedonia, 1990, 1993; Petter and Charles-Dominique, 1979).

### **Squealing in the ring-tailed lemur**

Squeals are sharp, tonal, loud, high-pitched, forceful, and conspicuous calls in the ring-tailed lemur (Andrew, 1963; Jolly, 1966; Macedonia, 1990, 1993; Petter and Charles-Dominique, 1979; **Figure 1**). Only sexually mature and sometimes juvenile ring-tailed lemur males are known to squeal, and they do so in both agonistic and sexual contexts (Gould, 1994, 2006; Jolly, 1966; Macedonia, 1990; Petter and Charles-Dominique, 1979). Males squeal towards females to determine if they are sexually receptive, and toward other males to indicate low-intensity agonism in competitive situations (Gould, 1994; Jolly, 1966; Macedonia, 1990; Sbeglia et al., 2010). Ring-tailed lemur squealing occurs almost exclusively in association with the multi-modal tail-waving display, which involves visual tail waving elements and olfactory scent marking

components in conjunction with the vocal squeal (Jolly, 1966; Macedonia, 1990; Petter and Charles-Dominique, 1979). Males squeal as they aggressively stare at other males and mark scent on their tails immediately prior to tail-waving displays (Jolly, 1966). Males also squeal when chasing inferiors who are subordinate in rank (Andrew, 1963). Petter and Charles-Dominique (1979) and Macedonia (1990, 1993) thought that males squealed to manifest their dominance towards other males. Petter and Charles-Dominique (1979) further noted captive males squealing out of “anger” (p.294) and as they attacked unfamiliar humans, further attesting to the aggressiveness of this vocalization. Squealing rate is thought to increase during the mating season, paralleling an increase of other forms of male-male aggression (Jolly, 1966). Although the ring-tailed lemur squeal is a relatively low-amplitude vocalization when compared with long-distance vocalizations such as the howl, some low-amplitude vocalizations are known to have substantial energetic costs in other animals (e.g. purring in cats; Peters, 2002; Remmers and Gautier, 1972). The squeal, as an agonistic signal used in male-male contest competition by ring-tailed lemurs (Jolly, 1966; Macedonia, 1990, 1993), has the potential to be a handicap signal, and as such, merits further investigation.

### **My study: Elucidating why male ring-tailed lemurs squeal**

Although past studies have explored the functions of scent marking in male ring-tailed lemurs (Mertl, 1976; Mertl-Milhollen, 2007; Palagi et al., 2003; Scordato and Drea, 2007), no studies to date have empirically evaluated the usage of the squeal vocalization by individual males, or tested how male squealing behaviour may relate to dominance. The goal of my study is to clarify why ring-tailed lemur males squeal at other males, and specifically to assess how intra-sexual selection theory may apply to ring-tailed lemur squealing rate. My study aims to clarify how and why males use squeal vocalizations through gathering data to test to following hypothesis.

### **Hypothesis: Squealing rate is an honest indicator of male dominance rank**

Squealing rate may honestly indicate male dominance rank in the ring-tailed lemur, as has been found for male-specific vocalization rates in chacma baboons (Kitchen et al., 2003). If this is the case, then I predict that high-ranking males will have higher squealing rates, and that squealing rate will be higher during times of male-male agonism.

Further to this hypothesis are several associated questions. Do males engage in agonistic interactions while squealing? If so, this would provide support for the idea of squealing being an agonistic vocalization in the ring-tailed lemur. Further to this question, when males squeal during agonistic interactions, are males who squeal more likely to win the agonistic interaction that squealing accompanies? If males who squeal during agonism are more likely to win, then this provides support for the notion that squealing is an aggressive rather than a submissive vocalization, and that a male's squealing rate indicates his superior fighting ability. Finally, do males with similar dominance ranks have a higher rate of squealing toward one another (i.e. a greater number of dyadic squealing interactions) than very differently ranked males? If squealing is an agonistic vocalization that accompanies male-male agonistic interactions, then we would expect the predictions of game theory to apply. Males with similar dominance ranks should squeal toward one another more than very differently ranked males.

Conversely, the null hypothesis states that squealing rate has no relationship with male dominance rank, such that males with higher dominance index scores do not have higher or lower squealing rates than males with lower dominance indices.

## **Methods**

### **Description of field site**

All data for this study were collected between March 1-July 1, 2010 at Beza Mahafaly Special Reserve, a protected governmental reserve in Madagascar's southwest (23°30'S lat., 44°40'E long.) (Sussman and Ratsirarson, 2006; Sussman et al., 2012). This reserve was established in 1978 and has been protected since 1986 (Gould et al., 2003; Sussman et al., 2012). It consists of two non-contiguous forest types, dry forest in the western area of the reserve (Parcel II, 500 ha) and riverine forest on the eastern side (Parcel I, 80 ha) (Sussman and Ratsirarson, 2006). However, the two non-contiguous parcels have recently been connected in an expansion of the reserve to now nearly 4000ha (Sauther, pers. Comm.). A system of labeled trails roughly divided Parcel I into 100m<sup>2</sup> squares, making this forest easy to navigate. Beza Mahafaly was an optimal site for recording primate vocalizations and collecting high-quality behavioural data because of its secluded location away from major roads. The small number of motorized vehicles in the area limited environmental noise.

Approximately 225 free-ranging ring-tailed lemurs in eleven 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 labeled with visible numbers, an identification system dating to the earliest ring-tailed lemur research at the reserve in the late 1980s (Cuzzo and Sauther, 2006; Cuzzo et al., 2010; Sauther and Cuzzo, 2009; Sauther et al., 2002; Sussman, 1991). The only individuals left uncollared were infants, yearlings, and some adult males who had recently migrated from groups outside of the reserve.

Any uncollared animals could be easily individually identified due to patches of black dye in different body areas on each animal, in addition to sex and size differences. Five groups from Parcel I were the focus of this study.

### **Description of study animals**

Behavioural focal follows were performed six days per week from dawn until dusk on all males aged three and older from five ring-tailed lemur troops (green, orange, purple, red, and yellow troops). Only one group was followed per day. Each group was studied 1-2 days per week. Resident males were sampled using the focal animal sampling method on a randomized, rotational basis from dawn until dusk (Altmann, 1974).

Focal data were collected from 25 sexually mature males in total (**Table 1**). Ages for most individuals are known from the decade-long work by Sauther and Cuzzo, who identify lemurs first as subadults (second year of age) when first captured, with age determined from a series of variables including dental development, sexual maturity (or lack thereof), body mass, and somatic development (Cuzzo and Sauther, 2006; Cuzzo et al., 2010; Sauther and Cuzzo, 2008, 2009). Thus collared lemurs aged two or greater are of known age. I estimated the age for all individuals with names beginning with “UMM” (unmarked male) as three or more. All “UMM” individuals were sexually mature males who were known to be new, non-natal members to collared study groups in Parcel I within the last year (Beza Mahafaly Special Reserve unpublished data). Both natal and non-natal male group members were included in all statistical analyses because some natal males were observed mating with female group members (Bolt, unpublished data). At Beza Mahafaly Special Reserve, ring-tailed lemur study group size ranged from 9-20 individuals, with 4-8 males, 4-10 females, and 0-3 infants present per group.

## Field methods

During focal sampling, each male subject was followed for thirty minutes at a time, with data recorded every 2.5 minutes on a programmed palm pilot (Palm Z-22) using one-zero sampling (Martin and Bateson, 2007) to document the actions that occurred during the previous time period, including the focal individual's behaviour (resting, vigilant, allogrooming, autogrooming, feeding, foraging, sunning, playing, attacking, fleeing, wrist marking, shoulder marking, genital marking, tail marking, tail waving, travelling, urinating/defecating, mounting, licking scent mark, other, out of sight), whether they were engaged in behaviour with others, and the identity of other individual(s) involved (if applicable). During focal sampling, the following vocalization types were recorded: moan, wail, howl, hmm, huh, purr, chirp, yip, cackle, squeal, twitter, plosive bark, chatter, gulp, rasp, shriek, click, click series, yap (following Macedonia, 1990). Animals were watched continuously during the focal period. The ring-tailed lemur ethogram was based on those used by Gould (1994), Jolly (1966), Parga (2006b), and Pereira and Kappeler (1997).

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 behaviour is occurring within a given time period (Sarfaty et al., 2012). Although one-zero sampling has received criticism (e.g. Altmann, 1974), this sampling method has also been empirically shown to be an effective technique for collecting data on primate behavioural rates (Leger, 1977; Suen and Ary, 1984), and provides an equally accurate measure of behaviour as more widely used sampling methods (reviewed in Rhine and Linville, 1980). One-zero sampling has been used in other studies of primate vocalizations as a means of measuring the rate of a short, repetitive vocalization (Suzuki and Sugiura, 2011) or to determine whether vocalizations occurred or not within a given time period (Clarke et al., 2012). Bernstein (1991) suggests that one-zero scoring should be used when behavioural acts are clustered and the bout, rather than each act, is of interest. Through using one-zero sampling in my study, each behaviour, squealing bout, and agonistic interaction could be reduced to a single, independent data point, allowing for a more accurate analysis.

Vocal recordings were made of all utterances by the focal animal during each focal follow when possible, using a Sennheiser ME66 directional microphone (Sennheiser Electronic

GmbH and Company, KG) and digital Marantz PMD660 recorder (Marantz Corporation, New York, USA). Recordings were made with a 44.1kHz sampling rate, 16-bit sample depth, and 64 kilobits/second MP3 compression. The sampling rate refers to the number of digital sound samples taken in per second, while the 16-bit sample depth refers to 65 536 different levels of quantization recorded (Oppenheim et al., 1996). MP3 compression was necessary due to storage space limitations on the digital recorder. Sound spectrograms for squeals were produced using Cool Edit Pro v.2.1 (Syntrillium Software, USA, 2003), with the spectrogram created using a Blackman window with 2048 frequency bins. A Blackman window is a mathematical function used in spectral analysis and used to generate spectrograms, while the number of frequency bins refers to the frequency resolution of the spectrogram, with 2048 values in total of different frequencies that are measured and used to generate the spectrogram (Oppenheim et al., 1996). 2048 frequency bins allowed for optimal frequency and time resolution of the ring-tailed lemur squeal vocalization, based on a visual inspection.

In my study, an agonistic interaction is defined as any behaviour involving contest competition between two individuals. This could consist of low-arousal behaviour (e.g. a displacement or lunge-withdraw) or higher-arousal behaviour (e.g. cuff, bite, or jump fight). An agonistic interaction involves one or more acts of avoidance, aggression, or defense between two individuals. A period without male-male agonism is defined as a time without contest competition between individuals.

### **Calculating male rank**

The male dominance hierarchy in a ring-tailed lemur troop is often linear, but is sometimes non-linear (Budnitz and Dainis, 1975; Gould, 1994; Jolly, 1966). In my study, dominance was determined from focal data using dominance index calculations, which take all decided agonistic and submissive interactions into account before assigning each male an individual dominance percentage within its troop (Zumpe and Michael, 1986). Dominance index was calculated using the following equation:

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

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

In calculating dominance indices, all agonistic behaviours (e.g. chase, lunge-withdraw, cuff) were treated equally (following Gould, 1994). Dominance indices were calculated separately for males in each group. Males with higher dominance percentages won more fights and had a higher ranking within their troops. Dominance index calculations for all males in each troop are presented in **Table 1**.

Ordinal dominance rank was determined from dominance index scores. Males within each group were assigned an ordinal ranking based on their dominance index score with relation to the other males in their group. In each group, the male with the highest dominance index score was assigned a dominance ranking of 1, the male with the second-highest dominance index score was assigned a dominance ranking of 2, and so on in descending order, until all males in each group were assigned an ordinal ranking.

### **Data analysis**

For each data set used in my study, data were not normally distributed, requiring the use of non-parametric tests. In addition, the sample size was small ( $n=25$  males), which meant that non-parametric tests were appropriate. For this reason, analyses in my study were performed using non-parametric statistics, such as Spearman rank correlations, Wilcoxon signed-rank tests, and Pearson chi-squared goodness-of-fit tests.

In my study, the Spearman rank correlation test was used to evaluate a prediction from my hypothesis, that high-ranking males will have higher squealing rates. The Spearman rank correlation test is used when there are two measurement variables (e.g. squealing rate and dominance index) and one nominal variable (e.g. individual) which groups measurement variables into pairs (McDonald, 2009; Sokal and Rohlf, 1995). The test determines if the ranks of each variable co-vary (e.g. if one value increases when the other decreases, or if one increases as the other increases) (McDonald, 2009; Sokal and Rohlf, 1995). The null hypothesis for the Spearman rank test states that the ranks of one measurement variable do not co-vary with the ranks of the other measurement variable (i.e. as one variable increases, the other is not more likely to increase or decrease) (McDonald, 2009; Sokal and Rohlf, 1995). For this test, the two variables were male ring-tailed lemur squealing rate and dominance index. When the Spearman rank test was performed, linear regression was also performed in order to visually summarize the relationship between the variables (McDonald, 2009).

In my study, the Wilcoxon signed-rank test was used to evaluate a prediction from my hypothesis, that squealing rate will be higher during times of male-male agonism. The Wilcoxon signed-rank test allows for the testing of differences between two nominal variables (e.g. individual and estrus day/non-estrus day) and a measurement variable (e.g. squealing rate) (McDonald, 2009; Sokal and Rohlf, 1995). The null hypothesis for the Wilcoxon signed-rank test states that the median difference between pairs of observation is zero (McDonald, 2009; Sokal and Rohlf, 1995). Under the null hypothesis, smaller values of  $z$  are less likely (McDonald, 2009; Sokal and Rohlf, 1995). For this test, the dependent variable was ring-tailed lemur squealing rate, and the independent variable was time (i.e. at a time of male-male agonism versus at a time without male-male agonism). I also used the Wilcoxon signed-rank test to determine whether male squealing rate was higher during agonistic wins when compared with agonistic losses. For this test, the dependent variable was ring-tailed lemur squealing rate, and the independent variable was agonistic success status (i.e. while winning an agonistic interaction versus while losing an agonistic interaction).

In my study, the Pearson chi-squared goodness-of-fit test was used to evaluate one of the questions associated with my hypothesis, whether males with similar dominance ranks will be more likely to have a higher rate of squealing toward one another (i.e. a greater number of dyadic squealing interactions) than very differently ranked males. Males were grouped into the number

of possible dyads involving different ranks overall. The Pearson chi-squared goodness-of-fit test is used when comparing observed values (i.e. the observed rate of squeal exchange between male-male dyads) to expected values (i.e. the expected rate of squeal exchange between male-male dyads, assuming that all males squealed at equal rates to all other males). The test determines if there is a significant difference between observed and expected values. The null hypothesis for the Pearson chi-squared test states that the frequency distribution of occurrences observed in the sample is not significantly different from the distribution that would be expected by chance (i.e. male dyads of similar dominance rank are not more likely to squeal at one another than would be expected by chance, assuming that all male-male dyads squeal at one another at equal rates). For this test, the categorical independent variable, rank difference between interacting ring-tailed lemur males, was compared against two categorical dependent variables, expected versus observed frequency of participation in squealing dyads.

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

To test whether males with similar dominance ranks were more likely than males with disparate dominance ranks to squeal at one another, all male-male dyads involving squealing were determined. To calculate expected values for squealing rate within each dyad, all focal males were considered equally likely to interact with all other males in their social group, and expected values were determined for how many squealing interactions (out of the total number of squealing interactions) would involve males separated by one rank position (i.e. rank 1 and 2 within a group, or rank 2 and 3 within a group, and so on), and how many would involve males separated by two, three, four, and five rank positions within a group. Following the methodology of Kitchen et al. (2003), all male-male squealing dyads as determined within each ring-tailed lemur group were pooled, so that of total focal data, all male-male dyads separated by one rank position were pooled for analysis, all male-male dyads separated by two rank positions were pooled for analysis, and so on.

All tests were two-tailed, and means were reported with standard deviations (SD). For all tests, the alpha level was set to 0.05. All statistical tests were performed using SPSS version 20 (IBM SPSS Statistics, IBM Corporation, Armonk, NY, USA, 2011).

## Results

### Squealing rate and male-male agonism

There was a correlation between male ring-tailed lemur dominance rank and squealing rate such that males with a higher dominance index score had a higher mean squealing rate (Spearman's rank correlation:  $r_s = 0.67$ ,  $n = 25$  males,  $p = 0.0001$ ; linear regression:  $r^2 = 0.405$ ,  $df = 23$ ,  $p = 0.001$ , **Figure 2**). In addition to male dominance rank being correlated with overall squealing rate, this correlation was significant when squealing rate using only squeals given during male-male agonism were considered (Spearman's rank correlation:  $r_s = 0.56$ ,  $n = 25$  males,  $p = 0.003$ ; linear regression:  $r^2 = 0.33$ ,  $df = 23$ ,  $p = 0.003$ , **Figure 3**).

Further, there was a significant difference in male squealing rate during times of male-male agonism when compared to times without male-male agonism (Wilcoxon test:  $z = -3.81$ ,  $n = 25$  males,  $p = 0.0001$ ; **Figure 4**). Mean squealing rate was higher at times with male-male agonism (2.86 squeals per hour  $\pm$  3.25,  $n = 25$  males) when compared to times without male-male agonism (0.17 squeals per hour  $\pm$  0.16,  $n = 25$  males). When tests were re-done with the outlier removed (male 273 removed from analysis [with value of 12 for squeal rate during male-male agonism]), results remained statistically significant (Wilcoxon test:  $z = -3.7$ ,  $n = 24$  males,  $p = 0.0001$ ). See **Appendix III** for data on individual male squealing rates, which were quite variable.

However, mean squealing rate was not significantly different during male-male agonistic wins when compared with squealing rate during agonistic losses (Wilcoxon test:  $z = -0.93$ ,  $n = 25$  males,  $p = 0.352$ , NS; **Figure 5**). Mean squealing rate was not significantly higher during wins (0.11 squeals per hour during wins  $\pm$  0.15,  $n = 25$  males) when compared with squealing rate during losses (0.08 squeals per hour during losses  $\pm$  0.12,  $n = 25$  males). When the outliers were removed (three males removed from analysis: male 263 with values of 0.65 and 0, male Umm2p with values of 0.2 and 0.27, and male 273 with values of 0.16 and 0.57), results remained non-significant (Wilcoxon test:  $z = -1.29$ ,  $n = 22$  males,  $p = 0.196$ , NS).

To test whether male ring-tailed lemurs with similar dominance ranks were more likely than males with disparate dominance ranks to squeal at one another, all male-male dyads involving squealing were determined. Dyadic squealing interactions were expected to occur equally between males of all ranks. When all male-male squealing dyads from the study group were pooled based on difference in dominance rank (i.e. so that all male-male dyads separated by only 1 dominance rank were grouped together, all male-male dyads separated by 2 dominance ranks were grouped together, and so on, following the methodology of Kitchen et al., 2003), there was no significant difference between expected and observed dyadic distribution of squeals overall, such that squeals were not statistically differently distributed between male-male dyads (Pearson chi-squared test:  $X^2 = 20$ ,  $df = 16$ ,  $n = 5$  rank differences,  $p = 0.22$ , NS; **Figure 6**). However, despite this lack of overall significant difference, when dyads were only one rank apart, males clearly squealed towards one another at a higher rate. In contrast, males with more disparate dominance ranks squealed at one another less often than expected.

## **Discussion**

### **Squealing indicates dominance rank and occurs during male-male agonism**

Results from my study indicate that dominant males had higher squealing rates, and that mean male squealing rate was higher during times of male-male agonism. These findings support the intra-sexual selection function of the quality handicap hypothesis, which suggests that male squealing rate honestly indicates male dominance status. My study shows that for ring-tailed lemurs, the squeal is used by males in correlation with both aggressive and submissive intra-sexual interactions.

When investigating squealing with respect to dominance rank differences between males, overall results for male-male dyadic interactions in squealing behaviour were not significant, but clear trends were apparent which supported the predictions of game theory. My results showed that males separated by one dominance rank squealed at one another a greater amount than expected, while males separated by two or more dominance ranks squealed at one another less often than expected. This outcome is consistent with the expectations of game theory as applied to squealing behaviour in the ring-tailed lemur. Because the squeal is a vocalization that accompanies male-male agonistic interactions, males with adjacent dominance ranks should

squeal toward one another more than differently-ranked males. This increased squealing between closely-ranked males could also be an artefact of increased aggression between closely-ranked males.

### **Comparing study results to previous research**

My study's result that ring-tailed lemurs squeal as a sign of agonism in male-male interactions is consistent with ring-tailed lemur squeal usage as reported by Jolly (1966) and Macedonia (1990, 1993). Jolly (1966) reported that males squeal when aggressively staring at and prior to aggressive tail-waving displays directed at other males, while Macedonia (1990, 1993) noted the squeal as an assertion of status when directed at other males. These findings correspond with accounts of squeal usage throughout *Mammalia*, in that squeals are most commonly used as agonistic signals. Squeals are used as submissive calls in agonistic encounters in a range of mammalian orders, including rodents, perissodactyls, carnivores, and primates (rodent: Morgret and Dengerink, 1972; perissodactyl: Hunsaker and Hahn, 1965; carnivore: Sheffield and King, 1994; primates and mammals: reviewed in Hall, 1941).

In primates including Old World monkeys, New World monkeys, anthropoids, and strepsirhines, squeals are used in agonistic encounters. Old World monkeys such as rhesus macaques (*Macaca mulatta*) and guenons (*Cercopithecus* spp.) squeal as both aggressive and submissive threat signals (guenon: Andrew, 1963; rhesus macaque: Bernstein et al., 1993), while anthropoids including siamangs (*Symphalangus syndactylus*) squeal as a sign of submission during fights (Andrew, 1963). New World monkeys such as the black-handed spider monkey (*Ateles geoffroyi*) and the common marmoset (*Callithrix jacchus*) squeal during fights, with squeals indicating both aggression and submission (black-handed spider monkey: Carpenter, 1935; common marmoset: Bezerra and Suoto, 2008). For strepsirhines, squealing signals aggression and/or submission in agonistic encounters. In dwarf lemurs (*Cheirogaleus* spp.), the squeal is an aggressive vocalization used to express intense threat, while in the red-fronted lemur (*Eulemur rufifrons*), the squeal expresses submission (dwarf lemur: Andrew, 1963; red-fronted lemur: Pereira and Kappeler, 1997). Squealing is used to signal both aggression and submission in gray mouse lemurs (*Microcebus murinus*), Senegal bushbabies (*Galago senegalensis*), and greater bamboo lemurs (*Prolemur simus*) (gray mouse lemur: Andrew, 1963; Senegal bushbaby: Charles-Dominique, 1977; greater bamboo lemur: Bergey and Patel, 2008). Results from my

study indicate that ring-tailed lemur squealing accompanied both aggression and submissive in agonistic interactions. With squeals accompanying both agonistic wins and losses in this species, ring-tailed lemur squealing use was like that of closely-related strepsirhine primates the red-fronted lemur and greater bamboo lemur. However, primate species from each suborder as well as species from other mammalian orders also squeal in similar contexts, indicating that squealing has widespread use as both an assertive and submissive vocalization. Ring-tailed lemur squealing thus conformed to broadly-observed taxonomic trends for primate squealing behaviour.

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

## **Conclusions**

The squeal in the ring-tailed lemur is a male-specific vocalization used by sexually mature individuals in the context of intra-sexual competition. Dominant males squealed at higher rates, and squealing rate increased during times of male-male agonistic interaction. The squeal is a meaningful signal in intra-sexual agonism for male ring-tailed lemurs, indicating both aggression and submission in male-male agonistic encounters.

## References

- Altmann, J. (1974). Observational study of behavior: sampling methods. *Behaviour* 49: 227-265.
- Andersson, M. (1982). Sexual selection, natural selection and quality advertisement. *Biological Journal of the Linnean Society* 17: 375–393.
- Andersson, M. (1994). Sexual selection. Princeton, NJ: Princeton University Press.
- Andrew, R. (1963). The origins and evolution of calls and facial expressions of the primates. *Behaviour* 20: 1-109.
- Bergey, C., and Patel, E. (2008). A preliminary vocal repertoire of the greater bamboo lemur (*Prolemur simus*). *Nexus* 1: 69-84.
- Bernstein, I. (1991). An empirical comparison of focal and *ad libitum* scoring with commentary on instantaneous scans, all occurrence and one-zero techniques. *Animal Behavior* 42: 721-728.
- Bernstein, I., Judge, P., and Ruehlmann, T. (1993). Kinship, association, and social relationships in rhesus monkeys (*Macaca mulatta*). *American Journal of Primatology* 31: 41-53.
- Bezerra, B., and Suoto, A. (2008). Structure and usage of the vocal repertoire of *Callithrix jacchus*. *International Journal of Primatology* 29: 671-701.
- Bishop, D., Cannings, C., and Maynard Smith, J. (1978). The war of attrition with random rewards. *Journal of Theoretical Biology* 74: 377-388.
- Bradbury, J., and Vehrencamp, S. (1998). Principles of animal communication. Sunderland, MA: Sinauer Associates.
- Brooks, R., and Endler, J. (2001). Direct and indirect sexual selection and quantitative genetics of male traits in guppies (*Poecilia reticulata*). *Evolution* 55: 1002-1015.
- Budnitz, N. and Dainis, K. (1975). *Lemur catta*: Ecology and behavior. In: Lemur biology. Tattersall, I., and Sussman, R. (eds.). New York: Plenum Press, pp. 219-235.
- Carpenter, C. (1935). Behavior of red spider monkeys in Panama. *Journal of Mammology* 16: 171-180.
- Charles-Dominique, P. (1977). Ecology and behavior of nocturnal primates: Prosimians of equatorial West Africa. London: Duckworth and Co. Ltd.
- Clarke, E., Reichard, U., and Zuberbühler, K. (2012). The anti-predator behavior of wild white-handed gibbons (*Hylobates lar*). *Behavioral Ecology and Sociobiology* 66: 85-96.
- Clutton-Brock, T., and Albon, S. (1979). The roaring of red deer and the evolution of honest advertisement. *Behaviour* 69: 145–169.

- Cuozzo, F., and Sauther M. (2006). Severe wear and tooth loss in wild ring-tailed lemurs (*Lemur catta*): a function of feeding ecology, dental structure, and individual life history. *Journal of Human Evolution* 51:490-505.
- Cuozzo, F., Sauther, M., Gould, L., Sussman, R., Villers, L., and Lent, C. (2010). Variation in dental wear and tooth loss in known-aged, older ring-tailed lemurs (*Lemur catta*): A comparison between wild and captive individuals. *American Journal of Primatology* 72:1026-1037.
- Davies, N. and Halliday, T. (1978). Deep croaks and fighting assessment in toads (*Bufo bufo*). *Nature* 274: 683-685.
- Darwin, C. (1871). *The descent of man, and selection in relation to sex*, 1<sup>st</sup> ed. London: John Murray.
- Enquist, M., and Leimar, O. (1983). Evolution of fighting behavior: decision rules and assessment of relative strength. *Journal of Theoretical Biology* 102: 387-410.
- Enquist, M., and Leimar, O. (1990). The evolution of fatal fighting. *Animal Behavior* 39: 1-9.
- Godin, J., and McDonough, H. (2003). Predator preference for brightly colored males in the guppy: a viability cost for a sexually selected trait. *Behavioral Ecology* 14: 194–200.
- Gosselin-Ildari, A., and Koenig, A. (2012). The effects of group size and reproductive status on vigilance in captive *Callithrix jacchus*. *American Journal of Primatology* 74: 613-621.
- Gould, L. (1994). Patterns of affiliative behavior in adult male ringtailed lemurs (*Lemur catta*) at the Beza-Mahafaly reserve, Madagascar. Ph.D. dissertation: Washington University, Missouri.
- Gould, L. (2006). Male sociality and integration during the dispersal process in *L. catta*: a case study. In: Ringtailed lemur biology. Jolly, A., Sussman, R., Koyama, N., and Rasamimanana, H. (eds.). New York: Springer, pp. 296-310.
- Gould, L., Sussman, R., and Sauther, M. (2003). Demographic and life-history patterns in a population of ring-tailed lemurs (*Lemur catta*) at Beza Mahafaly Reserve, Madagascar: A 15-year perspective. *American Journal of Physical Anthropology* 120: 182-194.
- Gould, L., and Zeigler, T. (2007). Variation in fecal testosterone levels, inter-male aggression, dominance rank and age during mating and post-mating periods in wild adult male ring-tailed lemurs (*Lemur catta*). *American Journal of Primatology* 69: 1325-1339.
- Grafen, A. (1990). Biological signals as handicaps. *Journal of Theoretical Biology* 144: 475-546.
- Grafen, A. (1991). Modelling in behavioural ecology. In: Behavioural ecology: an evolutionary

- approach, 3<sup>rd</sup> edition. Krebs, J., and Davies, N. (eds.). Oxford: Blackwell, pp. 5-31.
- Hall, C. (1941). Temperament: A survey of animal studies. *Psychological Bulletin* 38: 909-943.
- Hunsaker, D., and Hahn, T. (1965). Vocalization of the South American tapir, *Tapirus terrestris*. *Animal Behaviour* 8: 69-74.
- Huntingford, F., Turner, A., Sneddon, L., Neat, F. (2000). Prowess and the resolution of animal fights. In: *Animal Signals: signalling and signal design in animal communication*. Epsmark, Y., Amundsen, T., Rosenqvist, G., (eds.). Trondheim, Norway: Tapir, pp. 415-427.
- Hurd, P., and Enquist, M. (1998). Conventional signalling in aggressive interactions: the importance of temporal structure. *Journal of Theoretical Biology* 192: 197-211.
- Jolly, A. (1966). *Lemur behavior: A Madagascar field study*. London: University of Chicago Press.
- Jones, K. (1983). Inter-troop transfer of *Lemur catta* males at Berenty, Madagascar. *Folia Primatologica* 40: 145-160.
- Kitchen, D. (2004). Alpha male black howler monkey responses to loud calls: Effect of numeric odds, male companion behaviour and reproductive investment. *Animal Behavior* 67: 125-139.
- Kitchen, D., Seyfarth, R., Fischer, J., and Cheney, D. (2003). Loud calls as indicators of dominance in male baboons (*Papio cynocephalus ursinus*). *Behavioral Ecology and Sociobiology* 53: 374-384.
- Kitchen, D., Cheney, D., and Seyfarth, R. (2005a). Contextual factors mediating contests between male chacma baboons in Botswana: Effects of food, friends and females *International Journal of Primatology* 26: 105-125.
- Kitchen, D., Cheney, D., and Seyfarth, R. (2005b). Male chacma baboons (*Papio hamadryas ursinus*) discriminate loud call contests between rivals of different relative ranks. *Animal Cognition* 8:1-6.
- Kotiaho, J. (2000). Testing the assumptions of conditional handicap theory: costs and condition dependence of a sexually selected trait. *Behavioral Ecology and Sociobiology* 48: 188-194.
- Koyama, N. (1988). Mating behavior of ring-tailed lemurs (*Lemur catta*) at Berenty, Madagascar. *Primates* 29: 163-175.
- Leger, D. (1977). An empirical evaluation of instantaneous and one-zero sampling of

- chimpanzee behavior. *Primates* 18: 387-393.
- Macedonia, J. (1986). Individuality in a contact call of the ringtailed lemur. *American Journal of Primatology* 11: 163-179.
- Macedonia, J. (1990). Vocal communication and antipredator behavior in the ringtailed lemur (*Lemur catta*). Ph.D. dissertation: Duke University, North Carolina.
- Macedonia, J. (1993). The vocal repertoire of the ringtailed lemur (*Lemur catta*). *Folia Primatologica* 61:186-217.
- Martin, P., and Bateson, P. (2007). *Measuring Behavior: An Introductory Guide*. 3rd ed. Cambridge, UK: Cambridge University Press.
- Maynard Smith, J. (1982). *Evolution and the theory of games*. Oxford: Oxford University Press.
- Maynard Smith, J. (1994). Must reliable signals always be costly? *Animal Behaviour* 47: 1115-1120.
- Maynard Smith, J., and Harper, D. (1995). Animal signals: models and terminology. *Journal of Theoretical Biology* 177: 305-311.
- Maynard Smith, J., and Harper, D. (2003). *Animal signals*. Oxford: Oxford University Press.
- Maynard Smith, J., and Parker, G. (1976). The logic of asymmetric contests. *Animal Behavior* 24: 159-175.
- Maynard Smith, J., and Price, G. (1973). The logic of animal conflict. *Nature* 246: 15-18.
- McDonald, J. (2009). *Handbook of biological statistics* 2<sup>nd</sup> ed. Baltimore, MD: Sparky House Publishing.
- Mertl, A. (1976). Olfactory and visual cues in social interactions of *Lemur catta*. *Folia Primatologica* 26:151-161.
- Mertl-Milhollen, A. (2007). Lateral bias to the leading limb in an olfactory social signal by male ringtailed lemurs. *American Journal of Primatology* 69: 635-640.
- Mertl-Milhollen, A. (2006). Scent marking as resource defense by female *Lemur catta*. *American Journal of Primatology* 68: 605-621.
- Møller, A. (1988). Female choice selects for male sexual tail ornaments in the monogamous swallow. *Nature* 332: 640-642.
- Møller, A., and de Lope, F. (1994). Differential costs of a secondary sexual character: an experimental test of the handicap principle. *Evolution* 48: 1676-1683.
- Morgret, M., and Dengerink, H. (1972). The squeal as an indicator of aggression in mice.

- Behavior Research Methods* 4: 138-140.
- Oda, R. (1996). Effects of contextual and social variables on contact call production in free-ranging ringtailed lemurs (*Lemur catta*). *International Journal of Primatology* 17: 191-205.
- Oppenheim, A., Willsky, A., and Nawab, S. (1996). *Signals and Systems* 2<sup>nd</sup> ed. New York: Prentice Hall.
- Palagi, E., Telara, S., and Borgognini Tarli, S. (2003). Sniffing behavior in *Lemur catta*: seasonality, sex, and rank. *International Journal of Primatology* 24: 335-350.
- Parga, J. (2006a) Male mate choice in *Lemur catta*. *International Journal of Primatology* 27: 107-131.
- Parga, J. (2006b). Sexual selection in the ringtailed lemur (*Lemur catta*): female choice, male mating strategies, and male mating success in a female dominant primate. Ph.D. dissertation: University of Texas at Austin, Texas.
- Parga, J. (2010). Evaluation of male inter-troop transfer as a mating strategy in ring-tailed lemurs on St. Catherines Island, USA. *Folia Primatologica* 81: 146-162.
- Patel, E., Anderson, J., Irwin, M., and Owren, M. (2005). Quantifying the vocal repertoire of wild adult diademed sifakas (*Propithecus diadema diadema*) in Madagascar. *American Journal of Primatology* 66: 48 [abstract]
- Pereira, M., and Kappeler, P. (1997). Divergent systems of agonistic behaviour in lemurid primates. *Behaviour* 134: 225-274.
- Pereira, M., and Weiss, M. (1991). Female mate choice, male migration, and the threat of infanticide in ringtailed lemurs. *Behavioral Ecology and Sociobiology* 28: 141-152.
- Peters, G. (2002). Purring and similar vocalizations in mammals. *Mammal Review* 32: 245-271.
- Petter, J., and Charles-Dominique, P. (1979). Vocal communication in prosimians. In: *The study of prosimian behaviour*. Doyle, G., and Martin, R. (eds.). New York: Academic Press, pp. 247-305.
- Pride, R. (2005). Optimal group size and seasonal stress in ring-tailed lemurs (*Lemur catta*). *Behavioral Ecology* 16: 550-560.
- Remmers, J., and Gautier, H. (1972). Neural and mechanical mechanisms of feline purring. *Respiration Physiology* 16: 351-361.
- Rhine, R., and Linville, A. (1980). Properties of one-zero scores in observational studies of

- primate social behavior: The effect of assumptions on empirical analyses. *Primates* 21: 111-122.
- Sarfaty, A., Margulis, S., and Atsalis, S. (2012). Effects of combination birth control on estrous behavior in captive western lowland gorillas, *Gorilla gorilla gorilla*. *Zoo Biology* 31: 350-361.
- Sauther, M. (1989). Antipredator behavior in troops of free-ranging *Lemur catta* at Beza Mahafaly Special Reserve, Madagascar. *International Journal of Primatology* 10: 595-606.
- Sauther, M. (1991). Reproductive behavior of free-ranging *Lemur catta* at Beza Mahafaly Special Reserve, Madagascar. *American Journal of Physical Anthropology* 84: 463-477.
- Sauther, M., and Cuzzo, F. (2008). Somatic variation in living, wild ring-tailed lemurs (*Lemur catta*). *Folia Primatologica* 79: 55-78.
- Sauther, M., and Cuzzo, F. (2009). The impact of fallback foods on wild ring-tailed lemur biology: A comparison of intact and anthropogenically disturbed habitat. *American Journal of Physical Anthropology* 140: 671-686.
- Sauther, M., Sussman, R., and Cuzzo, F. (2002). Dental and general health in a population of wild ring-tailed lemurs: a life history approach. *American Journal of Physical Anthropology* 117: 122-132.
- Sauther, M., Sussman, R., and Gould, L. (1999). The socioecology of the ringtailed lemur: thirty-five years of research. *Evolutionary Anthropology* 8: 120-132.
- Sbeglia, G., Tang-Martinez, Z., and Sussman, R. (2010). Effects of food, proximity, and kinship on social behavior in ringtailed lemurs. *American Journal of Primatology* 72: 981-991.
- Scordato, E., and Drea, C. (2007). Scents and sensibility: information content of olfactory signals in the ringtailed lemur (*Lemur catta*). *Animal Behaviour* 73: 301-314.
- Sheffield, S., and King, C. (1994). *Mustela nivalis*. *Mammalian species* 454: 1-10.
- Snowdon, C. (2004). Sexual selection and communication. In: Sexual selection in primates: New and comparative perspectives. Kappeler, P., and van Schaik, C. (eds.). Cambridge: Cambridge University Press, pp. 57-70.
- Sokal, R., and Rohlf, F. (1995). Biometry: The principles and practice of statistics in biological research 3<sup>rd</sup> ed. New York: W.H. Freeman and Company.
- Suen, H., and Ary, D. (1984). Variables influencing one-zero and instantaneous time sampling outcomes. *Primates* 25: 89-94.

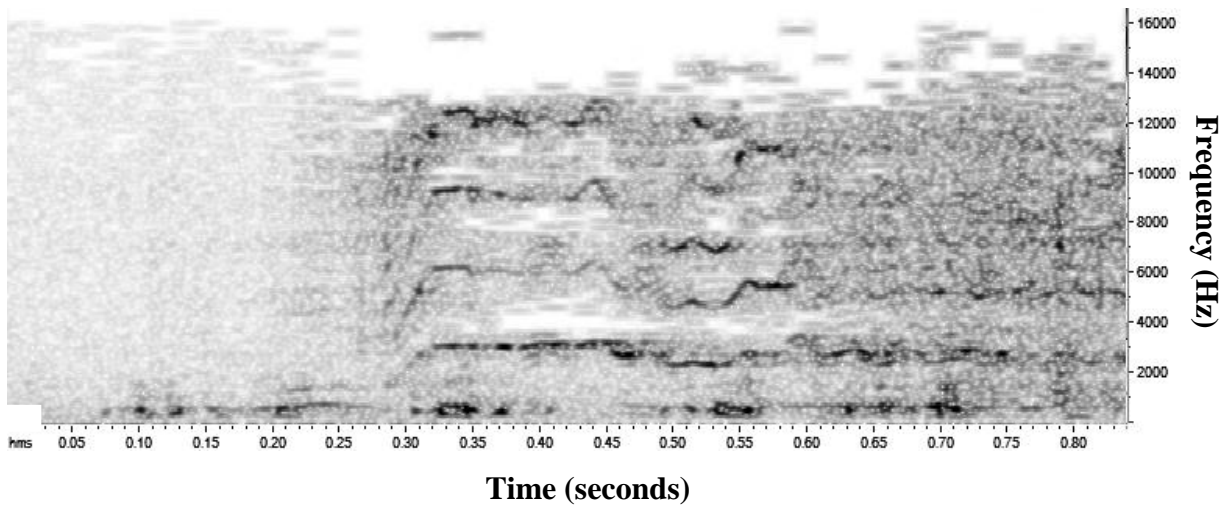
- Sussman, R. (1991). Demography and social organization of freeranging *Lemur catta* in the Beza Mahafaly Reserve, Madagascar. *American Journal of Physical Anthropology* 84: 43-58.
- Sussman, R. (1992). Male life history and intergroup mobility among ringtailed lemurs (*Lemur catta*). *International Journal of Primatology* 13: 395-413.
- Sussman, R., and Ratsirarson, J. (2006). Beza Mahafaly Special Reserve: A research site in southwestern Madagascar. In: Ringtailed lemur biology: *Lemur catta* in Madagascar. Jolly, A., Sussman, R., Koyama, N., Rasamimanana, H. (eds.). New York: Springer, pp. 43-51.
- Sussman, R., Richard, A., Ratsirarson, J., Sauther, M., Brockman, D., Gould, L., Lawler, R., and Cuozzo, F. (2012). Beza Mahafaly Special Reserve: A research site in southwestern Madagascar. In: Long Term Field Studies of Primates. Kappeler, P., and Watts D. (eds.). New York: Springer, pp. 45-66.
- Suzuki, M., and Sugiura, H. (2011). Effects of proximity and activity on visual and auditory monitoring in wild Japanese macaques. *American Journal of Primatology* 73: 623-631.
- Taylor, L. (1986). Kinship, dominance, and social organization in a semi-free ranging group of ringtailed lemurs (*Lemur catta*). Ph.D. Dissertation: Washington University, Missouri.
- Taylor, L. and Sussman, R. (1985). A preliminary study of kinship and social organization in a semi-free-ranging group of *Lemur catta*. *International Journal of Primatology* 6: 601-614.
- Van Horn, R., and Resko, J. (1977). Reproductive cycle of the ringtailed lemur (*Lemur catta*): sex steroid levels and sexual receptivity under controlled photoperiods. *Endocrinology* 101: 1579.
- Vehrencamp, S. (2000). Handicap, index, and conventional signal elements of bird song. In: Animal signals: Signalling and signal design in animal communication. Espmark, Y., Amundsen, T., and Rosenqvist, G. (eds.). Trondheim, Norway: Tapir Academic Press, pp. 277-300.
- Vehrencamp, S., Bradbury, J., and Gibson, R. (1989). The energetic cost of display in male Sage grouse. *Animal Behavior* 38: 885-896.
- Zahavi, A. (1975). Mate selection: A selection for a handicap. *Journal of Theoretical Biology* 53: 204-214.
- Zahavi, A. (1977). The cost of honesty. *Journal of Theoretical Biology* 67: 603-605.
- Zahavi, A., and Zahavi, A. (1997). The handicap principle: A missing piece of Darwin's puzzle.

Oxford: Oxford University Press.

Zumpe, D., and Michael, R. (1986). Dominance index: A simple measure of relative dominance status in primates. *American Journal of Primatology* 10: 291-300.

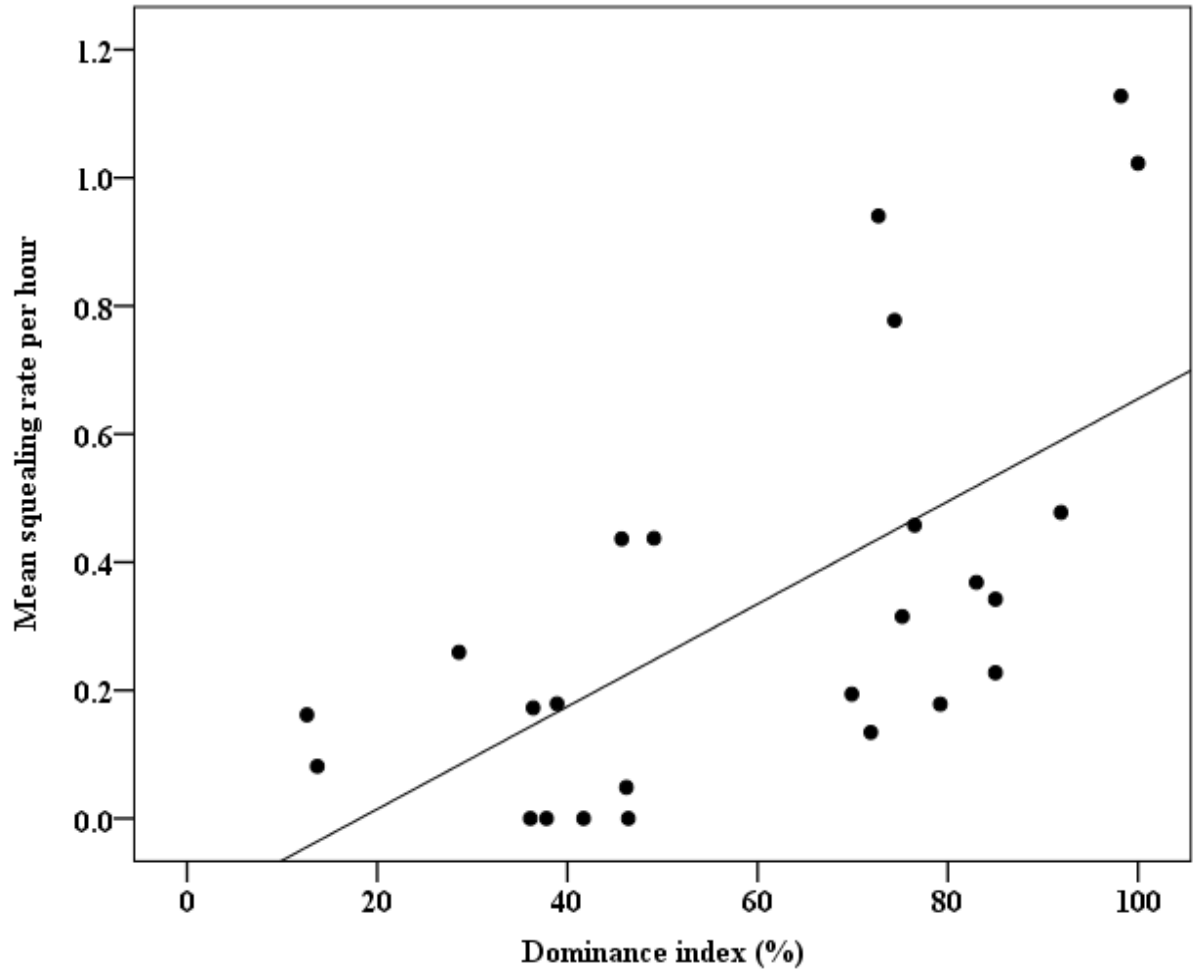
**Table 1. Male ring-tailed lemur study individuals at Beza Mahafaly Special Reserve,  
March-July 2010**

Troop	Individual name	Group membership status	Dominance index score in %	Rank within group	Known or approximate age in years
Green	Umm1g	Non-natal	91.9	1	≥4
Green	Umm2g	Non-natal	85	2	≥4
Green	175	Non-natal	71.9	3	≥8
Green	Umm3g	Non-natal	38.9	4	≥4
Green	203	Non-natal	36.4	5	≥8
Orange	263	Non-natal	98.2	1	≥7
Orange	259	Non-natal	83	2	7
Orange	Umm1o	Non-natal	49.1	3	≥4
Orange	291	Non-natal	45.7	4	≥7
Orange	318	Natal	37.8	5	3
Orange	226	Non-natal	12.6	6	≥12
Purple	Umm2p	Non-natal	100	1	≥4
Purple	Umm1p	Non-natal	76.5	2	≥4
Purple	Umm4p	Non-natal	69.9	3	≥4
Purple	323	Natal	46.4	4	3
Purple	322	Natal	41.7	5	3
Purple	Umm3p	Non-natal	36.1	6	≥4
Red	280	Non-natal	85	1	≥6
Red	273	Non-natal	72.7	2	≥6
Red	308	Natal	28.6	3	3
Red	307	Natal	13.7	4	3
Yellow	208	Non-natal	79.2	1	≥9
Yellow	Umm2y	Non-natal	75.2	2	≥4
Yellow	230	Non-natal	74.4	3	≥8
Yellow	Umm1y	Non-natal	46.2	4	≥4

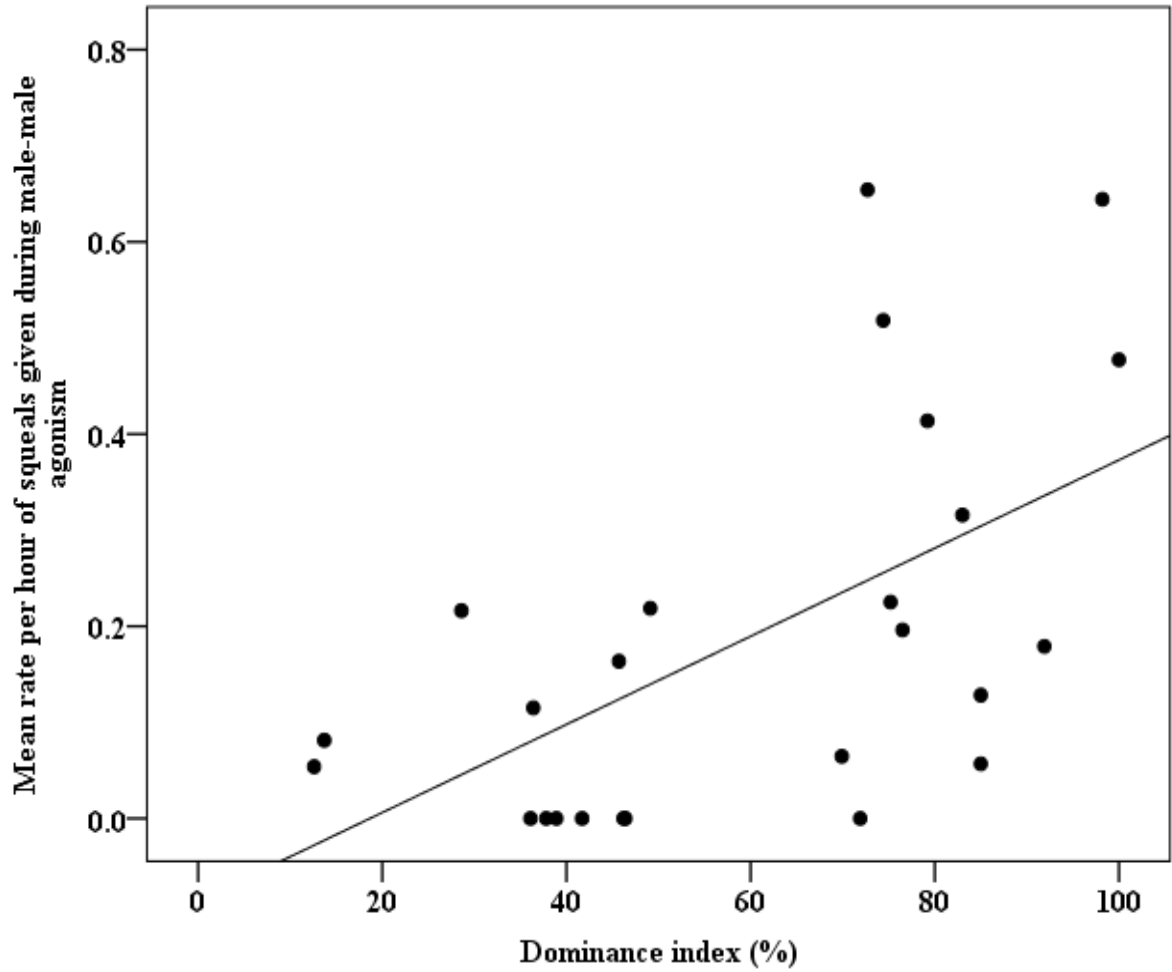


**Figure 1. Sound spectrogram of male ring-tailed lemur squeal, recorded with 44.1kHz sampling rate, 16-bit sample depth, and 64 kilobits/second MP3 compression, and with the spectrogram created using a Blackman window with 2048 frequency bins.**

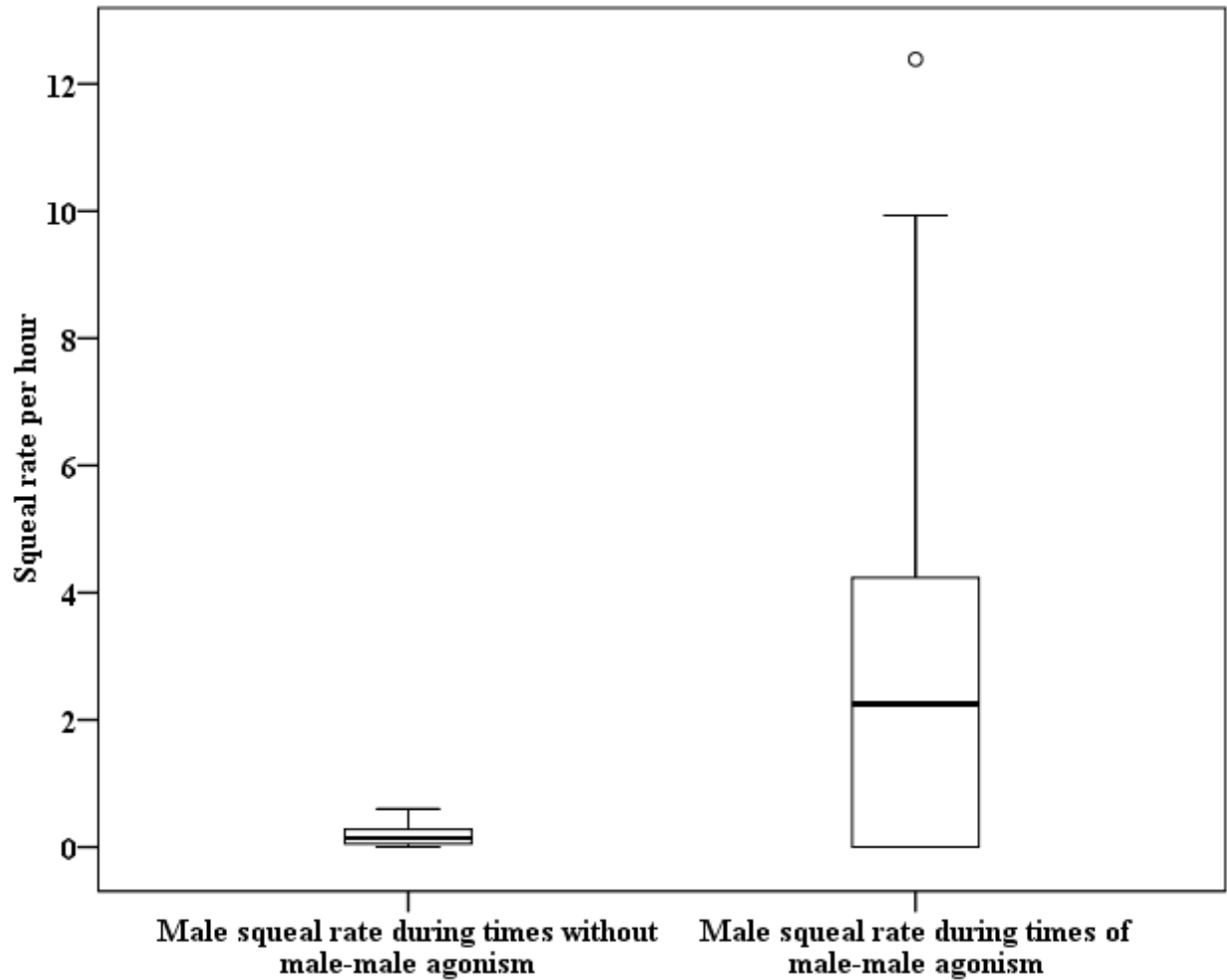
This spectrogram shows a squeal by male UMM1 from the purple group. A single squeal vocalization is represented from 0.28 - 0.84 seconds.



**Figure 2. Correlation between male ring-tailed lemur dominance index score and mean male squealing rate, with linear regression. Individual points represent individual males.**

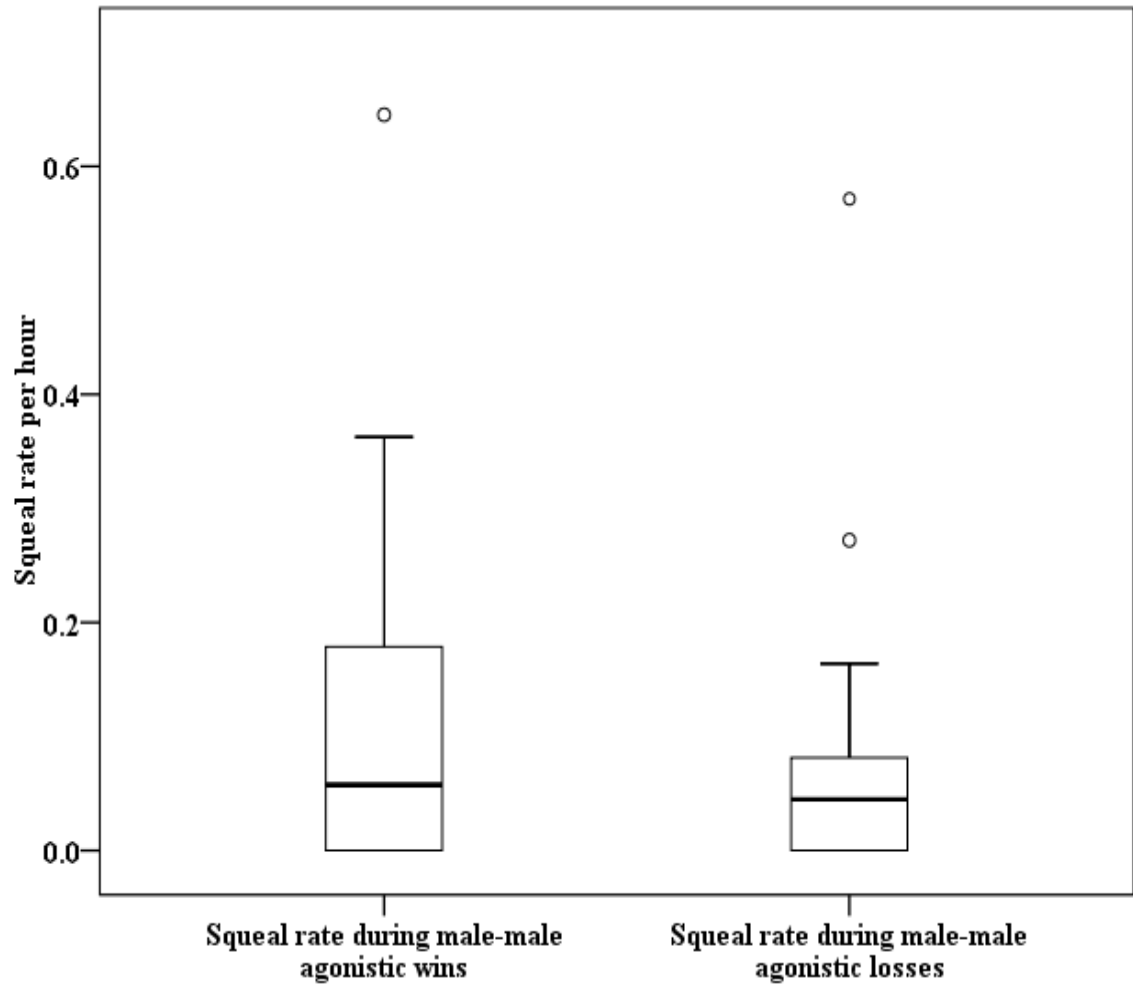


**Figure 3. Correlation between male ring-tailed lemur dominance index score and mean rate for squeals given during male-male agonism, with linear regression. Individual points represent individual males.**



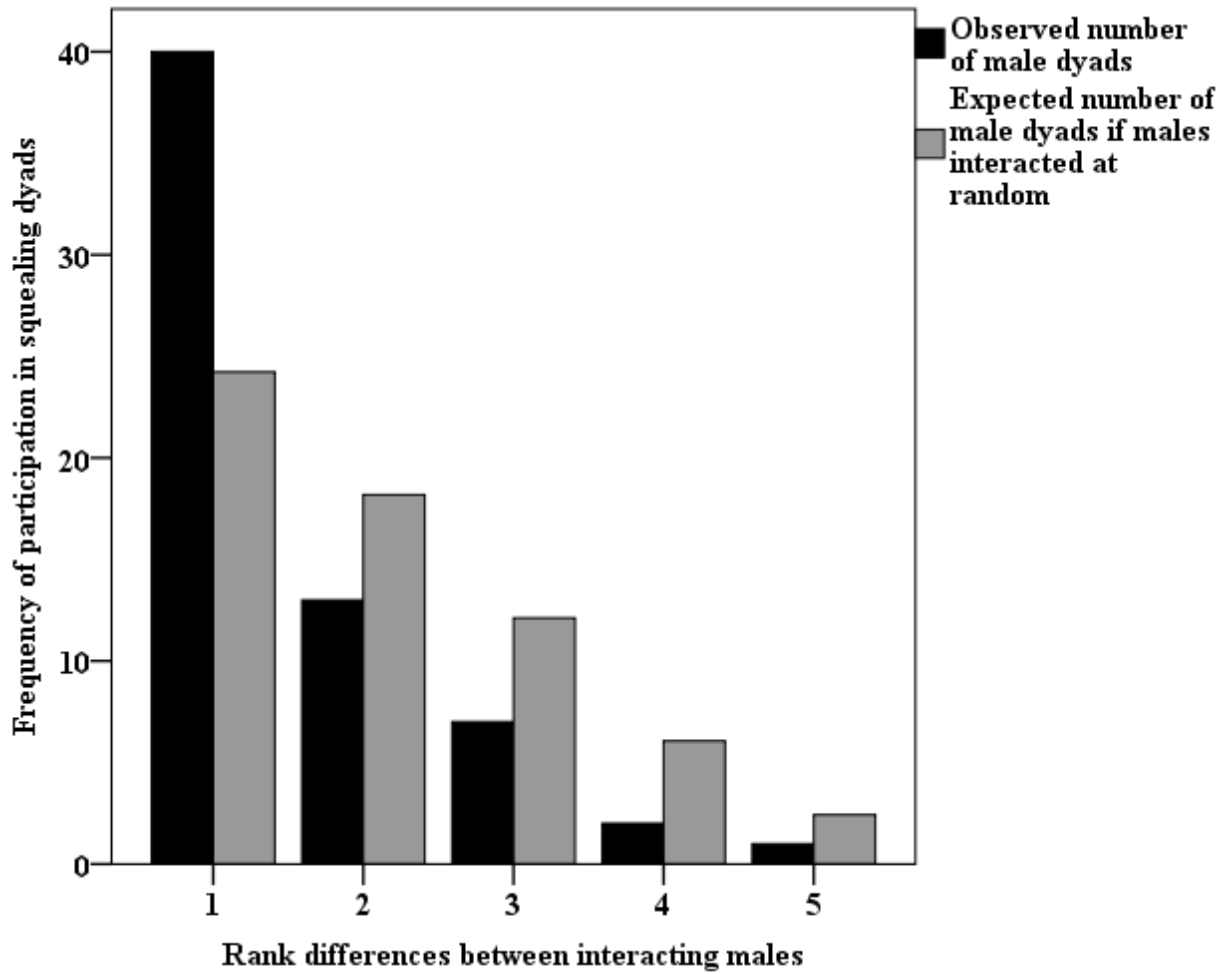
**Figure 4. Mean male ring-tailed lemur squealing rate per hour during periods of male-male agonism versus male squealing rate during times without agonism.**

Boxes represent inter-quartile ranges, lines represent median values, whiskers represent maximum and minimum values, and dots represent outliers.



**Figure 5. Mean male squealing rate per hour during male-male agonistic wins versus squealing rate during male-male agonistic losses.**

Boxes represent inter-quartile ranges, lines represent median values, whiskers represent maximum and minimum values, and dots represent outliers.



**Figure 6. The frequency of observed versus expected dyadic squealing incidents involving ring-tailed lemur males separated by varying numbers of positions in the dominance rank hierarchy.**

## Chapter 5. Conclusions and Future Directions

My dissertation examined the usage of three different vocalizations (purrs, howls, and squeals) by male ring-tailed lemurs (*Lemur catta*) at Beza Mahafaly Special Reserve in Madagascar (Sussman and Ratsirarson, 2006), and explored how the rates of these vocalizations related to male dominance rank. I also investigated these vocalizations with reference to sexual selection theory. I evaluated one vocalization with male-specific functions and two male-specific vocalizations: the purr (Chapter 2), the howl (Chapter 3), and the squeal (Chapter 4).

### Summary of findings

#### Chapter 2: Male use of the ring-tailed lemur purr

In chapter 2, I present evidence that male ring-tailed lemurs use the purr vocalization while engaging in intra-sexual agonistic behaviour. Purring rate significantly increased during male-male agonistic interactions. When purring was heard during male-male interactions, it was also significantly more likely to accompany agonistic success. Purring rate was also positively correlated with male dominance rank in ring-tailed lemurs, such that higher-ranking males purred at higher rates than lower-ranking males.

#### Chapter 3: The male ring-tailed lemur howl

In chapter 3, I present evidence that the male-specific howl vocalization is used as an inter-troop signal. The inter-group function of the mate defense hypothesis suggests that males howl toward males from other groups in order to arbitrate male-male competition for access to female mates (Delgado, 2006; Wich and Nunn, 2002). I predicted that howling rate of male group members would be higher during inter-troop encounters or when non-group members were present as opposed to contexts without non-group members present. I also predicted that a greater number of ring-tailed lemur males from the same social group would participate in howling bouts given during inter-group encounters as opposed to contexts without non-group members. I found strong support for the inter-group mate defense hypothesis with all predictions met. Ring-tailed lemur howling rate significantly increased during inter-troop encounters or when non-group members were visible and within 20 metres of the focal group. Further, a greater number of males participated in multi-male howling choruses when non-group

individuals were nearby. In fact, all observed howling choruses involving two or more males occurred when non-group members were present. Within each howling bout, the howls of individual males were offset, with each individual howling at his own pace (Macedonia, 1990). The minimum number of males in a group could therefore be detected in howling choruses.

My results for chapter 3 also indicated a lack of support for the intra-troop function of the mate defense hypothesis. For the intra-group mate defense hypothesis, I predicted that if howling was used as a form of self-advertisement between males in the same social group, it would be used in male-male agonism. Further, higher ranking males would have higher howling rates and longer howling bouts than lower ranking males. In other primate species, such as chacma baboons (*Papio ursinus*) and red howler monkeys (*Alouatta seniculus*), long call rate and bout length is known to be positively correlated with social standing (chacma baboon: Kitchen et al., 2003; red howler monkey: Sekulic, 1982; Sekulic and Chivers, 1986). However, howling rate and howling bout length were not correlated with male dominance rank in the ring-tailed lemur, nor was howling used in male-male agonistic contexts.

Finally, my results for chapter 3 indicated a lack for support for the mate attraction hypothesis. I predicted that if howling was used for mate attraction, males would howl at higher rates on days of known estrus, when they were more likely to gain sexual access to females. I also predicted that estrous females would be more likely to approach males during or after a howling bout, to show their attraction. However, I found that howling rate was not significantly higher on days of known estrus, nor were estrous females more likely to approach howling males during or after a howling bout.

#### **Chapter 4: The male ring-tailed lemur squeal**

In chapter 4, I present evidence that the male-specific squeal vocalization is used in contexts of intra-sexual agonism, such as immediately before or after male-male agonistic encounters. Male squealing rate significantly increased during periods of male-male agonism when compared to periods without agonism. Squealing was used as both an assertive and submissive vocalization in the ring-tailed lemur, with no significant difference in squealing rate during winning and losing agonistic interactions. Squealing rate was positively correlated with male dominance rank in ring-tailed lemurs, such that higher-ranking males had higher squealing rates than lower-ranking males.

### **Implications of my findings and directions for future study**

My dissertation tested the function and usage of three ring-tailed lemur vocalizations through examining vocalization rate in social context. My study shows that vocalization rate is a useful tool in empirically elucidating a vocalization's function. Future studies in primates and other animals which aim to describe the functions of vocalizations should use vocalization rate to help elucidate vocalization usage, rather than solely depending on anecdotal observation.

My dissertation also clarifies how the rates of the purr, howl, and squeal vocalizations relate to dominance rank in the male ring-tailed lemur. My results for chapters 2 and 4 indicate that both purring and squealing rates are correlated with dominance rank. Vocalization rate has been assessed with relation to individual dominance rank in other animals (red deer [*Cervus elaphus*]: Clutton-Brock and Albon, 1979), including primates (chacma baboon: Kitchen et al., 2003; red howler monkey: Sekulic, 1982; Sekulic and Chivers, 1986; gray mouse lemur [*Microcebus murinus*]: Zimmermann and Lerch, 1993). However, this line of inquiry should be pursued in a wider variety of primate and other animal species in future study.

Due to the function of the purr and the squeal vocalizations in intra-sexual competition in the ring-tailed lemur, it is likely that sexual selection has acted on purr and squeal vocalization rates in the evolutionary past, as has been hypothesized for the vocalizations of other animals used in intra-sexual competition (Snowdon, 2004). Howling also shows potential to be used in intra-sexual competition between ring-tailed lemur males of different groups, suggesting that sexual selection may have also acted on howling rate in the evolutionary past.

For the sexually-selected vocalizations of many animals (birds: Alatalo et al., 1990; Gottlander, 1987; Radesater et al., 1987; frogs: Ryan, 1988; Schwartz, 1986; red deer: McComb, 1991), vocalization rate is linked to female preferences and differential reproductive success for vocalizing males. These linkages between vocalization rate and female preference and vocalization rate and reproductive success may also apply to the purr and squeal calls of the ring-tailed lemur. Future study should explore the inter-sexual use of purr and squeal vocalizations in ring-tailed lemurs, and investigate how female choice and male mating success relate to vocalization rates. Further investigation should also explore the potential relationship between ring-tailed lemur squealing and purring rates and paternity.

Further study on the relationship between male ring-tailed lemur vocalizations and dominance should focus on the spectral qualities of vocalizations. In other primates such as the chacma baboon, the spectral characteristics of calls are linked to individual differences and reflect qualities such as dominance rank and body condition (Fischer et al., 2004). For ring-tailed lemurs, further investigation involving the spectrographic analysis of recorded vocalizations should investigate whether call components may indicate male behavioural attributes. Spectral characteristics such as fundamental frequency and formant dispersion, and temporal characteristics such as call length should be investigated for the purr, howl, and squeal vocalizations in the ring-tailed lemur. The possible links of these acoustic features with dominance rank, agonistic wins, mating success, and paternity should be evaluated in future study. Additionally, the purr, howl, and squeal vocalizations should be studied to determine how spectral and temporal characteristics relate to individual physical qualities in the ring-tailed lemur, such as age and size. My study assessed how variation in individual social qualities was reflected in vocalization rate, but physical qualities independently of social qualities (Fischer et al., 2004; Masataka, 1994) are also known to be bound to vocalization characteristics in other primate species (Ey et al., 2007; Hauser, 1993). Further investigation should elucidate how individual male physical qualities are reflected by vocalizations in ring-tailed lemurs.

In my study, I sought to improve understanding of how vocalizations are used by male ring-tailed lemurs, and how vocalization usage relates to the male dominance hierarchy in this species. The dominance and sexual selective properties of ring-tailed lemur vocalizations have never before been considered in the level of detail found in my dissertation. My work adds to the nascent quantitative literature on strepsirhine vocal communication in indigenous environments.

## References

- Alatalo, R., Glynn, D., and Lundberg, A. (1990). Singing rate and female attraction in the pied flycatcher: An experiment. *Animal Behavior* 39: 601–603.
- Clutton-Brock, T., and Albon, S. (1979). The roaring of red deer and the evolution of honest advertisement. *Behaviour* 69: 145–169.
- Delgado, R. (2006). Sexual selection in the loud calls of male primates: signal content and function. *International Journal of Primatology* 27: 5-25.
- Ey, E., Pfefferle, D., and Fischer, J. (2007). Do age- and sex-related variations reliably reflect body size in non-human primate vocalizations? A review. *Primates* 48: 253-267.
- Fischer, J., Kitchen, D., Seyfarth, R., and Cheney, D. (2004). Baboon loud calls advertise male quality: acoustic features and their relation to rank, age, and exhaustion. *Behavioral Ecology and Sociobiology* 56: 140-148.
- Gottlander, K. (1987). Variation in the song rate of the male pied flycatcher: Causes and consequences. *Animal Behavior* 35: 1037–104
- Hauser, M. (1993). The evolution of nonhuman primate vocalizations: Effects of phylogeny, body weight, and social context. *American Naturalist* 142: 528-542.
- Kitchen, D., Seyfarth, R., Fischer, J., and Cheney, D. (2003). Loud calls as indicators of dominance in male baboons (*Papio cynocephalus ursinus*). *Behavioral Ecology and Sociobiology* 53: 374-384.
- Macedonia, J. (1990). Vocal communication and antipredator behavior in the ringtailed lemur (*Lemur catta*). Ph.D. dissertation: Duke University, North Carolina.
- Masataka, N. (1994). Lack of correlation between body size and frequency of vocalization in young female Japanese macaques. *Folia Primatologica* 63: 115–118.
- McComb, K. (1991). Female choice for high roaring rates in red deer, *Cervus elaphus*. *Animal Behavior* 41: 79–88.
- Radesater, T., Jakobsson, S., Andbjør, N., Bylin, A., and Nystrom, K. (1987). Song rate and pair formation in the willow warbler. *Animal Behavior* 35: 1645–1651.
- Ryan, M. J. (1988). Energy, calling, and selection. *American Zoology* 28: 885–898.
- Schwartz, J. (1986). Male calling behavior and female choice in the neotropical treefrog. *Ethology* 73: 116–127.
- Sekulic, R. (1982). The function of howling in red howler monkeys (*Alouatta seniculus*). *Behaviour* 81:38–54.

- Sekulic, R., and Chivers, D. (1986). The significance of call duration in howler monkeys. *International Journal of Primatology* 7: 183–190.
- Snowdon, C. (2004). Sexual selection and communication. In: Sexual selection in primates: New and comparative perspectives. Kappeler, P., and van Schaik, C. (eds.). Cambridge: Cambridge University Press, pp. 57–70.
- Sussman, R., and Ratsirarson, J. (2006). Beza Mahafaly Special Reserve: A research site in southwestern Madagascar. In: Ringtailed lemur biology: *Lemur catta* in Madagascar. Jolly, A., Sussman, R., Koyama, N., Rasamimanana, H. (eds.). New York: Springer, pp. 43-51.
- Wich, S., and Nunn, C. (2002). Do male “long-distance calls” function in mate defense? A comparative study of long-distance calls in primates. *Behavioral Ecology and Sociobiology* 52: 474-484.
- Zimmermann, E., and Lerch, C. (1993). The complex acoustic design of an advertisement call in male mouse lemurs (*Microcebus murinus*, Prosimii, Primates) and sources of its variation. *Ethology* 93: 211–224.

**Appendix I. Individual male ring-tailed lemur purring rates and standard deviations**

Individual name	Mean purring rate per hour	All-occurrences of purrs during study period	Standard Deviation of purring rate per hour
Umm2g	0.63	11	1.20
Umm1g	0.24	4	0.44
175	0.07	1	0.26
Umm3g	0.06	1	0.24
203	0.12	2	0.33
263	0.70	13	0.89
259	0.47	9	1.39
291	0.49	9	0.71
UMM1o	0.33	6	0.97
318	0.29	5	0.69
226	0.00	0	0.00
Umm2p	0.48	7	0.64
Umm1p	0.07	1	0.26
Umm4p	0.19	3	0.41
323	0.00	0	0.00
Umm3p	0.19	3	0.54
322	0.00	0	0.00
280	0.56	13	1.47
273	0.82	20	1.27
308	0.17	4	0.49
307	0.24	6	0.52
230	0.57	11	0.69
208	0.49	11	1.71
Umm2y	0.59	13	1.18
Umm1y	0.10	2	0.44

**Appendix II. Individual male ring-tailed lemur howling rates and standard deviations**

Individual name	Mean howling rate per hour	All-occurrences of howling bouts during study period	Standard Deviation of howling rate per hour
Umm2g	0.009	1	0.09
Umm1g	0.009	1	0.09
175	0.009	1	0.09
Umm3g	0.000	0	0.00
203	0.018	2	0.13
263	0.008	1	0.09
259	0.000	0	0.00
291	0.000	0	0.00
UMM1o	0.000	0	0.00
318	0.000	0	0.00
226	0.000	0	0.00
Umm2p	0.000	0	0.00
Umm1p	0.000	0	0.00
Umm4p	0.000	0	0.00
323	0.008	1	0.09
Umm3p	0.008	1	0.09
322	0.008	1	0.09
280	0.030	3	0.17
273	0.040	4	0.20
308	0.050	5	0.33
307	0.030	3	0.17
230	0.000	0	0.00
208	0.025	3	0.16
Umm2y	0.000	0	0.00
Umm1y	0.000	0	0.00

**Appendix III. Individual male ring-tailed lemur squealing rates and standard deviations**

Individual name	Mean squealing rate per hour	All-occurrences of squeals during study period	Standard Deviation of squealing rate per hour
Umm2g	0.23	4	0.43
Umm1g	0.42	7	0.62
175	0.13	2	0.35
Umm3g	0.18	3	0.39
203	0.17	3	0.39
263	1.13	21	1.24
259	0.37	7	0.60
291	0.38	7	0.61
UMM1o	0.44	8	0.98
318	0.00	0	0.00
226	0.11	2	0.46
Umm2p	0.95	14	1.22
Umm1p	0.46	7	0.64
Umm4p	0.19	3	0.41
323	0.00	0	0.00
Umm3p	0.00	0	0.00
322	0.00	0	0.00
280	0.34	8	0.57
273	0.94	23	1.63
308	0.26	6	0.69
307	0.08	2	0.40
230	0.67	13	0.75
208	0.18	4	0.50
Umm2y	0.32	7	0.65
Umm1y	0.05	1	0.22

## Copyright Acknowledgments

A revised version of Chapter 3 of this dissertation has been previously published, with the copyright held by Springer Science+Business Media New York. This article is available at: <http://link.springer.com>

Bolt, Laura M. (2013). The function of howling in the ring-tailed lemur (*Lemur catta*).

*International Journal of Primatology* 34 (1): 157-169. DOI: 10.1007/s10764-012-9654-8

A revised version of Chapter 4 of this dissertation has previously been published, with the copyright held by John Wiley & Sons. This article will be in the December 2013 issue of *American Journal of Primatology* and is available online at:

<http://onlinelibrary.wiley.com/journal/10.1002/%28ISSN%291098-2345>

Bolt, Laura M. (2013). Squealing rate indicates dominance rank in the male ring-tailed lemur

(*Lemur catta*). *American Journal of Primatology* 9999: 1-11. DOI: 10.1002/ajp.22179