SIZING UP STRANGERS: SEXUAL SELECTION AND VOCAL SIGNALS IN
GELADA MALES

by

Marcela E. Benítez

A dissertation submitted in partial fulfillment
of the requirements for the degree of
Doctor of Philosophy
(Anthropology and Psychology)
in the University of Michigan
2016

Doctoral Committee:

    Associate Professor Jacinta C. Beehner, Chair
    Associate Professor Thore J. Bergman
    Assistant Professor Ben Dantzer
    Associate Professor Andrew J. Marshall
    Professor John C. Mitani

DEDICATION

For my parents, María Elena and Rubén

For the sobre mesas, the treasure hunts, the science kits, the pajaritos que se rompió la patitas, the soccer games, the asados, and the exotic pets. For filling my life with literature, art, music, adventure, and most importantly love.

And for my older brother, Leonardo

For showing me that magic is real.

Y para ti, Abuela

Por esa pasión, ternura, y fortaleza que hoy corren por mis venas.

ACKNOWLEDGMENTS

Over the past seven years, I have been incredibly fortunate to be surrounded by exceptional mentors, colleagues, and friends at the University of Michigan. Their knowledge, guidance, and support has been essential in every stage of my dissertation, and invaluable to my academic development and overall personal growth. I am grateful to have been part of not one, but two, incredible departments. To the faculty and staff, in Departments of Anthropology and Psychology, thank you for you continued support and for cultivating a community that encourages interdisciplinary research. To my peers and colleagues, thank you for making this journey one of the most formative and memorable experiences of my life.

Like most anthropologists, I have an interest in origin stories. Every academic points to a handful people that have sparked their research interests and laid down the foundation for their careers. I don't know what my future in this field holds, but I do know that my origin story begins here at Michigan and under the guidance of my brilliant advisors Dr. Jacinta Beehner and Dr. Thore Bergman. I arrived at Michigan with a broad interest in the relationship between hormones and cognition in nonhuman primates. From the moment I stepped into Jacinta's office, she worked with me to develop these interests into research questions and predictions that could be applied to geladas. She has continued to foster my research interests and aid in every stage of my dissertation—from brainstorming to grant writing, data collection to final revision. In the past few years, Jacinta has worked diligently in helping me become a better researcher

and a better writer. She has been a supportive, enthusiastic, and engaging advisor and I am so grateful to have had the opportunity to be mentored by such a distinguished female scientist.

I am also indebted to Thore, who officially took me on as his student in my third year. While much of my dissertation research stems from Thore's work, he has always encouraged me to develop my own research trajectory. I am grateful to Thore for always asking the challenging questions and encouraging me to think critically about my research and ideas. I was also fortunate to spend time in the field with Thore. From him, I learned how to record vocalizations, analyze calls, conduct playback experiments, and collect behavioral data. I could not have completed my fieldwork without his expertise, guidance, field stories, and games of Celebrity.

I am also thankful for the guidance of my committee: Dr. John Mitani, Dr. Ben Dantzer, and Dr. Andy Marshall. When Jacinta and Thore were on sabbatical in Ethiopia during my 5th year, John became my surrogate advisor. His writing and career advice, humor, and wonderful stories helped me push through the last few obstacles of graduate school. Because of John, I leave Michigan with a better understanding of and appreciation for both the field of primatology and the work of Irv Devore. To the newest members of my committee, Andy Marshall and Ben Dantzer, thank you for your continued feedback and professional guidance. I am fortunate that you both decided to come to Michigan, and even more so that you agreed to join my committee.

I owe so much of my sanity, health, and happiness throughout graduate school to my friends at the University of Michigan and in Ethiopia. To my gelada project big siblings—Amy Lu, Eila Roberts, Noah Snyder-Mackler, and David Pappano—who

paved the way through the program and through the Simiens, thank you for all the advice, feedback, recipes, and stimulating conversation. To Julie Jarvey, Elizabeth Johnson, Morgan Gustison, Caitlin Barale, Shayna Lieberman, and India Schneider-Crease, who made the field and the office feel like home, thank you for the crazy gibshas, the venting sessions, the work dates, and the late night dance parties. To all the Biological Anthropology Graduate Students that I have overlapped with here at Michigan—but especially Bethany Hanson, Dana Begun, Aaron Sandel, Rachna Reddy, and Maire Malone—and to my cohort buddies—Jess Beck and Ashley Schubert—thank you for being my co-pilots on this amazing adventure. I know you will all continue to be an important part of my professional and personal life in the years to come.

This dissertation would not have been possible without the help of my friends in Ethiopia. To the camp managers—Clay Wilton, Tara Hoshin, Levi Morris—thanks for holding down the fort and making sure data collection always ran smoothly. To our gelada experts—Eshete, Setey, and Ambaye—I am so grateful for your patience, expertise, and kindness. Thank for dropping everything when chaos ensued and running after the males to ensure that I always got the data. To the park rangers and their families, and to my friends in Gondar and Debark, thank you for taking me in and sharing your food, coffee, tej, and stories with me. I am a richer person for having known you.

Of the many people who helped with my research collection, my field assistant Megan Gomery deserves special recognition. As soon as we set foot in Ethiopia, it was clear to me that I was incredibly fortunate to have hired Megan to assist with my PhD data collection. Her independence, flexibility, and work ethic in those first few days

were impressive. The fact that she was able to maintain that level of commitment, hard work, and energy for almost two years is incredible. When I sprained my ankle, Megan collected all the necessary project data and independently ran the playback experiments. Because of Megan, my field season continued without a hitch and we were able to collect twice as many vocalizations, fecal samples, and hours of behavioral data than I had originally intended.

I have been so fortunate to grow up in a house filled with books, food, music, laughter, and love. Even more fortunate to have been surrounded by wonderful, intelligent, strong, passionate, and loving people. I have an amazing network of brilliant and caring family friends that have all left their mark. Thank you for the Christmas dinners, the solstice parties, the museum tours, the wine, and your never ending faith and support in my finishing.

To my mother and father, thank you for supporting me in all of my strange and crazy adventures— from soccer to monkeys, Ricky Martin to Messi, Beverly Glen Playgroup to Michigan. Thank you for igniting my curiosity, for fostering my interests, and supporting my dreams, even if that meant a career working with monkeys. To my brother, who has always paved the path and then gone off of it entirely, thanks for never letting me be satisfied with the easy answers. I look forward to discussing this thesis with you. To my sister, for showing me that, whether it be music or monkeys, passion and hard work always pay off. To my Abuela, for filling my life with magic, animals, telenovelas, and love. I am so grateful I got a chance to share this part of my life with you. Lastly, to my partner and best friend, Chelsea Fisher, for enriching my life in every way. I look forward to being your spousal hire someday.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

x

ABSTRACT

Sexual selection has led to the evolution of sexually-dimorphic traits, including ornaments, vocalizations, and displays, that reliably signal the condition or quality of the sender. By attending to these signals, animals gain information about the quality of a mate or the strength of a rival. Although sexually-selected signals are widespread across the animal taxa, signals in primates are rare. Primates typically rely on individual recognition, rather than signals, when assessing group mates. Consequently, our understanding of how primates convey, receive, and integrate information from signals into reproductive decisions remains poorly developed.

This research examines a putative signal for male geladas (*Theropithecus gelada*) living in the Simien Mountains National Park, Ethiopia: a loud call given during male displays. The unusually large groups found in gelada society may have favored the evolution of signals as a way for males to quickly assess the competitive ability of unknown rivals. Determining if loud calls are sexually-selected signals requires establishing that: (1) variation exists across males of different quality, (2) males are able to distinguish between high and low quality males based on these calls, (3) receivers base reproductive decisions on these calls, and (4) males with high quality calls have higher reproductive success. To address these criteria, this research combines acoustic, experimental, hormonal, and behavioral analyses in a comprehensive study of a sexually-selected signal in a primate.

This research has three main findings that further our understanding of the role of signals in primate communication. First, the rate of which males display and the acoustic properties of a male's call function as quality signals of a male's condition, androgen levels, and competitive ability. Second, gelada males, but not females, attend to differences in loud calls and do so with respect to both their own quality and the quality of the caller. Third, males with the highest quality calls sired the most offspring. These results indicate that gelada males attend to these loud calls when deciding which males to challenge. Geladas may be the exception among primates in relying exclusively on signals, rather than individual recognition, to assess rivals.

CHAPTER 1

INTRODUCTION & BACKGROUND

With many kinds of animals, man included, the vocal organs are efficient in the highest degrees as a means of expression.
-The Expression of Emotions in Man and Animals by Charles Darwin

As I have surveyed the primate literature relating communication signals to sexual selection, my assessment is that we have very little understanding of the role of sexual selection on primate communication that is comparable to our knowledge of other taxa.
-Sexual Selection and Communication by Charles T. Snowdon

There are two possible mechanisms that might explain how this behavior [loud call displays in geladas] discourages prospective challengers: either the absolute frequency with which a male engages in these chases is important, or, while engaging in a chase, the male is able to exhibit some sign that deters contenders [...] Unfortunately, the data to test this hypothesis are not, at present, available.
-Reproductive Decisions: An Economic Analysis of Gelada Baboons by Robin Dunbar.

INTRODUCTION

Although signals advertising male quality are widespread across a number of

vertebrate species (Vehrencamp 2000), sexually selected signals in primates are less

well-documented for several reasons (Snowdon 2004). First, quality signals in primates

are relatively rare (Setchell & Kappeler 2003). Primates typically live in small, stable

social groups, where that are able to rely on individual recognition of group-mates and

information from previous encounters (i.e., social knowledge) to make reproductive

decisions (Tomasello & Call 1997; Bergman & Sheehan 2013). Thus, social knowledge

presumably plays a greater role in sexual selection for primates than for species with

brief mating bouts or more ephemeral relationships (Snowdon 2004; Bergman & Sheehan 2013). As a result, primates may have had less selective pressure on the development of sexually selected signals (Bergman & Sheehan 2013). Second, understanding both *how* and *why* a signal evolved requires an integration of experimental manipulations and long-term behavioral observations that are logistically more challenging to conduct in wild primate species (Snowdon 2004).

In this dissertation, I investigate the role of sexually selected signals on the reproductive choices of male geladas (*Theropithecus gelada*) in the highlands of Ethiopia. Geladas are an ideal species for studying the role of sexually selected signals in primates for several reasons. First, the gelada social system may have favored the evolution of such signals for rival assessment (Bergman 2010; Bergman & Sheehan 2013). Geladas live in extremely large, multi-level, fluid societies comprised of dozens of reproductive units (Dunbar & Dunbar 1975; Kawai 1979; Dunbar 1984). Given that individual recognition appears limited in this species (Bergman 2010), signals likely evolved as a shorthand means to rapidly assess the condition of unfamiliar rivals or mates (Bergman & Sheehan 2013). Second, reproductive competition between gelada males consists of extremely costly, winner-take-all fights between harem-holding males ('leader males') and pre-reproductive bachelor males (Dunbar & Dunbar 1975). This situation favors both bachelors that choose the least dangerous reproductive males to attack and leader males that can deter attacks by advertising their quality.

One way in which leader males may deter challenges from bachelors is by engaging in a highly ritualized, loud call display that provides bachelor males a chance to assess potential rivals (Dunbar 1984). My research examines whether these displays

and their concomitant loud calls function as a sexually selected signal in male competition. Establishing whether loud calls are sexually selected signals requires establishing: (1) that signal variation exists across males of different quality, (2) that males are able to distinguish between high and low quality males based on these calls, (3) that receivers base reproductive decisions on these calls, and (4) that males with high quality calls have higher reproductive success (Snowdon 2004). To address these criteria, I combined acoustic, experimental, hormonal, and behavioral analyses in one of the most comprehensive studies of a sexually selected signal in a primate.

BACKGROUND

Sexual Selection and Signals

After developing the theory of natural selection (Darwin 1859), Charles Darwin realized that many traits, mainly sexually dimorphic traits, did not seem to promote survival. Darwin suggested that these traits evolved primarily to acquire mates, either by intimidating rivals and/or attracting females (Darwin 1871). Sexually dimorphic traits— mainly ornaments, armaments, and behavioral displays—are widespread across the animal taxa. Traits that are used in the context of sexual selection by influencing differential reproductive success are commonly known as sexually selected signals (Andersson, 1994).

To be maintained by natural selection, these signals must reliably signal information about the quality of the sender (Maynard Smith and Price 1973, Vehrencamp 2000). "Quality" can include an individual's current condition (i.e., strength or stamina; e.g., deep croaks in toads; Davies and Halliday 1978) and/or genetic quality

(i.e., good genes; e.g., tree frogs; Jaquiery *et al.* 2010). It has been hypothesized that sexually selected signals can only be reliable indicators of male quality if there is some cost or constraint that prevents low-quality animals from cheating and signaling high-quality.

Three signal types have been identified according to their costs: index, conventional, and handicap (Vehrencamp, 2000). Index signal are physical or physiological constrained traits that can convey information about intrinsic sender attributes such as age or body size (Maynard Smith and Harper, 1988, 1995; Maynard Smith 1991; Vehrencamp, 2000). The formant frequencies of male red deer (*Cervus elaphus*) roars, for example, function as index signals of male size (Reby and McComb 2003). Bigger stags have longer vocal tracts and as a result produce calls with lower frequency measures. Because body size conveys a greater advantage during fights, rivals can assess a male's fighting ability (i.e., body size) by attending to the acoustic properties these roars (Reby and McComb 2003).

Conventional signals carry a retaliation cost, whereby cheaters are punished for inaccurate signaling. In the paper wasp (*Polistes dominulus*), for example, low status males received higher levels of aggression when "cheating" by signaling facial patterns indicative of high status (Tibbets and Dale 2004). In general, conventional signals are rare. More common are *handicap signals,* signals that carry associated production costs. These signals can convey reliable information about the fighting ability, stamina, health, or condition of the sender because males in poor quality/condition cannot withstand the costs associated with signal production (Zahavi 1975; Zahavi and Zahavi 1977; Vehrencamp, 2000). In male baboons (*Papio cynocephalus*), for example, loud

call displays are energetically costly. Only males in good condition (e.g., dominant males) can call more often, call for longer, and produce calls with higher fundamental frequencies (Kitchen et al. 2003; Fischer et al. 2004). This handicap ensures that only animals of high quality or in good condition can sustain the costs involved in signaling.

By attending to these signals, males and females can gain valuable information about the quality of a potential mate or the relative strength of a rival prior to making important reproductive decisions (Maynard Smith & Price 1973; Bradbury & Vehrencamp 2011). If the signal is intended for a female audience (e.g., tail length in widowbirds; Andersson 1982), then females can assess the quality of a potential mates using signals prior to investing in offspring. If the signal is intended for a male audience (e.g., the roar of red deer; Clutton-Brook and Albon 1979), males can assess the condition or fighting ability of a potential rival. Because fighting can be costly to both losers *and* winners (e.g., Le Boeuf 1974), sexually-selected signals can reduce the cost of conflict by allowing males to assess one another before an encounter escalates to aggression (Maynard Smith 1982; Bradbury and Vehrencamp 1998).

Not all quality signals, however, are necessarily sexually selected signals. For example, male bull frogs emit advertisement calls that are reliable size assessment signals (Emlen 1968; Howard 1978). However, male bullfrogs do not assess fighting ability solely based on size related variation in acoustic signals (Bee 2002). While establishing signal quality is necessary in understanding the information being conveyed, assessing whether a signal is sexually selected requires understanding how conspecifics use information from these calls when making reproductive decisions (Rendall et al. 2009).

5

When studying sexually-selected signals, it is important to consider the perspective of both the signaler and the receiver. It is here that most studies on sexually-selected signals in primates have fallen short. Several primate studies have linked, for example, putative visual (e.g., bright skin color) and vocal signals (e.g., acoustic properties of calls) with aspect of male quality such as age, rank, health, and stamina. However, few studies have assessed whether these traits actually function in sexual selection.

To address this gap, Snowdon (2004) proposed specific criteria to demonstrate sexual selection in signaling in primates. First, the signal must be *sexually dimorphic*. Second, there must be *signal variation* between same sex individuals, high quality males should have high quality signals. Third, conspecifics must *discriminate between signals* of different quality. Forth, the signal must elicit *behavioral choices* in the recipient that are consistent with reproduction. If the signal is intended for a female audience, females should mate with males displaying higher quality signals. If the signal is intended for a male audience, males should avoid rivals signaling high competitive ability. Fifth, the signals must be *related to fitness* such that high quality signals result in greater reproductive success. To date, however, no study on a primate signal has yet to address all five of Snowdon's criteria.

In the next section, I will review the relevant literature on loud calls in primates. After this general review, I discuss why geladas are an ideal species for understanding the role of sexual selection in primate communication. Lastly, I outline the main questions and chapters of my thesis demonstrating how each address these criteria.

Sexual Selection and Primate Loud Calls

Many animals rely on information from vocal signals when making reproductive choices. Vocalizations can function as honest indicators of male quality when either the mode of delivery (e.g. display) or the acoustic properties of the call are costly to produce. In avian and amphibian species, vocal signals have been linked to body size (e.g. Linhart and Fuchs 2015), stamina (e.g., Vehrencamp et al. 1989), testosterone (Fusani et al. 1994), signal immune function (e.g., Mougeot et al. 2004), and overall health (Owen-Ashley et al. 2004). In primates, adult males produce long-distance vocalizations – hereafter, loud calls – that are hypothesized to function in sexual selection (Snowdon 2004; reviewed in Delgado 2006). For example, male howler monkeys (*Alouatta seniculus*) give loud roars (e.g., Sekulic 1982), gibbons (*Hylobates muelleri*) produce complex songs (e.g., Mitani 1985), and male baboons (*Papio spp.*) emit 'wahoo' vocalizations during chases with rivals (e.g., Hall & DeVore 1965). While loud calls have been studied by primatologists for decades, there is still considerable debate over how and why these calls may have evolved (Delgado 2006).

Loud calls are widespread across the primate order (Zimmermann 1995; Wich & Nunn 2002) and are characterized as being of lower frequencies than other calls in a species repertoire (Mitani & Stuht 1998). These calls can broadcast over large ranges suggesting that they may function in long-distance communication (Delgado 2006; Mitani & Stuht 1998; Waser 1977; Whitehead 1987). Indeed, there is considerable evidence suggesting that loud calls serve a spacing function both within (Mitani & Nishida 1993) and between groups (Waser 1975; Sekulic 1982; Mitani 1988; Whitehead 1989; Delgado 2006; Van Belle et al. 2014). However, loud call may also function in

direct caller assessment either by advertising attractiveness as a mate or competitive

ability to a rival (Delgado 2006).

The mate attraction hypothesis suggests that males produce loud calls primarily

to attract sexually receptive females (Delgado 2006). As is often the case in bird songs

(Vehrencamp 2000) and frog vocalizations (Sullivan & Kwiatkowski 2007), females

could attend to loud calls to assess the location or quality of a potential mate. However,

this hypothesis has received little empirical support (Snowdon 2004). In gibbons, for

example, unmated males call more often and for longer than mated males (*Hylobates*

klossi,, Tenaza 1976; *Hylobates lar,* Raemaekers et al. 1984), but there is no evidence

that females are attracted to them (Mitani 1988). Similarly, in orangutans (*Pongo*

pygmaeus), while there is some evidence to suggest that females are more likely to

approach males that call more often (Utami & Mitra Setia 1995), but female orangutans

do not respond to the playback of male calls (Mitani 1985).

Additional studies, however, suggest that loud calls evolved in the context of

male-male competition. In black howlers (*Alouatta pigra*), alpha males use loud calls to

assess the relative fighting ability of groups (Kitchen et al. 2004). In chacma baboons

(*Papio ursinus*), higher-ranking males call more often and are more likely to engage in

wahoo contests with males of similar rank (Kitchen et al. 2005). Studies of primate calls

have found that acoustic properties of these calls differ with a caller's body size (e.g.,

Japanese macaques, *Macaca fuscata*, Inoue 1988; Rhesus macaques, *Macaca*

mulatta, Fitch 1997; hamadrayas baboons, *Papio hamadryas*, Pfefferle & Fischer 2006;

chacma baboons, *Papio ursinus*, Kitchen et al. 2003), age (e.g., chacma baboons,

Kitchen et al. 2003, Fischer et al. 2002, Fischer et al. 2004; pig-tailed langur, *Simias*

concolor, Erb et al. 2013; Thomas langurs, *Presbytis thomasi*, Wich et al. 2003;

gibbons, *Hylobates lar*, Barelli et al. 2013), current condition (i.e. exhaustion; e.g.,

chacma baboons, Fischer et al. 2004; simakobus, Erb et al. 2013), and dominance rank

(e.g., chimpanzees, *Pan troglodytes,* Riede et al. 2007; Thomas langurs, Wich et al.

2003; crested macaques, *Macaca nigra*, Neumann et al. 2010; chacma baboons,

Kitchen et al. 2003, Fischer et al. 2004), suggesting that these calls may be linked to the

competitive ability of the sender. Taken together, these studies suggest that loud calls

function as sexually selected signals used in male-male competition in the contexts of

group defense or direct male assessment.

Despite the long-standing interest in primate loud calls, several questions remain

(Delgado 2006). First, while a growing number of studies have linked loud calls to male

condition, there are limited data across primates that indicate whether conspecifics

attend to information encoded in loud calls when making reproductive choices (Delgado

2006; Kitchen et al. 2013). In fact, relatively few studies have examined whether males

or females can discriminate between loud calls based on their acoustic properties

(Kitchen et al. 2013), a necessary step in establishing the overall function of these calls

(Snowdon 2004). Second, we know relatively little about how, or even if, individuals use

information derived from louds calls to make reproductive decisions. For loud calls to

function in direct male assessment, males should avoid or females should prefer the

males that produce the strongest signals (Snowdon 2004).

Lastly, sexually selected signals must ultimately result in differential fitness, such

that the strength of the signal must be directly associated with reproductive output.

However, since primates have long life-histories and complex social relationships,

quantifying lifetime reproductive success has been extremely challenging (Snowdon 2004). Previous studies have found a link between sexually selected signals and dominance rank, a proxy for reproductive success (Gerald 2001; Setchell & Dixson 2001; Kitchen et al. 2003), but to my knowledge, no study has examined the relationship between signal strength and fitness.

GELADA (THEROPITHECUS GELADA*)*

Geladas are terrestrial Old World primates that are currently only found in the highlands of Ethiopia (Dunbar 1993). A close relative of baboons (*Papio spp.*) geladas are the last remaining species in the genus *Theropithecus* (Delson et al. 1993). Geladas organize into extremely large (>1200 individuals) multi-level fission-fusion society that consists of several reproductive units (Crook 1966; Kawai et al., 1983). Reproductive units include a dominant leader male, 1-12 reproductive females, and 0-3 subordinate follower males. Units come together throughout the day to forage in *bands,* a collection of 5-30 units that spend at least 50% of their time together (Snyder-Mackler et al., 2012). Temporary aggregates of multiple units are known as *herds*.

Geladas are an ideal species for studying sexually selected signals for several reasons. In the largest aggregations of gelada society, individual recognition of conspecifics is probably not possible because of the cognitive costs of remembering so many individuals (Bergman et al. 2010). In support of this idea, recent research suggests that leader males in gelada society do not recognize other males around them – even males they encounter on a daily basis (Bergman et al. 2010). Thus, signals may

have evolved as a shorthand means to rapidly assess conspecifics (Bergman et al. 2009).

Second, reproductive competition between gelada males consists of extremely costly, winner-take-all fights between harem-holding males ('leader males') and pre-reproductive bachelor males (Dunbar & Dunbar 1975). Upon reaching adolescence, gelada males disperse from their natal unit and join all-male groups (*bachelor* groups) (Dunbar 1984; Pappano et al., 2012). Bachelor groups consist of 2-15 adult bachelor males and generally congregate on the outskirts of the units (Pappano et al. 2012). Bachelors are largely affiliative within the group however interaction between bachelors and leader males are largely hostile (Pappano et al. 2012).

For bachelor males, obtaining a unit of females requires challenging and replacing the leader male as the dominant male (i.e., 'takeover'). During takeovers, bachelor males are always the challengers and leader males are always on the defensive. Moreover, the winner always assumes the dominant leader male position, and the loser (if he survives) remains in the harem as a subordinate follower male (Dunbar 1984). This situation favors both bachelors that choose the least dangerous reproductive males to attack and leader males that can deter attacks by advertising their quality.

Third, gelada male reproductive output is (1) easy to quantify and (2) characterized by high reproductive skew. After takeovers, defeated leader males typically remain in the unit as follower males or disappear altogether, in which case they are presumed dead. The few cases where leader males were observed to re-enter another unit as a leader male involved males that had not yet sired offspring in their

original unit (Beehner, unpublished data). Thus, males have relatively discrete

reproductive windows (i.e., their tenure as a leader male) compared to other primates,

making it easy to quantify male reproductive output (i.e., number of offspring).

Furthermore, extra-unit paternity for this population is close to zero. Leader males sire

100% of offspring in single male units and 85% of offspring in units with followers

(follower males sire 15% of offspring) (Snyder-Mackler et al. 2012; Bergman et al.

2011). In sum, reproductive success for males is a function of their tenure as leader, the

size of their reproductive unit, and the presence of follower males in the unit (Snyder-

Mackler et al. 2012).

Finally, although signals are relatively rare in primates, gelada males have two

conspicuous traits that possibly serve as signals. The first is a red patch of skin on the

chest and neck. Previous work has demonstrated that leader males have redder chest

patches than non-reproductive males and that reproductive males with the largest

reproductive units have the reddest chest patches (Bergman & Beehner 2008; Bergman

et al. 2009). We know much less about a second putative signal – a loud display call

(Dunbar and Dunbar 1975) given by leader males during encounters with bachelor

males.

Gelada Male Vocal displays

Leader and bachelor males engage in ritualized displays (aka "yelping chases";

Crook 1966) that begin when a leader male leaves his unit of females and approaches a

group of bachelors on the outskirt of the band (see Dunbar 1984). The leader male

threatens the bachelors while bachelors congregate in a semicircle 1-2m in front of the

leader male. After an agitating few minutes of threatening, the leader male turns and solicits a chase. These chases are purely for display and rarely escalates to aggression (Dunbar 1984). The end of the display is marked by the leader male climbing to the highest point in the area and uttering a bout of high-pitched, two-phase loud calls ("display calls"; Dunbar and Dunbar 1975) before returning to his unit females.

Loud call bouts consist of 2-5 distinct vocalizations ("ee-yow") and leader males may give more than one bout during a display. The calls within the bout are mostly harmonic and are characterized by an inverted U-shaped frequency modulation (Aich et al., 1990). Loud calls are both the lowest in frequency in the gelada repertoire and exhibit the largest frequency range, increasing in frequency as calls progress throughout a bout (Gustison et al., 2012). Among adults, loud calls are only given by unit males (leaders and occasionally follower males). Neither females nor adult bachelor males produce this vocalization (Dunbar 1984). Occasionally, subadult and juvenile males will loud call but these calls do not solicit much interest from adults (Dunbar 1984).

We have several reasons for predicting that loud calls function in sexual selection, specifically in the context of male-male competition. First, gelada loud calls are *only* produced during aggressive encounter between males (Dunbar 1984). Loud calls are predominantly given during chases with bachelors but occasionally a leader male will call after chases with other follower males within his unit. However, almost all cases in which loud calls were directed towards follower males were following "messy" takeover when dominance was not clearly established (pers. observation). Unless

specified in the chapter, all analyses on loud calls were conducted only on calls directed towards a bachelor audience.

Second, these encounters elicit a great deal of interest from other males and are often contagious. Other leader males may follow one another in sequence, each in turn leaving his females to engage the bachelors and display. Displays are always initiated by leader males and only one male is involved at a time (Dunbar 1984). Third, bachelor males look significantly more at male vocal displays than copulations and male-male fights (Le Roux *et at*. 2012) suggesting that bachelor males may be extracting valuable information about leader male quality from these calls.

Loud calls and their concomitant displays are hypothesized to advertise a leader male's quality to rival bachelor males to discourage potential challenges (Dunbar 1984). There are two mechanisms by which these displays may function as sexually-selected signals either: (1) the acoustic properties of the loud call itself may contain information about a male's intrinsic condition, and/or, (2) the frequency of displays may indicate a male's relative strength as a competitor (Dunbar 1984). Although Dunbar proposed these possibilities over three decades ago, they have yet to be tested.

RESEARCH QUESTIONS & CHAPTERS

For gelada males, reproduction is contingent upon acquiring and maintaining access to a unit of females. Harem-holding leader males maximize reproductive success by obtaining a large unit or increasing their tenure length. Presumably, only males in top physical condition are able to both obtain a large unit *and* maintain control of the unit for a long period of time. It has been proposed that leader males discourage

prospective challengers using a highly-ritualized, loud call display given by leader males directed towards a bachelor audience (Dunbar 1984). **In this thesis, I will examine whether the gelada loud call display functions as a sexually selected signal in male competition.** Specifically, I answer four main questions to determine if gelada loud calls and their concomitant displays are sexually selected signals.

I address these questions in four separate chapters that are either accepted for publication (Chapter 3) or in the process of submission for peer-review (Chapter 2,4, and 5). Although I am the first author on all chapters, each chapter is a collaborative effort with several coauthors including my advisors Dr. Jacinta Beehner and Dr. Thore Bergman. For all remaining chapters, I use the pronoun "we" instead of "I" to denote this collaborative effort. I briefly describe each question and prediction below.

Question 1: Is there variation in loud call production among males of different quality?

For loud calls to function as sexually selected signals, there must be variation in how males produce these calls. Because vocal displays in geladas may be physically exerting, variation in (1) the *rate* of call production or (2) the *acoustic properties* of the loud call itself may be mediated by physical conditions (e.g., age, body size, stamina, status) and/or circulating levels of testosterone*.*

In **Chapter 2,** we investigate whether the *rate* males engage in these vocal displays indicates male condition. Given the physically demanding nature of these displays, we expect that displays are energetically costly to produce. Males should presumably engage more often in these displays when they are in peak physical condition. To test this hypothesis, we examined seasonal effects (rainfall and

temperature) as well as the overall effects of age and status on how often males engage in these displays. Furthermore, in this chapter we test the "testosterone-mediated hypothesis", which predicts that display rate behavior is influenced by circulating levels of the steroid hormone testosterone.

In **Chapter 3**, we investigate whether the *acoustic properties* of the loud calls of gelada males function as honest indicators of male quality and fighting ability. To test this hypothesis, we examined whether the acoustic properties of the gelada loud call vary in relation to individual, age, status, and/or exhaustion. We predict that the high-quality males in gelada society (e.g., dominant leader males) will produce distinct loud calls that differ along several acoustic properties. Specifically, we examined seven acoustic measures (e.g., fundamental frequency) and four temporal parameters (e.g., call duration) that have been previously shown to vary across condition in male primates. This second step represents an important validation for distinguishing the constraints associated with producing such vocalizations.

Questions 2: Do gelada males discriminate between loud call acoustic properties when assessing potential rivals?

In **Chapter 3**, we demonstrate that the acoustic properties of loud calls are honest indicators of a male's quality or condition. High-quality males produce calls that differ along several acoustic features. However, the fact that reliable information is available in loud calls is not sufficient to determine whether listeners actually attend to those signal features. We must also demonstrate that conspecifics can discriminate between signals based on these acoustic features. If males use vocal cues for

assessment, then males should discriminate between loud calls of variable quality. On the other hand, if females rely on these cues to assess the potential quality of a mate, females should attend to differences in these calls. We test this hypothesis in **Chapter 4** by examining whether gelada males and females can distinguish between high and low-quality calls. Using a playback experiment and natural observations of vocal displays, we evaluate whether loud calls function assess rivals and investigate the type of assessment strategy (e.g., mutual assessment, opponent-only assessment) used by males when attending to these vocal signals.

Question 3: Do geladas make behavioral choices based on information from display rates and/or loud call properties of rivals?

Importantly, if loud calls are sexually selected signals then the differences in loud call acoustic properties and/or the rate at which males display should be the basis for male decision-making. In other words, bachelors should decide which males to challenge and which males to avoid based on the strength of other males' signals. In **Chapter 2,** we examine whether males that display less often are more likely to be challenged by bachelor males. We conduct a similar analysis in **Chapter 5** on loud call quality and another putative signal for male geladas, the red patch of skin on the chest and neck (chest patch). By using a multimodal approach, we examine how bachelor males may use information from multiple signals to make the most informed reproductive choices.

Leader males may also rely on information from acoustic signals when deciding *when* to display. Loud call displays often act as a catalyst for other leader males to join

in with loud calls of their own. If leader males attend to the loud calls of the males around them, then we expect that high-quality leader males will be more likely to enter a loud call display when the display includes other males of high-quality. We test this prediction in **Chapter 3**.

Question 4. Do loud call properties and/or display frequencies predict reproductive success?

Ultimately, a sexually selected signal must result in disparities in reproductive output. If a strong signal effectively discourages challenges from bachelors, then a strong signal will also lead to longer tenures and higher reproductive success. We assess the relationship between signal strength and reproductive success in **Chapter 5.** Specifically, we examine whether display rate, call quality, and/or chest redness predict the length of a leader male's tenure and the number of offspring sired during that tenure.

STUDY SITE AND SUBJECTS

I conducted my dissertation research on a population of geladas living in the Simien Mountains National Park (SMNP), Ethiopia (13.3064° N, 38.2641° E). The SMNP is home to the largest community of geladas in Ethiopia (population estimated at 2460 geladas; Beehner et al. 2007). This population has been under continuous study since 2005 by the University of Michigan Gelada Research Project (UMGRP) directed by Dr. Jacinta Beehner and Dr. Thore Bergman. The UMGRP actively studies approximately 250 individually recognized geladas at any given time. Individuals are

habituated to observers on foot and have been under nearly daily observation since the onset of the study. The majority of my dissertation employs behavioral observations, vocal recordings, and fecal hormone analyses, collected on 29 adult males within our study community between February-December 2013. However, I draw from long-term project data (2006-2014), and from data from other males, when necessary to address my research questions.

Located in northern Ethiopia, the SMNP is characterized by jagged mountain peaks, deep valleys, and sharp precipices. At an altitude ranging from 3200-4500 meters, the SMPN encompasses an area of Afroalpine habitat (170 km^2) including open grassland plateau and a few remnant forests. The region experiences pronounced "wet" (80% of annual rainfall) and "dry" seasons each year (Beehner & McCann 2008; Hunter 2001). The wet and dry seasons are variable, but generally occur from June-September and October-May, respectively (Beehner & McCann 2008). Monthly average temperatures in the Simiens range from highs around 20°C (68°F) (March-May) to lows around 15°C (59°F) (July-September). Daily temperatures, however, can vary from up to 25°C and can drop below freezing at night (Iwamoto & Dunbar 1983). The SMNP is listed as a UNESCO World Heritage Site and is home to several endemic animals, including geladas and the Ethiopian wolf (*Canis simensis*) (1978).

SIGNIFICANCE OF RESEARCH

Compared to other taxa, sexually selected signals in primates are poorly understood, presumably because signals are rare, challenging to measure, and difficult to correlate with reproductive success. In this thesis, I examine if loud call displays in

gelada males function as sexually selected signals used in male competition. For a signal to be sexually selected, signals *must* (1) vary between same-sex individuals, (2) elicit differential responses in conspecifics, (3) influence mating decisions, and (4) impact reproductive success (Snowdon 2004). By combining cognitive experiments, hormonal analysis, and behavioral observations, this dissertation addresses all four of these criteria and stands as one of the most extensive studies on a sexually selected signal in a wild primate. Specifically, in this thesis we validate signal quality, quantify the cost of signal production (energy and/or testosterone), assess how conspecifics use signal information to make reproductive choices, and determine how signal strength relates to reproductive fitness. Lastly, we present some of the first evidence linking reproductive success to signal strength in a wild primate.

CHAPTER 2

THE FUNCTION AND COSTS OF GELADA MALE VOCAL DISPLAYS

INTRODUCTION

Sexual selection has led to the evolution of elaborate sexually-dimorphic traits, including morphological, vocal, and behavioral signals (Andersson 1994). These signals can influence access to mates by affecting either attractiveness (i.e., ornaments used in mate choice) or competitive ability (i.e., badges of status used in competition for mates, Andersson 1994). Consequently, males in many animal species invest substantial resources in sexually-selected displays involving signals (Andersson 1994). Across a range of taxa, males that display for longer, at greater intensities, or with greater complexity than other males are more successful at attracting mates or deterring rivals (e.g. insects, Berg et al. 2005; Delaney et al. 2007; Mowles & Jepson 2015; birds, Rintamaki et al. 1999; Gentner & Hulse 2000; frogs, Gerhardt 2000; Schwartz et al. 2001; Prohl 2003; mammals, Clutton-Brock & Albon 1979; Clutton-Brock et al. 1982; Mcelligott et al. 1999; Teichroeb & Sicotte 2010).

To be maintained by natural selection, these displays must reliably signal information about the condition and/or quality of the sender (Maynard Smith and Price 1973, Vehrencamp 2000). Vocal displays, displays that combine both rigorous physical movements and repeated vocalizations, can reliably signal male quality if there is some

cost or constraint that prevents lower-quality individuals from "cheating" and signaling high-quality (Zahavi 1975, Grafen 1990, Vehrencamp 2000, Johnstone 1995). Signals that are constrained by physical attributes (e.g., body size), commonly referred to as index signals (Vehrencamp 2000), provide honest information about physical characteristics of the sender. For example, the acoustic properties of male red deer roars are constrained by body size, with bigger males producing calls that are lower in pitch and longer in duration (Reby and McComb 2003). A signal can also be reliable if it is costly to produce, ensuring that only males of high quality or good condition can sustain the costs involved in signaling (handicap signal; Zahavi 1975, 1977, Grafen 1990). For instance, the display itself may require stamina and good physical condition, preventing weak males from engaging readily in these displays (reviewed in Payne and Pagel 1997). Indeed, there is evidence in a range of taxa to suggest that vocal displays are energetically costly to produce (Ryan 1988; Prestwich 1994; Payne & Pagel 1997; Davies & Halliday 1978; Halliday 1987; Marler & Ryan 1996; Humfeld 2013). Several studies have shown, for example, that males display less often when body reserves are low (Reby & McComb 2003; Reid 1987; Kotiaho et al. 1998; Wagner & Hoback 1999; Godfrey & Bryant 2000; Crocker et al. 2012), foraging success is low (Kacelnik 1979; Mace 2008), and temperatures are cold (Gottlander 1987; Reid 1987; Vehrencamp et al. 1989; Cowlishaw 1996).

Display can be additional costly if associated with the steroid hormone testosterone. Testosterone plays a central role in regulating behavioral traits related to competition for mates by influencing both the stamina and motivation to engage in these displays (Wingfield et al. 1987, 1990; Buchanan et al. 2001). Despite the clear

competitive benefits of testosterone maintaining high levels is costly. High testosterone can result in a reduced immune function (Folstad & Karter 1992), increase stress levels (Braude et al. 1999), increase risk or injury and mortality (Marler & Moore 1988), and a greater overall energetic expenditure (Marler & Moore 1988; Buchanan et al. 2001). As a result, presumably only males in good physical condition can buffer the associated costs of maintaining high levels of testosterone (Folstad & Karter 1992).

Males in many nonhuman primate species also engage in vocal displays that are hypothesized to function as sexually-selected signals (e.g., Ursine Colobus, *Colobus vellerosus*, Teichroeb & Sicotte 2010); mountain gorilla, spp., Sicotte 2002; Robbins 2003; chacma baboons, *Papio hamadryas ursinus*, Kitchen et al. 2003; gibbons spp. Raemaekers et al. 1984; Mitani 1988; Cowlishaw 1996). Several studies have shown, for example, decreased display behavior with decreasing rank (chacma baboons, Kitchen et al. 2003; Fischer et al. 2004; macaques, *Macaca nigra*, Neumann et al. 2010; guerezas, Colobus guereza, Harris et al. 2006; ursine colobus monkeys, *Colobus vellerosus*, Teichroeb & Sicotte 2010), suggesting that there is a relationship between competitive ability and vocal displays in these species. Other studies have examined the context surrounding display to infer its function (Mitani and Nishida 1993; Erb et al. 2013; Teichroeb and Sicotte 2010; Raemaekers et al. 1984). For example, male ursine colobus monkeys, display more often and more vigorously in the presence of other males, but not females, suggesting that these displays likely function in male-male competition (Teichroeb and Sicotte 2010). There is little evidence, however, that displays function in direct male assessment (Kitchen et al., 2003) and few studies have examined exactly *how* these displays signal male condition (simakobu, *Simias concolor*,

Erb et al. 2016; gibbons, *Hylobates spp*: Cowlishaw 1996, Whitten 1982; Ursine colobus, Teichroeb & Sicotte 2010).

In this chapter, we examine whether vocal displays in geladas (*Theropithecus gelada*) are handicap signals that function to deter challenges from rival males (i.e., male-male competition). Geladas live in large, multilevel societies comprising dozens of reproductive units (one dominant leader male, 1-12 females, and occasionally 1-3 subordinate follower males) nested within a foraging band (Dunbar & Dunbar 1975; Kawai 1979; Mori 1979; Dunbar 1984). On the outskirts of these units are all-male groups which are made up of adult bachelor males. Reproductive competition between gelada males consists of extremely costly, winner-take-all fights between leaders and bachelors ("takeover"; Dunbar & Dunbar 1975). This situation favors both bachelors that choose the least dangerous males to attack and leader males that can deter attacks by advertising their condition (Dunbar 1984).

One way in which leader males may deter challenges from bachelors is by engaging in a highly-ritualized, vocal display that provides bachelor males with a chance to assess the strength and stamina of potential rivals (Dunbar & Dunbar 1975).These ritualistic displays typically begin when a leader male approaches, threatens, and solicits a chase from a group of bachelor males (Dunbar 1984). During these displays, males run, throw rocks, climb trees and shake branches while simultaneously uttering a series of high-pitched, two-phrase loud calls unique to both the species and the context ('ee-yow' calls; Dunbar & Dunbar 1975).

There are two possible mechanisms that might explain how these display function to discourage prospective challengers: either the rate of which males engage in

these displays indicates a male's relative strength as a competitor, and/or the vocalization given within the display contains information about male quality or condition (Dunbar 1984). In this chapter, we focus on this first hypothesis that display *rate* is important in deterring challenges from bachelors (Dunbar 1984). In 1984, Robin Dunbar published preliminary data suggesting that males that displayed less often were more likely to be overthrown. We expand on these preliminary findings, with a larger sample size and longer period of observation, to investigate the functional benefits of participating in these displays.

In addition to examining the function of these displays, we investigate whether display behavior is associated with costs; mainly, energetic costs and/or hormonal condition. To investigate energetic constraints, we examined differences in display rate due to seasonal changes, mainly rainfall and temperature. Geladas are the only graminivorous primates with over 90% of their diet comprising of high-protein fescue grasses (Iwamoto 1993). With such a restricted diet, geladas appears to be more vulnerable to environmental changes than other primate species (Mau et al. 2009). Geladas modify their diet across the year due to changes in precipitation, feeding predominantly on preferred above-ground resources (blades, seeds, and stems) during the wet season (Jun-Oct) and below-ground (roots and storage organs) during the dry season months (Hunter 2001). This dietary shift may lead to an energy shortfall in the dry season months, that precludes optimal competitive performances in the dry season months (Pappano & Beehner 2014).

Changes in temperature can also carry energetic constraints. Geladas are found only in high-altitude environments where temperature is variable throughout the day and

can approach freezing at night (Iwamoto & Dunbar 1983). When ambient temperatures are cold, warm bodied animals must either reduce their activity or increase their food intake to maintain body temperature (Terrien & Jeremy 2011). On the other hand, when ambient temperatures are hot, animals may struggle to prevent overheating, and therefore reduce their energy expenditure (e.g., Sykes monkeys, *Cercopithecus mitis*, and guerezas: Mueller et al., 1983; chacma baboons: Hill 2006). Thus, both high highs and low lows can effect energetic expenditure.

Vocal displays in geladas may also be testosterone-dependent. In primates, testosterone has been shown to mediate aggressive behaviors (e.g., Dixson 1980; Muller & Wrangham 2004; Pappano & Beehner 2014), reproductive trajectories (Pappano & Beehner 2014), and vocal production (e.g., Barelli et al. 2013) but significantly less is known about its role in display behavior. Among bachelor males in gelada society, testosterone is correlated with levels of bachelor-initiated aggression and is a reliable predictor of a male reproductive trajectories (Pappano & Beehner 2014). Among leader males, we expect a similar relationship between testosterone and vocal displays, given that vocal displays are, by definition, aggressive encounters initiated by leader males.

If vocal displays function to deter challenges from rival males, we predict that males that display more often should be less likely to be taken over. How often a male displays, however, is likely a tradeoff between his *motivation* to engage rivals and the *costs* associated with displaying. If unbound by constraints, males should be motivated to display at higher rate when the threat of being challenged by bachelors is high. Three factors may influence a male's motivation to display: status, group size, and takeover

risk. Specifically, we expect that leader males, males that have everything to lose from being overthrown, should display more often than subordinate follower males. Among leader males, we expect that males in the largest units should display the most frequently. Males with more females in their unit have a higher potential reproductive rate making larger units more desirable to bachelor males (Dunbar 1984). Indeed, larger units are taken over more frequently than smaller one (Dunbar 1984; Bergman et al., 2009). Finally, while geladas are not seasonal breeders, takeovers in geladas follow a distinct seasonal pattern, with bachelor-initiated aggression occurring predominantly at the end of the dry season months ("takeover season"; Pappano & Beehner 2014). We expect that males will display more often during the months in which the risk of takeover is highest (February-May).

However, if participation in vocal displays is costly, a male's ability to display may be constrained by his physical condition: mainly age, androgen levels, and energetic state. We expect that prime aged (8-12 yrs) males will display more often than older males (>12yrs) and that, regardless of age, males with higher testosterone will engage significantly *more* in these displays than low testosterone males. Second, we expect a male will display more often when nutritional intake is high, and energetic expenditure is low. Specifically, we predict that males will display *more* often in the wet season months, when above-ground food is readily available. In terms of temperature, we predict that gelada males will display *less* often as minimum temperature decreases, due to the additional metabolic costs of dealing with cold stress, and when maximum temperatures increase, due to increased activity costs.

METHODS

Subjects and Study Site: Data were collected from a population of geladas living in the Simien Mountain National Park, Ethiopia. The University of Michigan Gelada Research project has been collecting long-term behavioral and demographic data on this population since January 2006. For this study, we followed 29 males (18 leaders, 11 followers) from February 2013-January 2014. All males were individually recognized and habituated to observers on foot.

The Simien Mountain National Park encompasses an area of Afroalpine habitat, including open grassland plateau and a few remnant forests. The region experiences pronounced wet and dry seasons each year. The wet seasons generally occur during June-September and are characterized by above average rainfall (cumulative rainfall, wet season= 2169 mm, dry season= 301 mm) and low temperatures (mean maximum temperature, wet season= 14.8°C, dry season= 18.6°C)(Hunter 2001; Beehner & McCann 2008; Pappano & Beehner 2014). In general, temperature in the Simiens are variable throughout the day (daily maximum temperature ranged from 8.9-25.0°C) and approach freezing at night (daily minimum temperature ranged from 4.1-8.2°C) (Beehner & McCann 2008; Pappano & Beehner 2014). Climate data were collected using a rain gauge and digital thermometer at a central location in the geladas' home range. Rainfall (mm) and temperature data (daily maximum and minimum, °C) were collected daily, with a mean for each month calculated for temperatures (Max Temp, Min Temp) and a cumulative total for each month calculated for rainfall (Rain; Beehner & McCann 2008).

Vocal Display Behavior: We collected all-occurrence behavioral sampling on 395

observed vocal display events involving known males between February 2013 and

January 2014. A display event began when one or more males engaged the bachelors

in a chase, and a display ended when all males involved returned to their previous

activity. For each display event, we recorded which known males participated in the

display, which males were present and did not participate, and whether the display was

directed towards bachelors or directed towards other unit males.

Vocal displays were predominantly given in the presence of bachelor males

(n=279 display events from 29 males). Leader males occasionally engaged in similar

display behaviors (e.g., chasing and loud calling) during aggressive encounters with

their follower male(s) (n=116 unit display events). However, these chases occur

predominantly following "messy" takeovers where dominance is not clearly established

and multiple followers are attached to a group (*pers. observation*). Because these

displays have been hypothesized to deter challenges from bachelors (Dunbar 1984), we

focused our analysis on the 279 display events that were aimed at bachelor males. For

each unit male, we recorded the number of times he displayed per month and the

number of hours that male spent in the presence of bachelor males.

Status and takeovers. Status categories for unit males (i.e., leader or follower) were

determined using behavioral observations of group membership and dyadic dominance

interactions each month. The dominant male in a unit was assigned as the leader male.

Any subordinate males were assigned as follower males. Follower males included both

"old" followers (i.e., the deposed leader) or "young" followers (i.e, subordinate immigrant males that join a unit)

Takeovers are discrete events where a bachelor challenges and subsequently overthrows a dominant leader male. After takeovers, the deposed leader either returns to a bachelor group, disappears entirely (and is presumed dead), or remains in the unit as a subordinate follower male. We observed 8 takeovers involving known leader males during the study period. However, we had sufficient vocal display rate data (>2 mos of observations) from only 4 of the 8 males prior to them being overthrown. In 3 takeovers the deposed leader remained in the unit as a follower male. For those males, status during the takeover month was assigned depending on the date of takeover.

Unit size. As a proxy for unit size, we used the number of adult females within each group. Females were considered adults when they began to exhibit sexual swellings, suggesting that they had reached sexual maturity. We recorded unit size separately for each unit each month to account for the changing number of females due to female maturations, unit fissions, and female deaths. Unit size for leader males ranged from 2-13 females. We assigned all follower males a 0 for unit size.

Age: Age was estimated to the nearest half year based on secondary sexual characteristics such as canine eruption, physical size, pelage coloration, and cape length (Dunbar & Dunbar 1975; Beehner et al. 2015). For the 29 males in this study, males age ranged from 7.5-16.0 years.

Testosterone: We collected bimonthly fecal samples from all target males (735 total

samples, mean 26 samples / male) for the extraction and analysis of testosterone

metabolites. Hormones were collected using a "field-friendly" method for fecal steroid

hormone extraction and preservation (Beehner & Whitten 2004; Beehner & McCann

2008) that has been previously used in this population of geladas (Beehner et al. 2009;

Pappano et al. 2010; Pappano & Beehner 2014). All samples were subsequently frozen

(-10°C) in the field until shipped to the University of Michigan for radioimmunoassay

(RIA) analysis. Prior to RIA, steroids were eluted from cartridges with methanol. All

samples were assayed for testosterone metabolites using a modified protocol for a

commercially-available RIA kit (Pantex anti-Testosterone RIA) and results are

expressed as ng/g dry feces (Pappano et al. 2010). The antibody in this kit has been

analytically validated for use in geladas (and found to be both linear and accurate;

(Pappano et al. 2010; Pappano & Beehner 2014). Intra-assay coefficients of variation

(CV) for a high- and low-concentrated quality control were 8.2% and 9.4%, respectively.

Corresponding figures for inter-assay CVs were 11.7% and 10.4%.

Data Analysis

First, we examined whether the males that displayed less often were more likely

to be targeted by bachelors. To do this, we compared mean monthly display rates for

leader males that remained leaders (N=10) to display rates for leader males that were

overthrown (N=4) using a Mann-Whitney U exact probability test. We calculated a mean

display rate for each male using his total number of displays divided by his total number

of hours spent with bachelors each month. We excluded from this analysis any new leader males that entered a unit during the study period (N=4).

We then conducted a General Linear Mixed- effects Model (GLMM) analysis, using a Poisson distribution, to investigate the relationship between the functional significance of a male's display and the cost of doing so. Our dependent variable was the monthly display counts per male offset by the total hours that male spent with the bachelors each month. Specifically, we had seven variables of interest. First, we included factors that should influence a male's motivation to display: mainly, *status* (leader / follower)*, unit size* (0-13), and *takeover risk* (number of takeovers across known units for each month). Second, we included factors that could constrain a male's ability to display: *age* (rounded to nearest half year), mean monthly *testosterone* (log-transformed, ng/g), *rain* (cumulative monthly rainfall, mm), *max temp* (mean monthly maximum temperature, ˚C), and *min temp* (mean monthly minimum temperature, ˚C). We controlled for repeated measures from each male by including male ID as a random intercept.

We examined the correlation among variables prior to model fitting to determine whether any were highly correlated, which may lead to inaccurate model results. We found a strong correlation ($r>0.6$) between *max temp* and *min temp* (Pearson's correlation: $r=0.78$). Because of this, we ran two set of GLMMs, one that included *max temp* (M1) and one that included *min temp* (M2). For both models, we compared univariate models that considered only a single fixed effect to multivariate models that considered all combinations of fixed effects. We compared all candidate models using Akaike information criterion (AICc) and considered the models with the lowest AICc to

be the best fit for our data set. We then compared the top models from both sets (M1 and M2) using a likelihood ratio test.

For all GLMMs, we visually inspected each model using a Q-Q plot, histogram of residuals and scatterplot of fitted versus residual values. For all models, residual values were normally distributed. We performed all statistical analysis using R (v. 3.0.3). All models were run using the lme4 package (v. 1.1-7). We used the MuMIN package (v. 1.12.1) to compare all candidate models and ggplot2 (v. 2.1.0) and sjplot packages (v. 2.0.0) to create figures.

RESULTS

Males that remained leaders exhibited significantly higher display rates than males that were taken over (Mann-Whitney test, U= 2.000, SE= 7.040 p=0.008; Figure 2.1). We found no difference in the age of males between these two groups (Mann-Whitney, U=14.000, SE= 7.040, p=0.454). However, it is important to note that our sample size was quite small here.

The best predictors of male display rate were *status*, *age*, *testosterone*, *rain*, and *max temp* (or *min temp*)(Figure 2.2). Models with both *max temp* and *min temp* performed substantially better than the intercept only null model (ΔAICc=50.25). Comparing these two top models, the model including *max temp* performed better than the model including *min temp* (χ^2=2.99, p<0.001). *Min temp* was included in the best model but had no significant effect on how often a male displayed (GLMM; *min temp*, β=-0.092, SE=0.055, t=-1.668 p=0.095). For *rain*, *testosterone*, *status*, and *age*, the

beta coefficients were nearly identical between models (Table 2.1). Here, we focus on

the model including *max temp* only, but include both model results in Table 2.1.

Leader males displayed more than follower males (leaders, β=0.787, SE=0.249,

t= 3.160, p=0.001; Figure 2.3) but neither *unit size* nor *takeover risk* was included in

either model, and when included, were non-significant (unit size, β=-0.052, SE=0.042,

t= -1.244, p=0.214; *takeover risk*, β=0.073, SE=0.073, t= 1.003, p=0.316). We found a

negative relationship between *display rate* and *age*, such that older males displayed

more less than younger males (age, β=-0.163, SE=0.055, t=-2.970, p=0.003; Figure

2.4). In addition, we found that males with high testosterone levels displayed more often

than males with low testosterone (*testosterone*, β=0.629, SE=0.205, t=3.069, p=0.002;

Figure 2.5). We also found a positive relationship between *rain* and *display rate*. Males

displayed more during months with higher cumulative rainfall than they did during

months with lower rainfall (*rain*, β=0.183 , SE=0.059, t= 3.076, p=0.002; Figure 2.6).

Mean maximum temperature also influenced display behavior with males displaying

more often as temperatures decreased (*max temp*, β=-0.151, SE=0.063, t=-2.392,

p=0.017; Figure 6).

DISCUSSION

Our results support the hypothesis that vocal displays in geladas function to deter

challenges from rivals. Consistent with previous findings on vocal displays in this

species (Dunbar 1984), we found that males that displayed less often were more likely

to be targeted by bachelor males. Given this, we expect that males should display most

often when the threat to their fitness is highest, in this case when they are leaders, have

the largest units, and when challenges are more likely. However, this is not what we found. Although leaders did, indeed, display more than followers, unit size and takeover risk did not influence their display rate.

Rather, it appears that vocal display rates may carry heavy production costs. We found that all males displayed more often during periods of high rainfall (high food availability) and warmer temperatures, suggesting that there are energetic costs associated with engaging in these displays. It appears that only prime-aged leaders males with high testosterone can withstand the costs associated with displaying at higher frequencies. Taken together, these data suggest that vocal displays in geladas function as handicap signals that reliably advertise a male's current condition (e.g., hormonal profiles) and overall competitive ability.

Does vocal display rate function to deter rivals?

In primates, displays have been hypothesized to function in attracting females and/or competing with males. Despite several studies showing that dominant males display at higher frequencies than subordinate males, whether males actually assess rivals based on display rate has remained largely untested (Snowdon 2004). Similar to previous research on displays in primates, we found that leader males, the dominant males in gelada society, displayed more often than subordinate follower males. Moreover, *among* leader males, the males that displayed the least often were the most likely to be subsequently overthrown.

These results mirror those from Dunbar's (1984) preliminary findings on gelada display rates and likelihood of takeover (Dunbar, 1984, page 180, Figure 66). Both

results stem from small sample sizes – this study examined 13 males (9 that remained leaders and 4 that were takeover) while Dunbar observed 9 males (7 that remained leaders and 2 that were takenover. Nevertheless, the fact that two small sample sizes should produce nearly identical results is compelling evidence supporting the hypothesis that males that display more often are more successful at deterring rivals. There are also a few differences to consider when comparing our results to those of Dunbar. In this study, display rate was calculated as displays per hour spent in the presences of bachelor males (13 units, 436 bachelor hours observed, over 12 months). Dunbar's (1984) rates were calculated using the total observation hours (9 units, 154 observation hours, 5 months). This resulted in overall differences in display rates between the two studies: however, the relative difference between males during each study period was not affected. Males that displayed less often, regardless of how display rate was calculated, were more likely to be replaced.

Leader males that are more successful at deterring bachelors will maintain access to females the longest, and thus have the highest reproductive success. Once a leader is targeted for a takeover, it appears that he stands very little chance at success, because generally these attacks involve multiple bachelor's chasing and fighting the leader until the point of exhaustion (Dunbar 1984). Note however, that the early stages of takeover challenges are rarely observed, and we do not know how often such attempts fail (i.e., the leader fights off the bachelor and retains his unit). Regardless, the optimal strategy for gelada leader males is to avoid being targeted by bachelors in the first place. Therefore, to the extent that displays successfully deter bachelor attacks, leader males should display more often when their tenure is at risk (Dunbar 1984).

However, males in large units did not display more often than males in smaller ones, nor did males display more during months when takeover risk was higher. This suggests that there may be heavy costs associated with engaging these displays.

Are vocal displays energetically costly to produce?

Supporting previous research on this population of geladas (Pappano and Beehner 2014), we found that the majority of takeovers occurred during the dry season months (Feb-May 2013). It would be in a leader male's best interest to display most often during these months, but this is not what we found. Rather, we found a positive association between display rates and cumulative rainfall (i.e., rainy season; Figure 6) indicating that leader males displayed significantly *less* in the dry season, despite the fact that male-male competition was highest. We suggest that there may be energetic constraints on how often a male can perform displays, possibly due to a negative energy balance experienced during the dry season months – a hypothesis that remains to be tested.

Although we currently lack data on food quality in the Simiens, we know that an increase in rainfall is positively associated with more green grass cover, and hence increased food availability for geladas (Hunter 2001). In the dry season months, males spend more time foraging and moving (e.g., they have longer daily ranges) suggesting that energetic expenditure is also higher (Iwamoto & Dunbar 1983).

In addition to rainfall, maximum daily temperature also influenced how often males displayed. Specifically, males displayed less often as maximum daily temperature increased. In other species, animals reduced energetically expensive activities at temperatures exceeding $30^{o}C$ (Hill 2006). It seems unlikely that this decline in display

rate during hotter months reflects heat stress as temperatures in Simiens never exceeded 25°C. One possibility is that males display less often on hot days because they are travelling further. Previous research has shown that geladas significantly increase their daily journey length during warmer months (Hunter, 2001). However, more research would need to be done to test this hypothesis.

We expected minimum temperature to have a strong effect on display rate due to increase metabolic costs of thermoregulation. Minimum temperature was included as a predictor in the best fit model, however, we found only a slight decline in display rate as minimum temperature dropped, and these results were not significant. Compared to maximum temperature (range: 12.94°C- 22.74°C), minimum temperatures were not as variable (range: 5.8°C -9.91°C; Figure 2). The fact that we see any effect of minimum temperature, when monthly minimum temperatures differed very little, suggests that minimum temperature might have a greater effect in influencing display frequency than we can detect in this analysis. Previous research has shown that temperature-dependent metabolic requirements impose a major constraint on gelada behavior and physiology. Geladas alter their feeding behavior, overall activity rates (Iwamoto & Dunbar 1983), and exhibit higher "stress hormones" (i.e., glucocorticoids) (Beehner & McCann 2008) when the minimum temperature drops. Mean minimum temperatures may not accurately represent the metabolic costs incurred by males on any given day. Future analysis might benefit from assessing daily displays rates to determine whether day-to-day changes in temperatures influence display behavior.

These seasonal changes in display performance are similar to what has been previously documented in calling rates for other primate species. For example, gibbons

(*Hylobates spp.*) have been found to call at higher rates when temperatures were warmer and when high-energy food was more abundant (Cowlishaw 1996). However, for other primate species, like simokobu monkeys (*Simias concolor*), there is no evidence to suggest that seasonal changes influence vocal behavior, as energy constraints did not appear to affect calling rates (Erb et al. 2016). However, few studies have examined whether the behaviors associated with calling (i.e., vocal display) are affected by food availability, energetic expenditure, and metabolic costs. Vocalizations, in general, entail relatively low energetic costs (Ward et al. 2003), yet that cost should be substantially higher in taxa in which males vocalize for extended periods of time, like gibbons, or when vocalizations are coupled with physically demanding behavior, like chacma baboons (*Papio ursinus,* Kitchen et al., 2003) and geladas. To test this hypothesis (that vocal displays are energetically costly), it will be necessary to either quantify heart rate during such displays (using heart rate monitor collars) and/or examine energy balance in males that display more and less often. For example, urinary C-peptide of insulin, a biomarker of energy balance (Girard-Buttoz et al. 2011; Emery Thompson and Knott 2008), may be useful for assessing the energetic costs of vocal displays for animals that display frequently.

Are vocal display mediated by testosterone?

We found that males with high testosterone displayed more often than males with lower testosterone, suggesting that displays are both testosterone *and* condition-dependent signals. Several primate studies have suggested that testosterone may mediate display behavior (Kitchen et al. 2003; Wich et al. 2003). For example, in

chacma baboons, high-ranking males have higher testosterone levels and are more likely to participate in loud call contests than low-ranking males (Kitchen et al. 2003; Beehner et al. 2006). To our knowledge, our data here provides some of the first direct evidence linking testosterone and display behavior in a nonhuman primate species.

In gelada males, testosterone follows seasonal patterns with leader males exhibiting lower testosterone levels during the dry season months presumably because males are unable to upregulate testosterone during periods of low food availability (Pappano & Beehner 2014). Display rates appear to mirror these seasonal changes in testosterone, with males displaying more often during the months in which testosterone was highest (Figure 2.6). Given the positive relationship between rainfall, testosterone, and display rates among gelada males, variation in body condition is the most likely cause of differences in testosterone production and display behavior. Similar results have been found in birds (Ligon et al, 1990) and frogs (Marler & Ryan 1996), where both testosterone and display rates increase with increased food availability.

Currently, we do not know the directionality of the response between energetic condition and testosterone. On the one hand, gelada males with higher testosterone may display more often and expend more energy (Energetic Hormone Vocalization Model; Emerson & Hess 2001). This does not appear to be the case in geladas since testosterone increased a few months prior to display rates doing so (Figure 2.6). A more likely explanation is that gelada males that display more often have higher testosterone as a result. But, further studies are needed to test any causal hypothesis.

One question remains: how do bachelors *know* how often males display? One possibility is that bachelors use this information immediately – and are more likely to

challenge the males that do not display. However, we know that this is not true. The

"display season" – where leader males display the most often – is very different from the

"takeover season". Yet, we see a relationship between display rate and likelihood of

subsequent takeover. Another possibility is that bachelor males keep track of individual

males and remember how often each one displays. However, given the size and

complexity of the gelada social system, and given experimental results that indicate

males do not recognize one another (Bergman 2010), it is unlikely that bachelor males

are tracking individual male condition across time. Yet a third possibility is that the loud

calls themselves produced during these displays encode information about male

condition and/or quality. If this is the case, we expect the acoustic properties of loud

calls to function as quality signals and that call quality is directly correlated with how

often males display. We address these predictions in the next chapter.

TABLES

Table 2.1. Results from best fit models.

	Model 1 (Max Temp)					Model 2 (Min Temp)			
	beta	*Se*	*t-value*	*p-value*		*beta*	*Se*	*t-value*	*p-value*
Fixed Parts									
(Intercept)	-3.65	0.91	-4.01	6.01e-05		-3.74	0.92	-4.07	4.71e-05
Status (Leaders)	0.77	0.25	3.16	**0.002**		0.79	0.25	3.14	**0.002**
Age	-0.16	0.06	-2.97	**0.003**		-0.16	0.06	-2.89	**0.004**
Testosterone	0.63	0.21	3.07	**0.002**		0.65	0.21	3.04	**0.002**
Rain	0.18	0.06	3.08	**0.002**		0.26	0.48	5.37	**8.01 e-08**
Max Temp	-0.16	0.07	-2.39	**0.017**					
Min Temp						-0.09	0.06	-1.67	0.095
Random Parts									
Number of males				29					29
Number of obs.				260					260

FIGURES
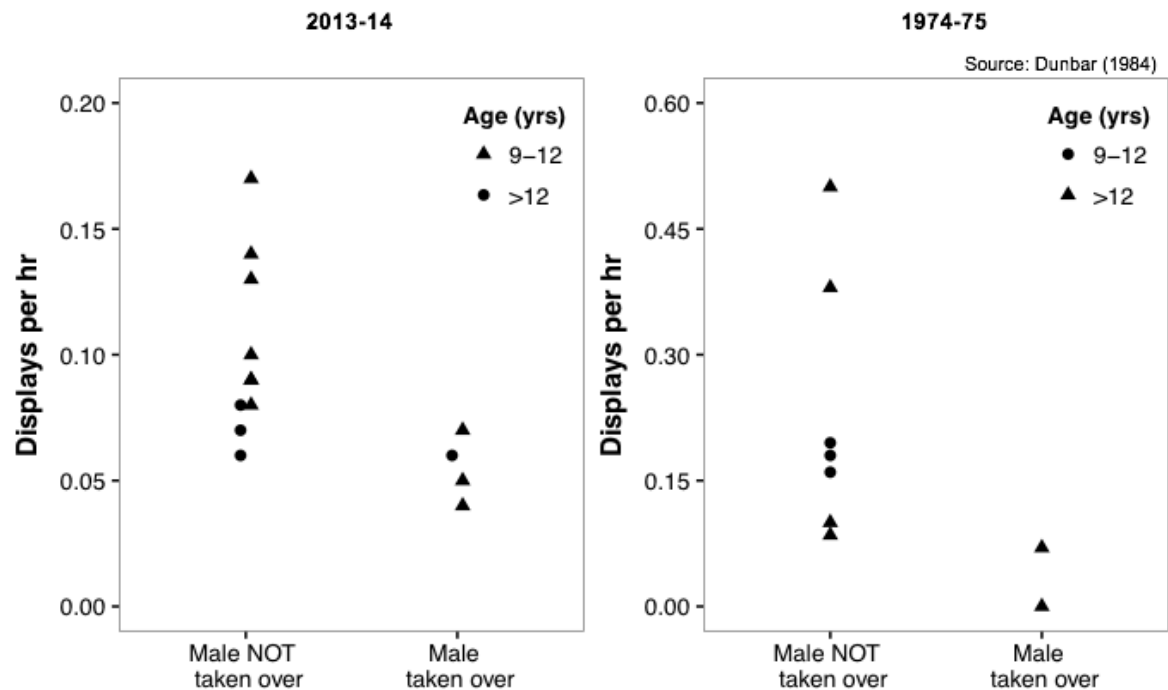
Figure 2.1. Display rate for leader males that remained leader (not taken over) and leader males that were taken over.(a) Data from this study, based on 436 observation hours where bachelors were present. (b) Data reproduced from Dunbar 1984 (Figure 66, pg 180), based on approximately 154 observation hours spent with units (not time with bachelors). Note that the y-axes are different scales for the two datasets, due to the difference of how rate was calculated. Both datasets demonstrate that males NOT taken over produce displays at higher rates. Circles represent prime-aged leader males (9-12 years) and triangles represent older leader males (>12 years) (see Beehner et al., 2015 for more details on age estimates).

Response Variable: Male displays per month
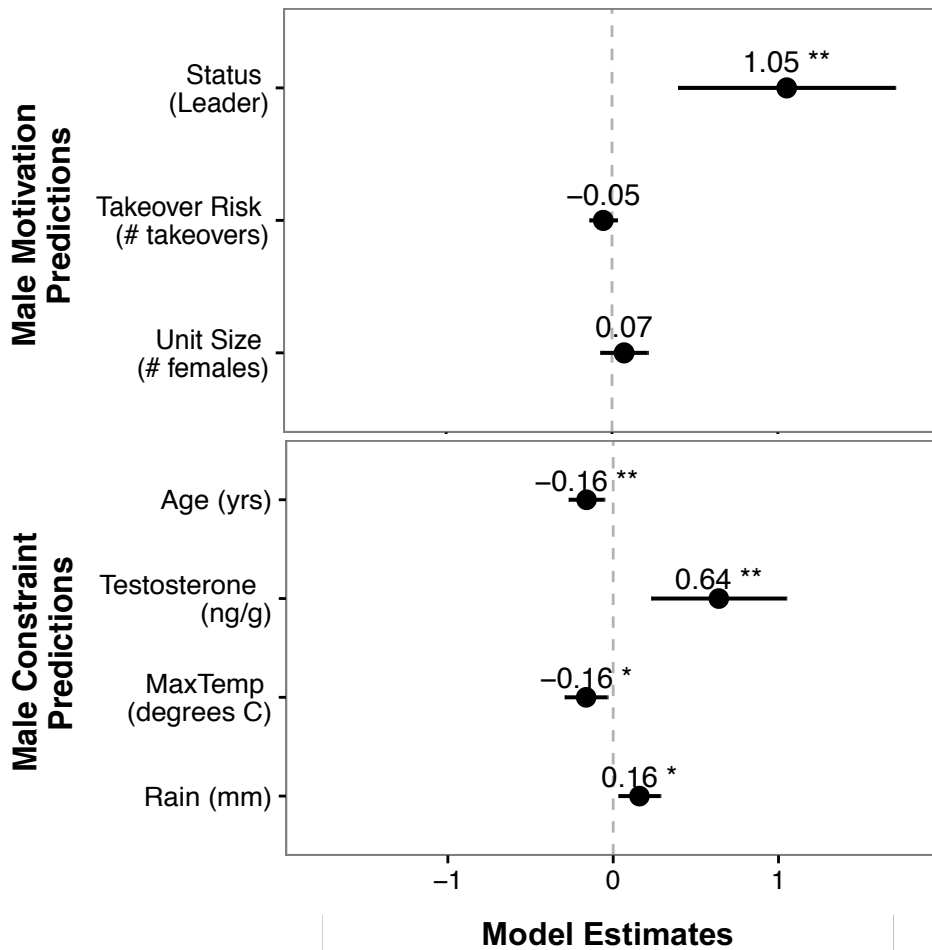
Figure 2.2. Model estimates +/- SEM for full model GLMM results for model including max temp. Estimates show the effects on how often males display in a given month (controlling for hours spent with bachelors). All variables were included in the same model. We have separated model estimate results to highlight the variables of interest for each set of predictions. *, **, *** note significance at 0.5, 0.01, and <0.001 respectively.
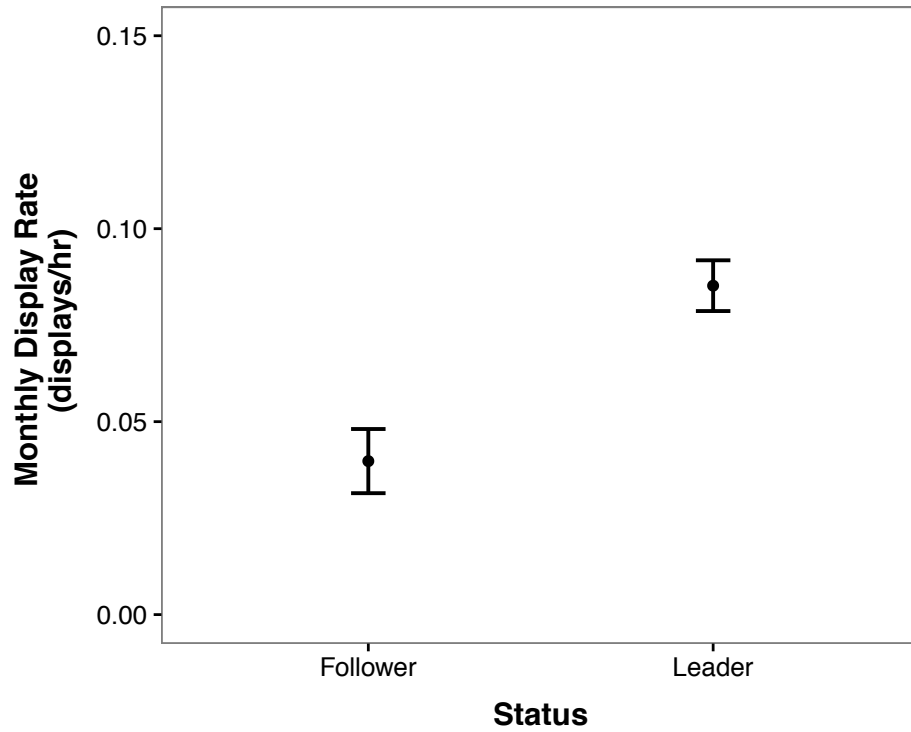
Figure 2.3. Status difference in monthly display rate. Leader males display more often than follower males. Error bars represent +/- SE.
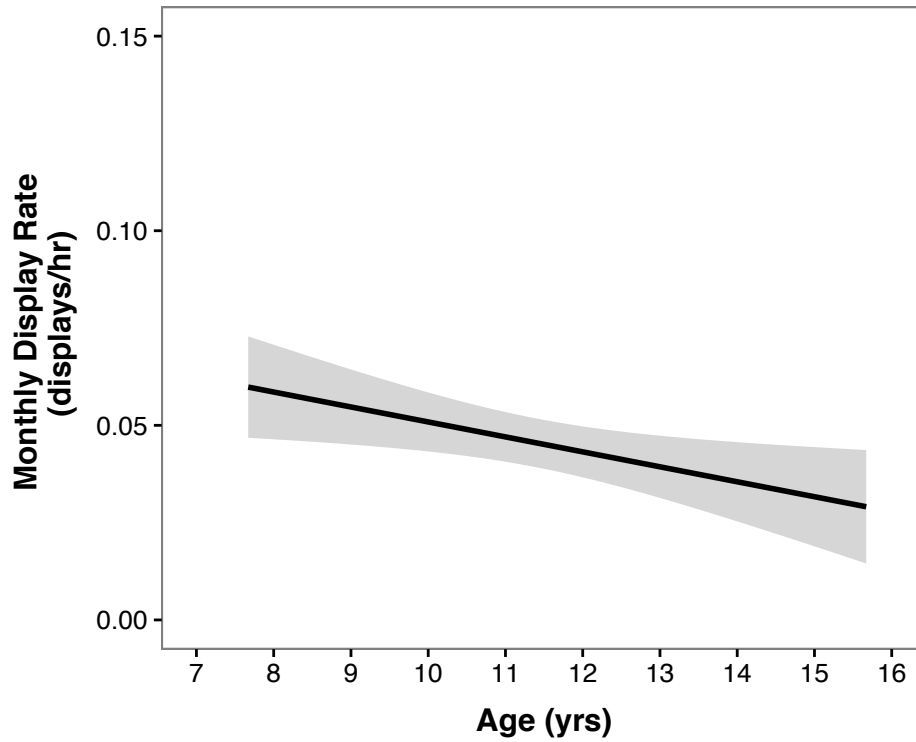
Figure 2.4. Age-based changes in month display rate. Younger males display more often than older males. Shaded area represents +/- SE.
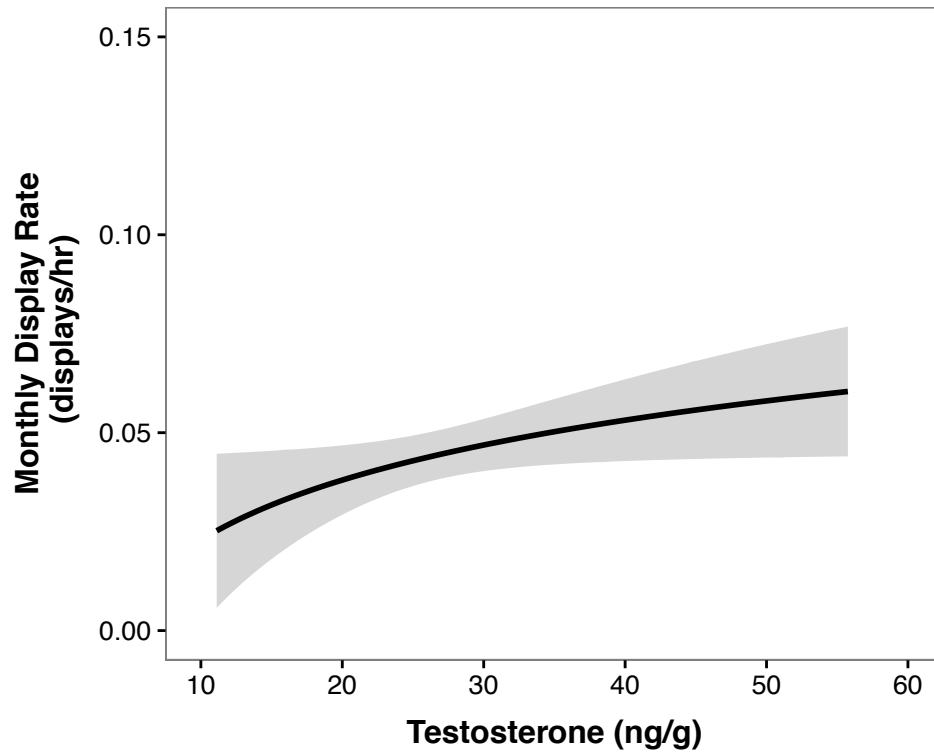
Figure 2.5. Average monthly testosterone and display rate. Males with higher testosterone displayed more often. Shaded area +/- SE.
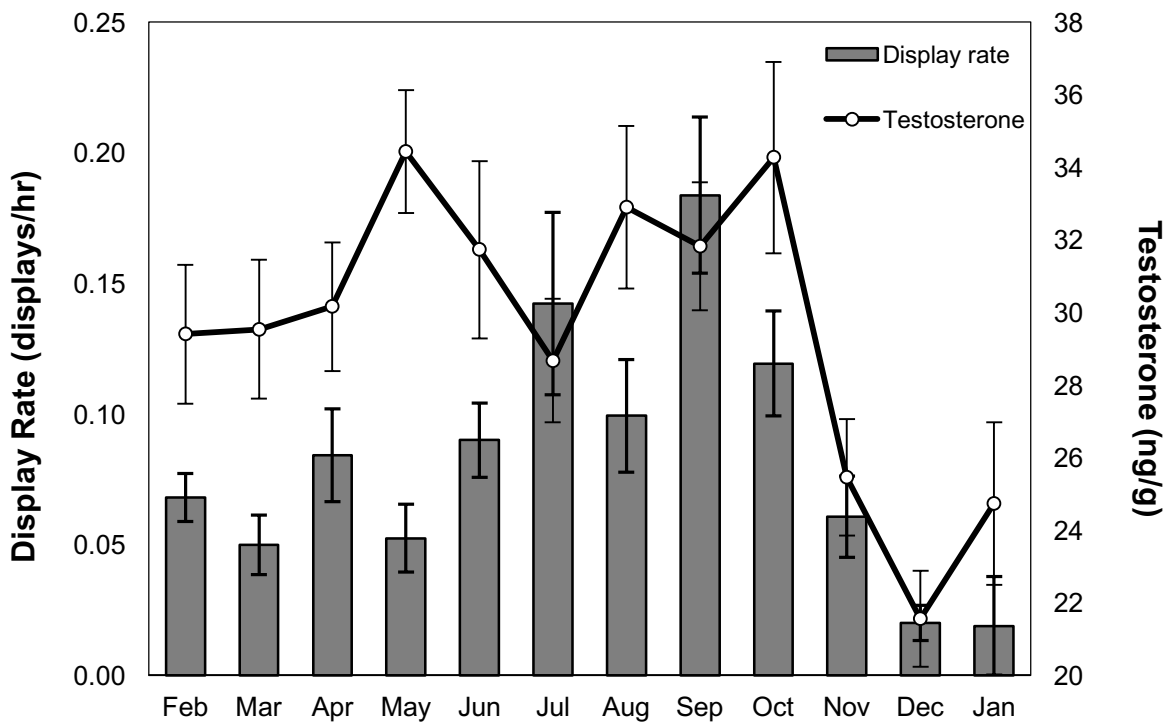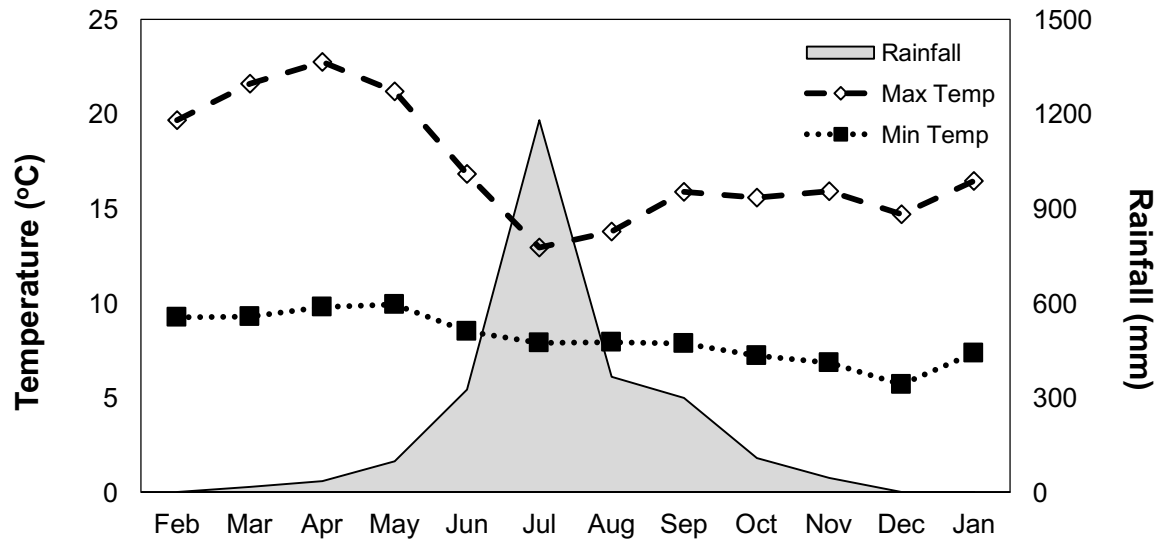
Figure 2.6. Monthly changes in weather (Fig 2a), average display rate (+/- SEM) and average testosterone (+/- SEM; Fig 2b) for leader males from February 2013- January 2014. Males display more often during the wet season (Jun-Sep) months when rainfall is high and max temp is low. Testosterone also increase in the wet season months.

CHAPTER 3

ACOUSTIC AND TEMPORAL VARIATION IN GELADA LOUD CALLS

ADVERTISE MALE QUALITY

INTRODUCTION

In many species of birds, amphibians, and mammals, individuals make

reproductive decisions based on information gleaned from vocalizations (e.g., red

deer, *Cervus elaphus*: Reby et al. 2005; grey treefrog, *Hyla chrysoscelis*:

Gerhardt et al. 2000; red grouse, *Lagopus lagopus scoticus*: Mougeot et al.

2004). Vocalizations can function as *quality signals* (Zahavi 1975; Vehrencamp

2000) if there is an associated cost or constraint on vocal production that

prevents low-quality individuals from producing a strong acoustic signal (e.g.,

nightingales, *Luscinia megarhynchos,* Thomas 2002; canary, *Serinus canaria*,

Ward et al., 2003; bottlenose dolphin, *Tursiops truncates*, Holt et al., 2015).

Acoustic signals can function in two distinct contexts related to sexual-selection –

mate choice by signaling individual quality to females (e.g., red deer, *Cervus

elaphus*, McComb 1991; grey treefrog, *Hyla versicolor*, Gerhardt et al. 2000; red

grouse, *Lagopus lagopus scoticus*, Mougeot et al. 2004) or male-male

competition by signaling competitive ability to rivals (e.g. Blanchard's cricket frog,

Acris crepitans blanchardi, Wagner 1992; red deer, Reby et al. 2005). For

example, in primates, adult males produce long-distance vocalizations (i.e., "loud

calls") that may be used in both contexts (e.g., Kitchen et al. 2003; Fischer et al. 2004; Delgado 2006). Potential rivals or mates likely attend to loud calls because, in addition to providing information about caller identity (e.g., Erb et al. 2013; Wich et al., 2003; Fischer et al., 2002; Spillmann et al., 2010; Bouchet et al., 2012; Barelli et al., 2013; Neumann et al., 2010) and context (e.g., Fischer et al., 2002; Wich et al., 2003), acoustic properties of the call often correlate with a caller's body size (e.g., Japanese macaques, *Macaca fuscata*, Inoue 1988; Rhesus macaques, *Macaca mulatta*, Fitch 1997; hamadrayas baboons, *Papio hamadryas*, Pfefferle & Fischer 2006; chacma baboons, *Papio ursinus*, Kitchen et al. 2003), age (e.g., chacma baboons, Kitchen et al., 2003, Fischer et al. 2002, Fischer et al., 2004; pig-tailed langur, *Simias concolor*, Erb et al., 2013; Thomas langurs, *Presbytis thomasi*, Wich et al. 2003; gibbons, *Hylobates lar*, Barelli et al., 2013), current condition (i.e., exhaustion; e.g., chacma baboons, Fischer et al., 2004; simakobus, Erb et al., 2013), and dominance rank (e.g., chimpanzees, *Pan troglodytes,* Riede et al. 2007; Thomas langurs, Wich et al. 2003; crested macaques, *Macaca nigra*, Neumann et al., 2010; chacma baboons, Kitchen et al., 2003, Fischer et al., 2004).

Despite a long history of research on sexually-selected vocalizations in primates, several questions remain. First, although many primate species are known to emit loud calls, it is not clear how many of these actually function in mate selection or rival assessment. Unlike avian and amphibian taxa that depend heavily on vocal signals, the vast majority of primate species rely on individual recognition and social knowledge when making reproductive choices (Tomasello

& Call 1997; Bergman & Sheehan 2013). Thus, for primates that live in relatively small, stable, social groups, loud calls may function as a means to obtain information about caller *identity* rather than the condition or fighting ability of the caller. However, individual recognition likely has a reduced role in large primate groups where recognition of every group member may not be possible (e.g., geladas, *Theropithecus gelada*, Bergman 2010). Moreover, large primate societies (where individual recognition is expected to be low) are exactly the situations where we expect selection to favor the evolution of loud calls to function as quality signals. In the absence of individual recognition, loud calls can allow conspecifics to quickly assess the relative condition of an unknown rival or the quality of a potential mate.

Second, we have yet to establish if there are universal indicators of strength or high-quality in vocal signals across primates. Some acoustic features, particularly those relating to body size, should be similar across primate species. Yet, we lack the comparative data to assess if there are any similarities in how loud calls convey information about identity, current condition, or dominance rank across closely related species. Currently, we have detailed acoustic analyses (e.g., spectral analysis) for only a handful of primate species-specific loud calls (langurs, Erb et al., 2013; sportive lemurs, *Lepilemur ssp.*, Méndez-Cárdenas et al., 2008, titi monkeys, *Callicebus nigrifrons,* Caselli et al., 2014), and we have even fewer from species where loud calls may function in direct assessment (chacma baboons, Kitchen et al. 2003, Fischer et al., 2004; and Thomas langurs, Wich et al., 2003). There are some similarities in properties of vocal signals

across species; for example, call duration and calling rates are known to decline as a male fatigues (Fischer et al., 2004; Erb et al., 2013). Yet, for the most part, vocal features show variation across species. For example, high-ranking chacma baboons produce relatively high frequency calls (Fischer et al., 2004), while high-ranking crested macaques produce low frequency calls (Neumann et al., 2010). Whether these differences are species-specific or context-specific remain unknown.

Here, we seek to broaden our understanding of the features and function of primate loud calls by examining the loud calls of male geladas. Specifically, we test whether variation in acoustic and temporal measures of their calls has the potential to function as an honest indicator of a male's quality. Note that throughout this manuscript we will not be able to adequately distinguish true quality (i.e., genetic quality) from condition (e.g., current energetic/health condition), and thus we use this term loosely to encompass both possibilities. Geladas are well suited for studies of quality signals in primates for two reasons. First, the gelada social system may have favored the evolution of such signals for direct assessment (Bergman & Sheehan 2013; Bergman et al., 2010). Geladas live in extremely large, multi-level, fluid societies comprising dozens of reproductive units. Each unit consists of one dominant 'leader male', several adult females, their offspring, and occasionally one or more subordinate 'follower males' (Dunbar 1983; Dunbar and Dunbar 1975; Kawai et al. 1983; Mori 1979a). These units are nested together within a foraging unit known as a band and several bands may come together to form herds as large as 1200 individuals

(Dunbar 1983; Kawai *et al.* 1983; Snyder-Mackler et al. 2014). In the largest aggregations of gelada society, individual recognition plays a reduced role compared to smaller primate groups (Bergman et al., 2010; le Roux & Bergman 2012). Second, reproductive competition between gelada males consists of extremely costly, winner-take-all contests between leader males and pre-reproductive 'bachelor males' (Dunbar & Dunbar 1975). These contests favor bachelors that challenge the leader males that are either poor condition or low quality; and that, presumably, are unable to advertise high quality.

One avenue for advertising quality is for a leader male to engage in a highly ritualized loud-call display that allows bachelor males to assess his strength (Dunbar 1984). A display begins when the leader male approaches, threatens, and solicits a chase from a group of bachelor males (Dunbar 1984). During these displays, males run, throw rocks, climb trees and shake branches while simultaneously uttering a series of high-pitched, two-phase loud calls ('ee-yow' calls; Dunbar and Dunbar 1975). For geladas, loud calls are always given within a bout (2-8 calls per bout), and a male can give multiple bouts during the same display (Figure 3.1a). Loud calls are often "contagious" with multiple males sequentially engaging the bachelors in a chase prior to calling. Although bachelors also vocalize during these displays (i.e., "how bark"), leader males (and sometimes subordinate follower males predominantly) utter the two-syllable loud calls during these chases. Loud calls displays occur on a daily basis when bachelors are present and multiple display events per day is common (Benitez, unpublished data).

Given the active nature of these display, we expect that loud calls with certain acoustic and temporal features may function as a reliable indicator of male stamina and competitive ability (cf. Kitchen *et al.* 2003). Previous research on this population of geladas has shown that bachelor males pay attention to loud calls significantly more than other salient vocal cues (i.e., copulation calls) suggesting that bachelors may extract information about the condition of the sender from the acoustic properties of these calls (le Roux & Bergman 2012). To test this hypothesis, we looked for variation in the acoustic properties of loud calls in relation to a male's quality.

Specifically, we examined 12 call parameters and 3 bout parameters (see Table 1) that have been previously shown to vary due to individual or condition (e.g., age, status, and stamina) in chacma baboons (Fischer et al., 2004). There are remarkable similarities between the loud calls of geladas and baboons (i.e., wahoos) in both delivery and context. Loud calls in both species consist of several bouts of 2 syllable calls predominately given by males during chases with rivals (Hall and DeVore, 1965, Fischer et al., 2002, Dunbar 1984, Aich et al., 1990). Similar to the contest wahoos of baboons, gelada loud calls are only given during aggressive encounters with adult males (Dunbar 1984). Much like this parallel study in baboons, we expected to identify several acoustic features of gelada loud calls that accompany a male's condition.

If loud calls are honest signals of a male's competitive ability in geladas, we expect acoustic features to vary among individual, age, status, and exhaustion. First, we investigated which acoustic parameters varied between

individuals. We expected significant individual differences in one or more acoustic measures, mainly fundamental frequency and peak frequency (i.e. frequency with the greatest amplitude value), because these two were found to differ with condition in chacma baboons (Fischer et al., 2002) and simakobu colobines (Erb et al., 2013). Second, we examined acoustic differences in calls due to age (adolescent, mid-prime, and late- prime males). Due to difference in overall body size between adolescent and prime aged males (Ey et al., 2007), we expected calls to vary with (and thus potentially convey information about) the relative age of the caller. Specifically, we predicted that prime aged males, both mid- and late prime, would produce calls with lower frequency measures than adolescents due to difference in the length or development of the vocal tract (Fitch & Hauser 2002). In addition, since temporal features of calls can vary with lung capacity, and the size of the lungs is closely related to body size (Fitch & Hauser 2002), we expected prime aged males to produce longer calls and/or more calls per bout than adolescent males (cf. Kitchen et al., 2003). Third, we examined acoustic differences in relation to status. Similar to Chapter 2, we examine status qualitatively (between leaders and followers) and quantitatively (for leaders with different number of females). We broadly use the term "status" to refer to these qualitative and quantitative differences in mating opportunities. We expect that high-status males will produce acoustically distinct calls from low-status males. Fourth, we tested whether call features changed during chase displays, presumably due to exhaustion (i.e., by comparing calls from the beginning of a bout and/or display to calls from the end of a bout and/or display

from the same male). Based on the assumption that loud calls are energetically costly to produce, we expected that only males in the best physical condition would have the stamina and strength to produce certain acoustic properties. Thus, we expected the calls of leader males to differ in both acoustic and temporal measures from those of follower males and that similar acoustic features will degrade across a long chase event, presumably as a male fatigues.

METHODS

Study Site and Subjects

Data were collected from a population of wild geladas living in the Simien Mountains National Park, Ethiopia. The University of Michigan Gelada Research project has been collecting long-term behavioral, demographic, and hormonal data on this population since January 2006. For this study, we collected vocalizations opportunistically from 79 males (29 adolescents, 50 adults) from April 2008-December 2013. All males were individually recognized and habituated to observers on foot.

Age and Status

For all males in the study, age was estimated to the nearest half year based on secondary sexual characteristics such as canine eruption, physical size, pelage coloration, and cape length (Dunbar & Dunbar, 1975; Beehner et al., 2015). For age, we classified males as *adolescents* (<8y), *mid-prime adults* (8-12y) or *late-prime adults* (>12y). For unit males, status categories (leader,

follower) were determined by behavioral observations of group membership and dyadic dominance interactions. Leader males include all males with unlimited reproductive access to the females in the unit. Follower males include additional adult males in a unit that are subordinate to the leader male. Follower males are typically former unit leaders but can be young males that submissively join and remain with a unit (Mori 1979b).

In addition to the broad categories of male status, we generated a more fine-tuned quantitative measure of male status for leader males by recording the number of adult females in each unit. We considered females adults when they began to exhibit sexual swellings, suggesting that they had reached sexual maturity.

Acoustic Analyses

We opportunistically recorded loud calls from all males across the study period. We recorded loud calls using a Sennheiser ME-66 directional microphone and a Marantz PMD 660 digital recorder (sampling rate 44.1 kHz and 16-bit resolution). At the time of the recording, we noted (1) the identity of the caller, (2) the activity of male while calling (e.g., approach, chase, or fight), (3) the position of the bout within the chase event (e.g., first, second, etc.), and (4) the position of the call within the bout. Prior to analysis, we audibly and visually inspected calls using Avisoft SASLab Pro (Avisoft Bioacoustics, Berlin, Germany) acoustic software. We generated spectrograms in Avisoft with a fast Fourier transformation size of 1024 points (frequency range= 22 kHZ; frequency

resolution= 43 Hz, bandwidth=56 Hz, Frame size=100%, Window=Hamming;

temporal resolution= 2.903ms, overlap=87.5%). We selected only complete

recordings that were devoid of background noise (e.g., bird song) and

interruptions (e.g., calls from other individuals). We accumulated 785 loud call

recordings (across 272 bouts) of sufficient quality from 79 males for acoustic

analysis.

We conducted acoustic analyses at the level of the bout (*bout analysis*)

and at the level of the individual call (*call analysis*). For the bout analysis, we

measured three bout parameters (Table 1, the *number of calls per bout*, the *call

interval*, and the bout *range in pitch*; Figure 3.1a). First, for each bout we

calculated *the number of calls* given per bout (range from 2-7). Second, we

calculated a mean *call interval* per bout. Intervals were measured from the end of

the 'yow' element of the previous call to the beginning of the 'ee' element of the

next call. Third, we calculated the *range in pitch* throughout the bout. For all calls

within the bout we measured the mean fundamental frequency (see below). We

then subtracted the call with the highest fundamental frequency (always the last

call in the bout) from the call with the lowest fundamental frequency (always the

first call in the bout) to measure vocal range in pitch throughout a bout.

For the call analysis, we submitted the spectrogram of the 'yow' element

(i.e., the predominant component of the call) of each call to a custom

software program (LMA) that extracts acoustic parameters from vocal signals

(Fischer et al., 2013) (Figure 3.1). In LMA, we examined the mean and maximum

values of five additional acoustic parameters related to frequency, energy, and

pitch (see Shrader & Hammerschmidt, 1997). First, we examined the first

dominant frequency band which is the lowest frequency band characterized by

amplitudes that exceed a given threshold (sum of means plus 1SD) as calculated

from the the adjacent frequency bins. In tonal calls, the lowest dominant

frequency band corresponds to the fundamental frequency. Second, we

examined the *peak frequency* of each call which is the frequency in each time

segment of the spectrogram that has the greatest amplitude value (i.e., the most

acoustic energy). Third, we measured the *distance between the 1st and 2nd*

dominant frequency band. Forth, we examined the *frequency range* for each call

which marks the first time the frequency amplitude exceeds a dynamic threshold

until the last time the frequency amplitude falls below this threshold (i.e., main

acoustic energy per time segment). Note that *frequency range* is a within call

measure *and range in pitch* (above) is a measure of vocal range throughout a

bout. Fifth, we assessed the *1st distribution of frequency amplitude* which is

measured by determining the frequency amplitudes across the spectrum for each

time segment. From these values, the frequency was calculated where the

distribution of frequency amplitude reached the first quartile (25%) of the total

distribution.

Lastly, we manually extracted the mean fundamental frequency (i.e.,

lowest frequency of a harmonic series) of each call by visually inspecting pitch

contour using PRAAT v. 5.0.29 (www.praat.org). The minimum and maximum

values for the fundamental frequency were set according to the pitch contour as

observed on the spectrogram. In total, our analysis consisted of 2 bout

parameters and 12 call parameters (Table 1).

In addition, we manually extracted the mean fundamental frequency (i.e.,
lowest frequency of a harmonic series) of each call by visually inspecting pitch
contour using PRAAT v. 5.0.29 (www.praat.org). The minimum and maximum
values for the fundamental frequency were set according to the pitch contour as
observed on the spectrogram. In total, we examine 12 call parameters (Table 1)
related to duration, frequency, energy, and pitch.

Data Analyses

Factor analysis. Prior to all analyses, we checked the distribution of each
parameter and, where necessary, we transformed the data to approximate a
normal distribution. Next, to remove redundancy between the acoustic
parameters (i.e., many of the acoustic properties were highly correlated), we ran
a factor analysis (FA) using all 12 call parameters. The FA was run in SPSS
using a varimax rotation. The two factors that emerged from this analysis (*factor
scores*) are listed in Table 2.

Individual differences. To test for differences between calls due to individual,
we used discriminant function analysis (DFA). DFA is commonly used in
behavioral and bioacoustics research to determine whether calls differ between
subjects, groups, and context (Mundry & Sommer, 2007). The benefit of DFA is
that it addresses how reliably groups can be distinguished and which acoustic

parameters are important in those classifications. However, DFA can be

inaccurate when using non-independent data (i.e., multiple calls from the same

individual to test group differences; Mundry & Sommer, 2007). To account for

non-independence, we subsequently ran a permuted discriminant function

analysis (pDFA) controlling for bout number using an R algorithm written by

Roger Mundry (Mundry & Sommer, 2007). *P*-values of the pDFA were based on

cross-validated calls and determined using 1,000 permutations into which the

original data were included as one permutation. To balance the variance in the

number of calls from each individual in the dataset, we used a subset of our data

for each DFA analysis. In the DFA data sets, we used only the first 3 calls / bout /

male to balance any acoustic changes due to the position of the call within the

bout. For individual differences, we conducted a DFA on calls collected from

prime aged males from which at least 13 calls were recorded (i.e. at least one

more than the number of acoustic parameters examined in the DFA). For the 7

males that fit this criterion, all had at least 18 calls of sufficient acoustic quality for

analysis. For males with more than 18 calls, we randomly selected 18 calls to

balance individual contribution (N=7, n=126 calls).

Age and Status. To investigate whether call and bout parameters varied in

relation to age and status, we constructed a series of linear mixed models

(LMMs). First, we compared calls of adolescent males (<8 yrs, N=29, n=84 calls),

mid-prime adult males (8-12 yrs, N=39, n=531 calls), and late-prime adult males

(>12 yrs, N=11, n=170 calls) to assess if age influenced the acoustic properties

of these calls. For call parameters, we used the factor scores from the FA as the dependent variables, *age* and *call position* (nested within bout) as fixed effects, and *caller* as a random effect. We included *call position* as a continuous predictor to control for variation in acoustic changes within a single bout.

We further examined the differences in bout parameters between adolescent, mid-prime, and late-prime male calls, by constructing three additional models with either *call interval*, *range in pitch*, or *number of calls* as dependent variables, *age* as a fixed effect and *bout id* and *caller* as random effects (adolescent, n=36 bouts; mid-prime, n=188 bouts; late-prime, n=48 bouts). For *range in pitch*, we only included bouts from males in which all calls within the bout were of sufficient quality to be analyzed (Table 1; N=57, n=218 bouts). For *number of calls per bout,* we conducted a general linear mixed model with a negative binomial distribution.

Second, to investigate whether the acoustic properties of calls differed due to status, we constructed five additional LMMs on a subset of the data that included *only* calls from adult males (leaders, N=33, n=552 calls; followers, N=17, n=114 calls). For call parameters, we constructed two LMMs, one for each factor score from the FA analysis as the dependent variable and status (leader or follower) and number of females as a predictor variable. We controlled for *age* (fixed effect), call position nested within bout (fixed effect), and *caller id* (random effect). To examine the effect of status on bout parameters, we constructed three additional models with each bout parameter as the dependent variable, *status, number of female,* and *age* as a fixed effects, and *bout id* and *caller* as random

effects (leaders, n=204 bouts; followers, n=32 bouts).

Exhaustion. To evaluate differences in loud calls due to exhaustion, we conducted a pair-wise comparison on all males from whom we had recorded at least three consecutive bouts during an observed chase event (N=10). For each male, we compared the first call given during the first bout to the first call given during the last bout of a display (n=20 calls). We used a non-parametric exact probability paired t-test (Wilcoxon Signed Rank Test) due to our small sample size (Mundry & Fischer, 1998). We expected that acoustic and/or temporal features of calls would degrade as a male fatigues during a chase event. For each male and for each chase event, we compared the factor scores of calls given during the first bout with the factor scores of calls given during the last bout. Note that these calls are from the same male for the same chase event. We limited our analysis to the first call within the bout to control for call position. In addition, we compared between the first and last bout of a chase event the *number of calls* given per bout, the *range in bout*, and the *call interval*.

All models were fitted using a Gaussian error function. We visually inspected each model using a Q-Q plot, histogram of residuals, and scatterplot of fitted versus residual values. Residual values for all models were normally distributed. All models were conducted in R v.3.2.0 (R Core Team, 2015) using the function 'lmer' in the lme4 packages v.1.1-11 (Bates et al., 2015). The DFA and Wilcoxon Signed Rank Test were conducted in SPSS v.23.0 (IBM SPSS Statistics, 2015) while the pDFAs were run in R using an algorithm written by

Roger Mundry.

RESULTS

Factor analysis

The factor analysis resulted in two factors with Eigenvalues >1 together explaining 73.6% of the total variance. All spectral parameters measured showed high loadings on Factor 1 which explained 63.2% of the variance. Factor 2 showed high loadings on 'ee' and 'yow' duration only and explained and additional 10.4% of the variance (Table 2). Based on the loadings of these parameters on the rotated components, we characterized and labeled Factor 1 as *spectral measures* and Factor 2 as *temporal measures*. In other words, a high score along Factor 1 / *spectral measures* indicates that calls have higher dominant frequency bands, greater distance between the 1st and 2nd dominant frequency bands, higher fundamental frequency, higher peak frequency, a greater range in pitch, and energy concentrated at higher frequencies. A high score in Factor 2 / *temporal measures* signifies longer 'ee' and 'yow' elements resulting in overall longer calls.

Individual differences

The DFA revealed one factor with Eigenvalues >1. This first function contributed to 54% of the variance and exhibited a high positive loading (>0.4) on four parameters (mean fundamental frequency, mean peak frequency, mean distribution of the 1st dominant frequency band, and mean 1st quartile energy).

The second function (Eigenvalue=0.7) contributed to 27.1% of the variance and exhibited a high absolute loading only on the duration of the 'yow' element. The results from the pDFA indicated that calls were significantly different between individuals, with 38.1% of cross-classified calls assigned correctly (P=0.001; 14% expected by chance alone)

Age and Status

The first set of LMMs revealed that both the position of the call within the bout and age influenced the acoustic properties of the calls. Specifically, we found that as throughout the loud call bout, calls increased in overall frequency (*spectral measures*: β=0.38, s.e.=0.02, P<0.001; Figure 3.2). However, we found no effect of call position on *temporal measures* (Table 3.3).

Adolescent males produce calls with higher *spectral measures* (Figure 3.3a) and shorter *temporal measures* (Figure 3.3b) than both mid-prime (*spectral measures*, β =-1.12, s.e.=0.18, P<0.001; *temporal measures*, β 0.51, s.e.=0.18, P=0.005; Table 3) and late-prime (*spectral measures*, β =-1.53, s.e.=0.20, P<0.001; *temporal measures*, β 0.82, s.e.=0.22, P<0.001) males. Within adult males, we found that late-prime males have calls with the lowest *spectral measures* (Mid- prime, β = 0.82, s.e.=0.13, P<0.001) but did not differ in *temporal measures*. We found no effect of age on any of the three bout parameters (Table 3.3)

Regardless of age, leader males produce calls that are lower in *spectral measures* (β =-0.61, s.e.=0.25, P<0.02; Figure 3.4a) and shorter in *temporal*

measures (β =-0.52, s.e.=0.24, *P*=0.004; Figure 3.4b) than follower males. In addition, leader males produced more calls per bout (β =1.32, s.e.=0.12, *P*=0.020; Figure 3.4c) and exhibited a greater range in pitch throughout a bout (β= 0.29, s.e.=0.10, *P*=0.007; Figure 3.4d) than follower males (Table 3.3). Call position within a bout was again a significant predictor of *spectral* (β= 0.37, s.e.=0.02, *P*<0.001) but not *temporal* measures in the status models (β= 0.01, s.e.=0.0, *P*=0.794).

Among leader males, males in units with more females produced calls with the lowest *spectral* measures (β =-0.11, s.e.=0.05, *P*=0.034; Figure 3.5a). We found no effect of number of females on *temporal measures* (β =-0.05, s.e.=0.04, *P*=0.260). We found that leaders with more females exhibited the greatest range in pitch throughout a bout (β= 0.04, s.e.=0.02, *P*=0.029; Figure 3.5b). We found no effect of number of females on number of calls per bout or call interval (Table 3.3)

Exhaustion

We found significant differences between the first and last bout of a chase event with respect to *spectral measures*, *temporal measures*, number of calls per bout, mean call interval (Table 3.3). Specifically, we found that as a male fatigued across the chase event, he produced calls with higher *spectral measures* (Wilcoxon Signed Rank Test; *T*=55, N=10, Ties=0, *P*<0.01; Figure 3.6a) and longer *temporal measures* (*T*=50, N=10, Ties=0, *P*=0.02; Figure 3.6b). In addition, males gave fewer calls per bout (*T*=28, N=7, Ties=3, *P*=0.02; Figure

3.6c) and had a longer interval between calls (T=47.5,N=10, Ties=0, P=0.04; Figure 3.6d) during the last rather than the first bout of the display. We found no difference in range in pitch (T=-1.27, N=10, Ties=0, P=0.2).

DISCUSSION

Our results are consistent with the hypothesis that loud calls are quality signals in male geladas. Gelada loud calls can reliably signal the sender's competitive ability because the highest quality males produced the strongest vocal signal. Specifically, dominant leader males – the only males with reproductive access to females – produced significantly more calls per bout, produced acoustically different calls that were lower in several frequency measures (e.g. peak frequency, quartile energy), and exhibited a greater vocal range (range in pitch throughout a bout) compared to subordinate follower males. Among leader males, we found that males with access to the largest unit of females produced the lowest frequency calls and the greater range in pitch throughout a bout. Similar acoustic "decay" was observed from prime aged to adolescent males and from "fresh" to "fatigued" adults suggesting that these acoustic features can reliably indicate male condition due to either physical constraints (e.g., body size) and/or energetic costs (e.g., stamina).

In birds, amphibians, and some mammalian species, several acoustic features, such as fundamental frequency (i.e., pitch), have been linked to variation in body size. Since fundamental frequency depends on the length and tension of the vocal folds, the longer the larynx, the lower the fundamental

frequency of the caller (e.g., Fitch & Hauser, 1995). Similar to what has been found in chacma baboons and other primates, in geladas the differences in body size across males also influenced acoustic features; adolescent males, with smaller body sizes, produced higher frequency calls than prime aged males. However, among a sample entirely of adults, body size alone cannot account for the differences in acoustic properties that are related to exhaustion –our analysis of exhaustion was within the same male across a single chase event. Thus, although we do not discount the effects of body size entirely, we are also confident that additional factors contribute to variance in the quality of loud calls.

Similar to previous research conducted on the loud calls of chacma baboons (Fischer et al., 2004), we found evidence that gelada loud calls were energetically costly to produce with calls exhibiting significant spectral and temporal changes as a male fatigued. However, unlike chacma baboons where fundamental frequency declined during a loud call display (Fischer et al., 2004), we found that in geladas the calls produced at the end of a chase event (during the last bout) were significantly *higher* in frequency measures, including fundamental frequency, than calls produced during the beginning of a chase event (during the first bout). As was found in chacma baboons, we found significant differences between the calls of high- and low-status males. In contrast to high-ranking male baboons, high-status male geladas produced calls that were *lower* in frequency measures. Moreover, gelada males with the longest tenures (i.e., late-prime leaders) produced the calls with the lowest frequency measures. Taken together, these results suggest that while frequency measures

may be important indicators of stamina and competitive ability in primate loud

calls, exactly *how* these acoustic features change in response to caller condition

may differ, even among closely related species.

Notably, the loud calls of male geladas exhibit a large and rapid increase in

frequency measures (e.g., 86% mean F0 change) throughout a bout, such that

call position had a significant effect on the acoustic properties measured.

Previous studies have shown slight decreases in frequency measures over

multiple seconds of repeated calling in other primates (chacma baboons, Fischer

et al., 2004; langurs; Erb et al., 2013), presumably due to lung deflation.

However, in geladas frequency measures increase throughout a bout, with

significant changes occurring between successive calls in a period as short as

0.7 seconds. These results suggest that *vocal range* may be a key factor for

distinguishing quality in gelada vocal displays. Recent work on the larynx and

vocal tract of cervids (e.g., red deer) has shown that for the same larynx to

produce calls with high and low fundamental frequencies requires an enormous

amount of muscular effort to stiffen the vocal ligaments and a large lung capacity

to overcome phonation threshold pressure (Titze and Riede, 2010). In other

words, showcasing vocal range may accurately represent an increase in lung

capacity, laryngeal control, and/or vocal muscular strength. We found that high-

status males produced the smallest range in fundamental frequency *within* each

call, but the largest range in fundamental frequency *between* calls across the

same bout. We suggest that, for geladas, a key feature of a high quality loud call

may be the ability to maintain a controlled, even tone for a single call while

simultaneously displaying a large range in fundamental frequency across the bout. Thus, for geladas, the entire bout, and not just the individual calls that make it up, may function as a quality signal. Similar findings have been documented in chimpanzees, where the highest-ranking males are those that can drive their voices to a higher maximum fundamental frequency during a pant hoot vocalization (Riede et al., 2007). An interesting avenue of future research might be to assess why showcasing vocal range may be important in some primates but not others.

In terms of temporal features, the number of calls given per bout appears to be a better indicator of male stamina than the duration of the calls within a bout. As males fatigued during a chase event, the number of calls per bout decreased, resulting in an overall shorter bout even though individual calls' duration increased. Furthermore, follower males had calls with longer temporal measures, but ultimately gave fewer calls per bout than the leader males. Given that these temporal features are likely constrained by lung capacity, a tradeoff may mediate how many calls an individual can produce and the duration of each of those calls. For geladas, producing more calls per bout may be more energetically taxing than investing in a longer call.

We also found differences in acoustic measures across individual males. Similar to other primate studies, fundamental frequency (e.g., Thomas langurs, Wich et al., 2002; chacma baboons, Fischer et al., 2002; simakobu, Erb et al., 2013; gibbons, Barelli et al., 2013), peak frequency (e.g., crested macaques, Neumann et al., 2010), the position of the first dominant frequency band (e.g,

chacma baboons, Fischer et al., 2002; crested macaques, Neumann et al., 2010), and first quartile energy (e.g., chacma baboons, Fischer at al., 2002) all contributed to the discrimination of individuals. Individual acoustic differences may allow bachelors to identify and monitor how often specific males engage in signaling displays. If males that signal less often are challenged more often (Dunbar 1984), then individual identification may be a necessary piece of information contained within each call. However, given that individual recognition is limited in this species (Bergman et al., 2010), bachelors may be attending to the acoustic cues related to call quality rather than individual identity. In other words, males that call more frequently may avoid getting replaced (Dunbar 1984) simply because they have higher quality calls.

One limitation of this study (which holds true for much of the research on primate loud calls) is that it is strictly correlational. To test the hypothesis that a loud call is indeed a sexually selected signal, a relationship between the quality of the caller and the quality of the call is *necessary* (otherwise listeners would not benefit from attending to such calls), but it is not *sufficient*. A relationship might be spurious or it might not be attended to by any potential receivers. However, the consistency of acoustic changes across age, fatigue, and status are evidence that the patterns vary in a predictable way. For the future, playback experiments are necessary to demonstrate that geladas attend to these differences in loud calls. Nevertheless, two lines of evidence suggest that loud calls in geladas likely function as signals in rival assessment. First, bachelor males pay close attention to signaling bouts between rival males (le Roux & Bergman, 2012) suggesting

that bachelors may be extracting information about male condition from these calls. Second, the males that were able to maintain their units the longest (arguably the highest quality males), produced the strongest acoustic signals, suggesting that males with high-quality calls are the most successful at deterring challenges from rivals. If this is the case, we then expect bachelor males to distinguish between high and low quality males based on the acoustic and temporal patterns described here.

TABLES

Table 3.1. Spectral (of 'yow' element) and temporal parameters analyzed in this study.

Bout Parameter	Definition
Number of calls per bout	Number of calls given per bout
Call interval *mean*	Mean duration (s) of intervals between calls within a bout
Range in pitch	Range in pitch (Hz), measured by the difference in mean fundamental frequency between the call with the lowest F0 (e.g. 1st call) and the call with the highest F0 (e.g. last call) during a bout

Call Parameters	Definition
Duration - 'ee'	Duration (s) of the 'ee' element of the call
Duration - 'yow'	Duration (s) of the 'yow' element of the call
Fundamental frequency *mean*	Mean frequency (Hz) of the first frequency band
Dominant frequency band *mean*	Mean frequency (Hz) of the dominant frequency band
Dominant frequency band *maximum*	Maximum frequency (Hz) of the dominant frequency band
Peak frequency *mean*	Mean peak frequency (Hz)
Peak frequency *maximum*	Maximum peak frequency (Hz)
Distance between frequency bands *mean*	Mean distance (Hz) between the first and second dominant frequency bands
Distance between frequency bands *maximum*	Maximum distance (Hz) between the first and second dominant frequency bands
Frequency range *mean*	Mean frequency range (Hz) within the call
1st quartile frequency *mean*	Mean frequency (Hz) under which 25% of the energy for each call is located
1st quartile frequency *maximum*	Maximum frequency (Hz) under which 25% of the energy for each call is located

Table 3.2. Results of the Factor Analysis (FA)

| Call parameters	Factor 1 *Spectral measures*	Factor 2 *Temporal measures*
Duration - 'ee'	-0.06	**0.77**
Duration - 'yow'	0.05	**0.78**
Fundamental frequency	**0.59**	-0.15
Dominant frequency band *mean*	**0.96**	0.00
Dominant frequency band *maximum*	**0.94**	0.04
Peak frequency *mean*	**0.96**	-0.01
Peak frequency *maximum*	**0.90**	0.04
Distance between frequency bands	**0.87**	0.02
Distance between frequency bands	**0.79**	0.05
Frequency range *mean*	**0.67**	-0.12
1st quartile frequency *mean*	**0.96**	0.00
1st quartile frequency *maximum*	**0.96**	0.52
Eigenvalues	*7.59*	*1.25*
Variance explained (%)	*63.20*	*10.40*

Table 3.3. Summary of changes in acoustic properties due to age, status, and exhaustion.

Parameters	Age 1 (mid-prime[1])	Age 2 (late-prime[1])	Status 1 (leader[2])	Status 2 (number of females)	Exhaustion (fresh[3])
Spectral Measures	**<0.001 ↓**	**<0.001 ↓**	**0.018 ↓**	**0.034 ↓**	**0.005 ↓**
Temporal Measures	**0.005 ↑**	**<0.001 ↑**	**0.003 ↓**	0.259	**0.022 ↓**
Number of calls	0.471	0.129	**0.020 ↑**	0.983	**0.008 ↑**
Call interval	0.502	0.750	0.897	0.071	**0.041 ↓**
Range in pitch	0.609	0.341	**0.007 ↑**	**0.029↑**	0.203

P-values are estimates derived from the LMMs[1,2] and the Wilcoxon signed-rank test[3.] Significant differences are highlighted in bold. The arrows show direction of changes for significance. Age differences are compared to adolescent male calls. Status differences are compared to follower male calls. Exhaustion values are a within individual analysis comparing calls from a male at the beginning of a display (fresh) to calls at the end of a display.

a
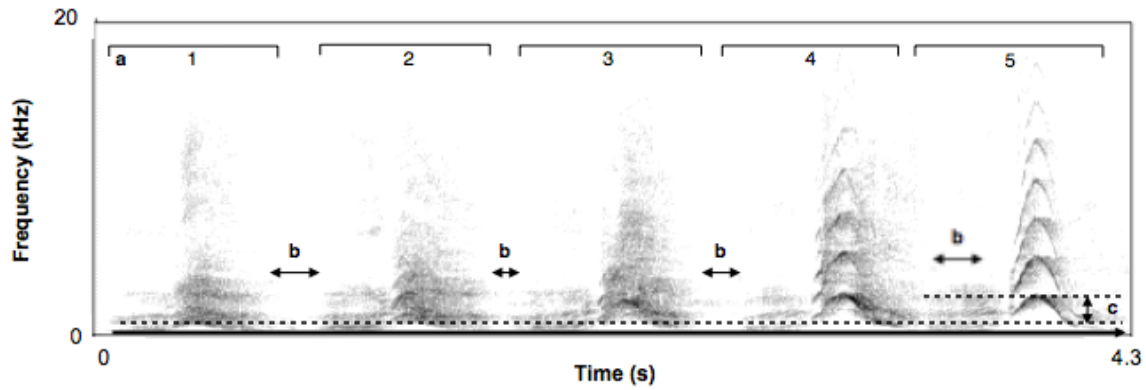
b
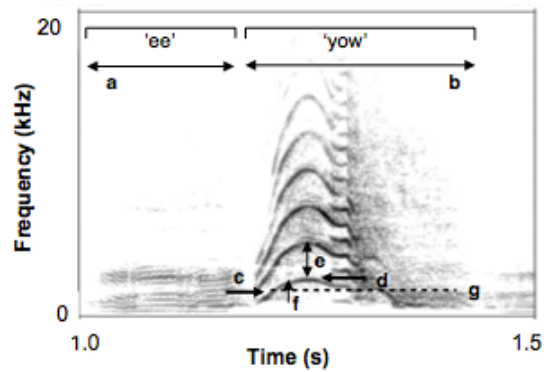
Figure 3.1. Spectrograms of gelada loud calls. Fig a depicts a bout containing five calls indicating the bout parameters measured in the acoustic analysis: a) number of calls per bout, b) inter-call interval (averaged in analysis), and c) range in pitch. Fig b depicts a gelada loud call indicating the call parameters measured in the acoustic analysis: a) 'ee' duration, b) 'yow' duration, c) fundamental frequency and dominant frequency band for this call, d) peak frequency, e) distance between frequency bands, f) frequency range, and g) 1st quartile frequency.
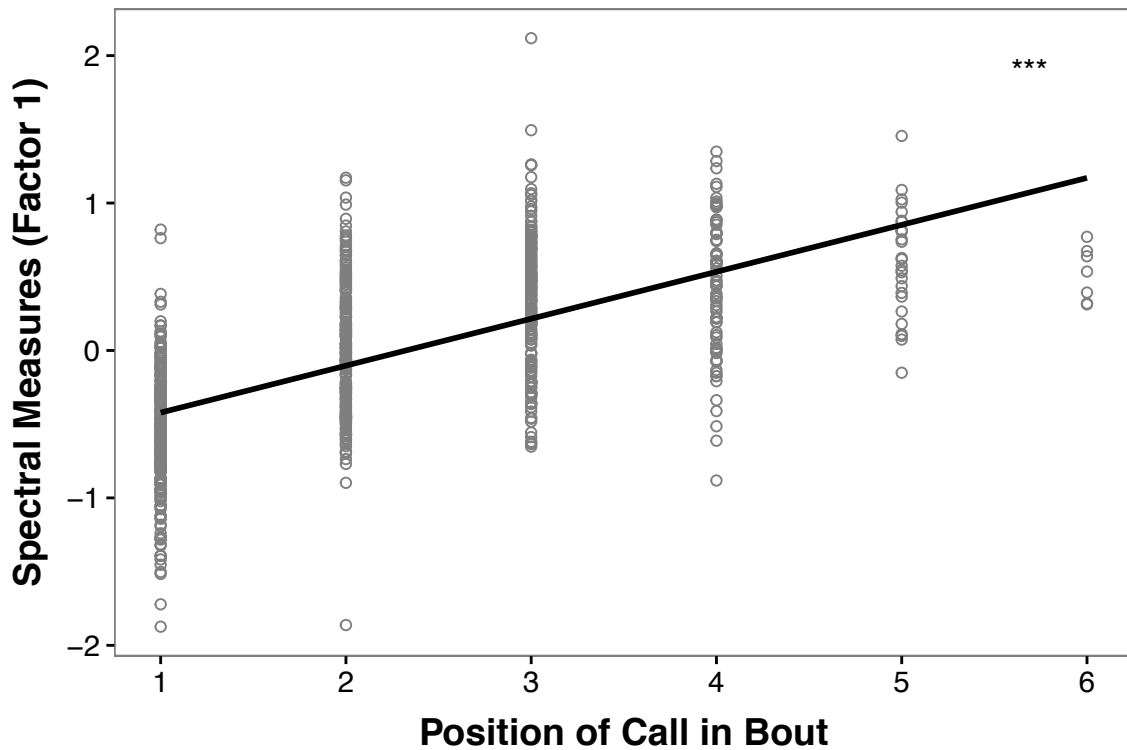
Figure 3.2. Variation in spectral measures (factor 1) due to the position of the call within a bout. A low score in factor one signifies a call that is lower in pitch, lower in peak frequency, has a lower dominance frequency band, energy concentrated at lower frequencies, a smaller range in pitch, and a smaller distance between frequency bands. Spectral measures significantly increased throughout a bout, p<0.001.
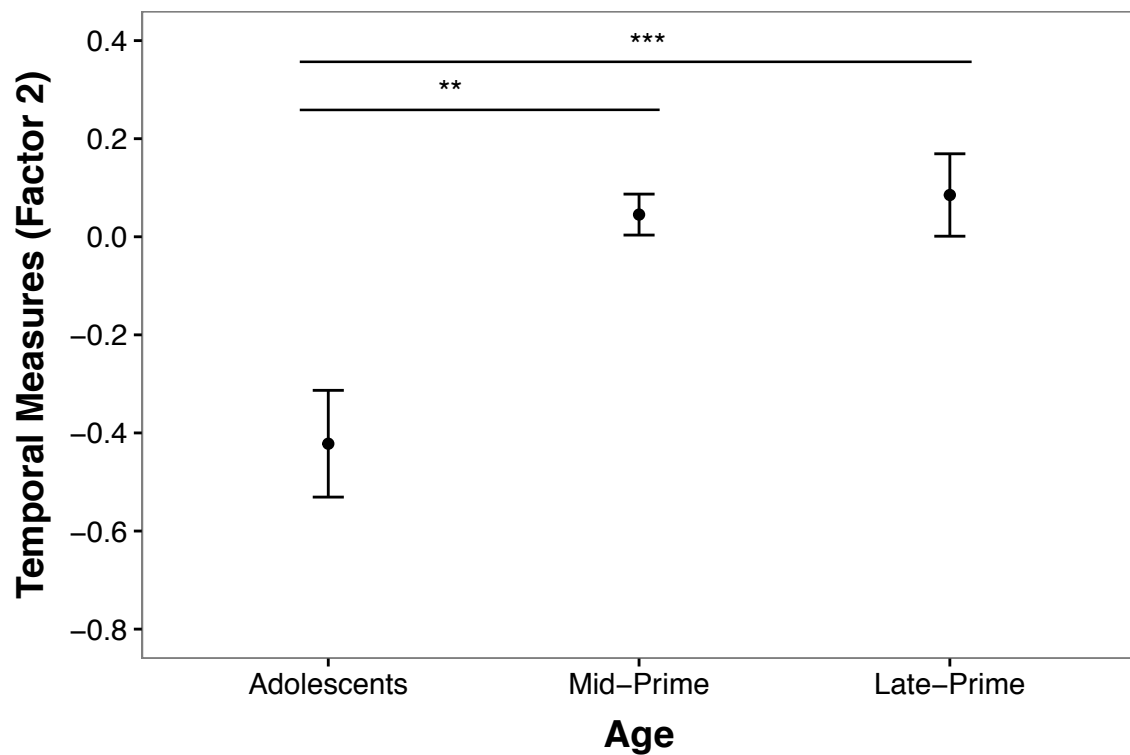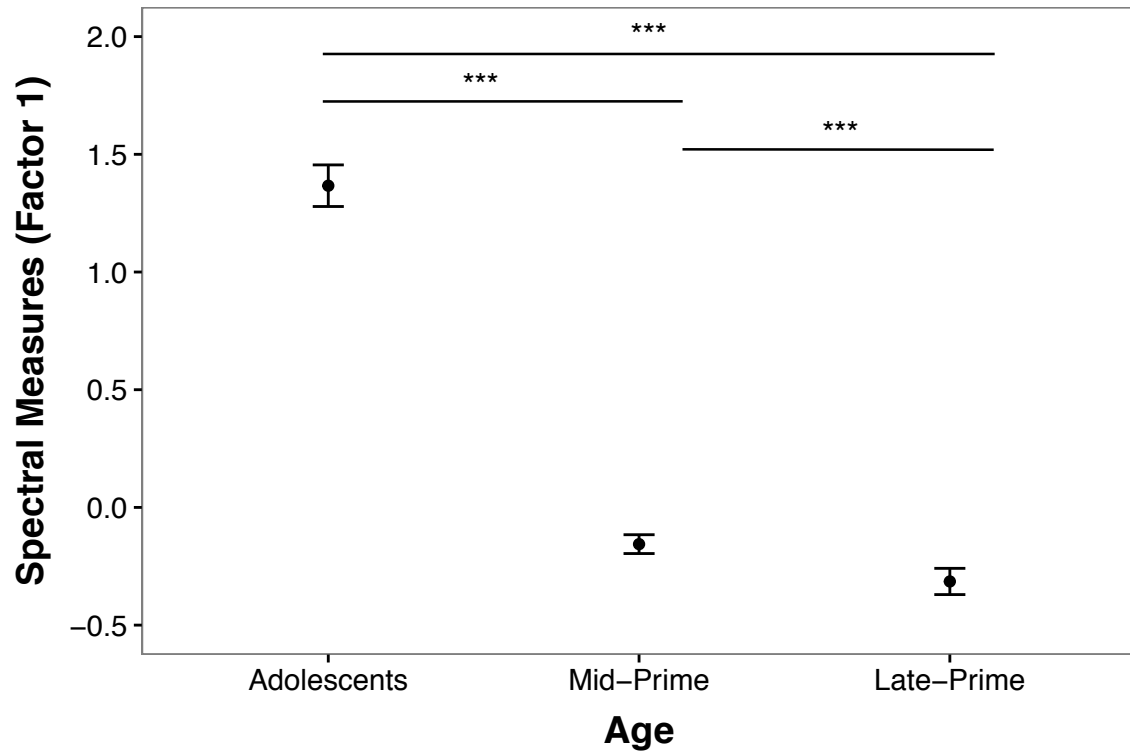
Figure 3.3. Age-based difference in spectral (Fig 3a) and temporal (Fig 3b) call parameters expressed as mean (± SEM) factor scores. ***Significant at p<0.001 and ** at p<0.01.

a
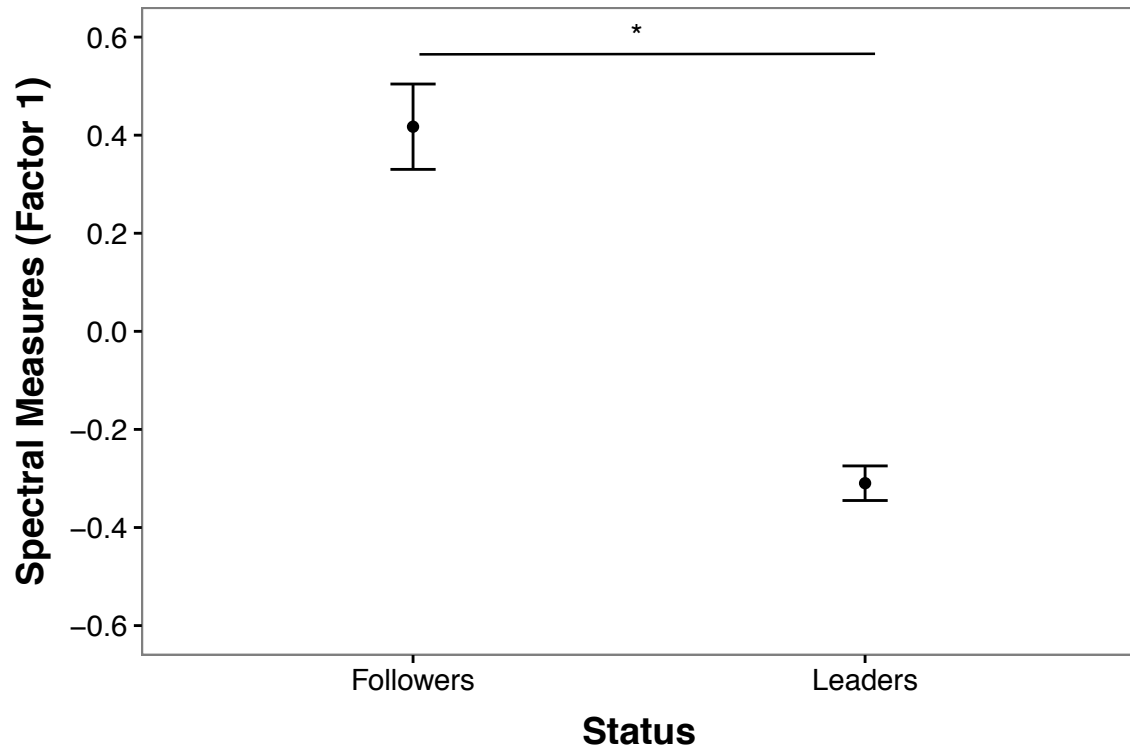
b
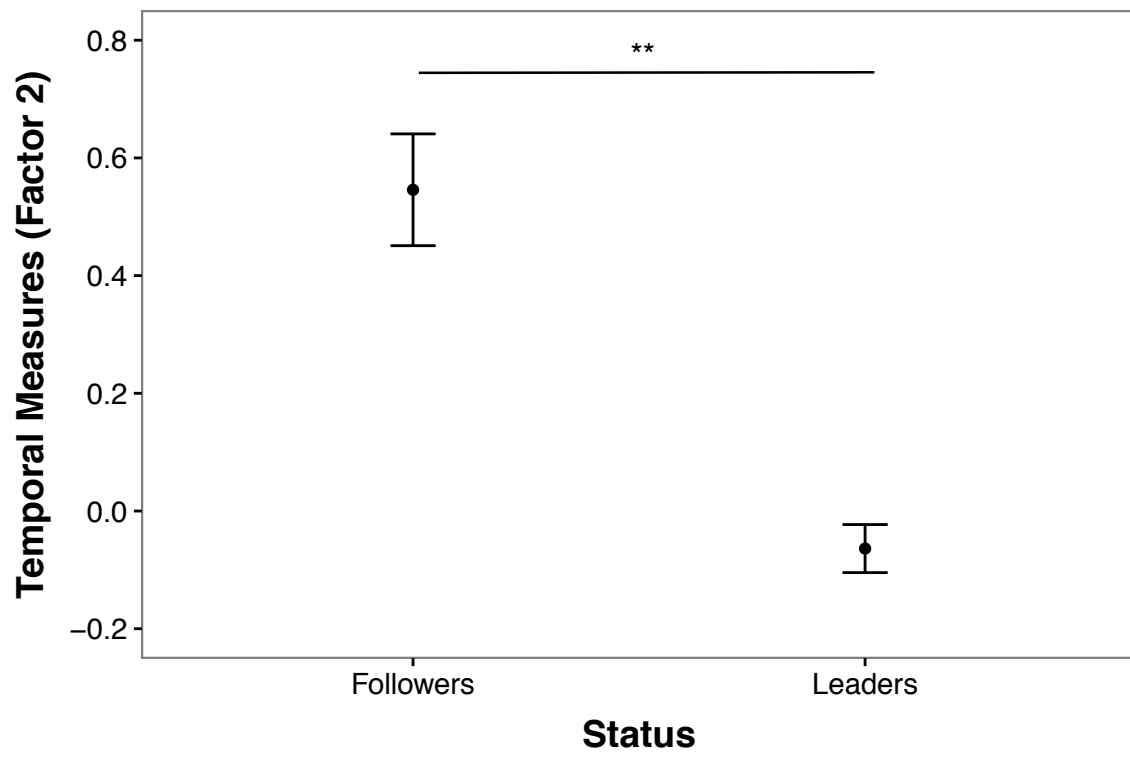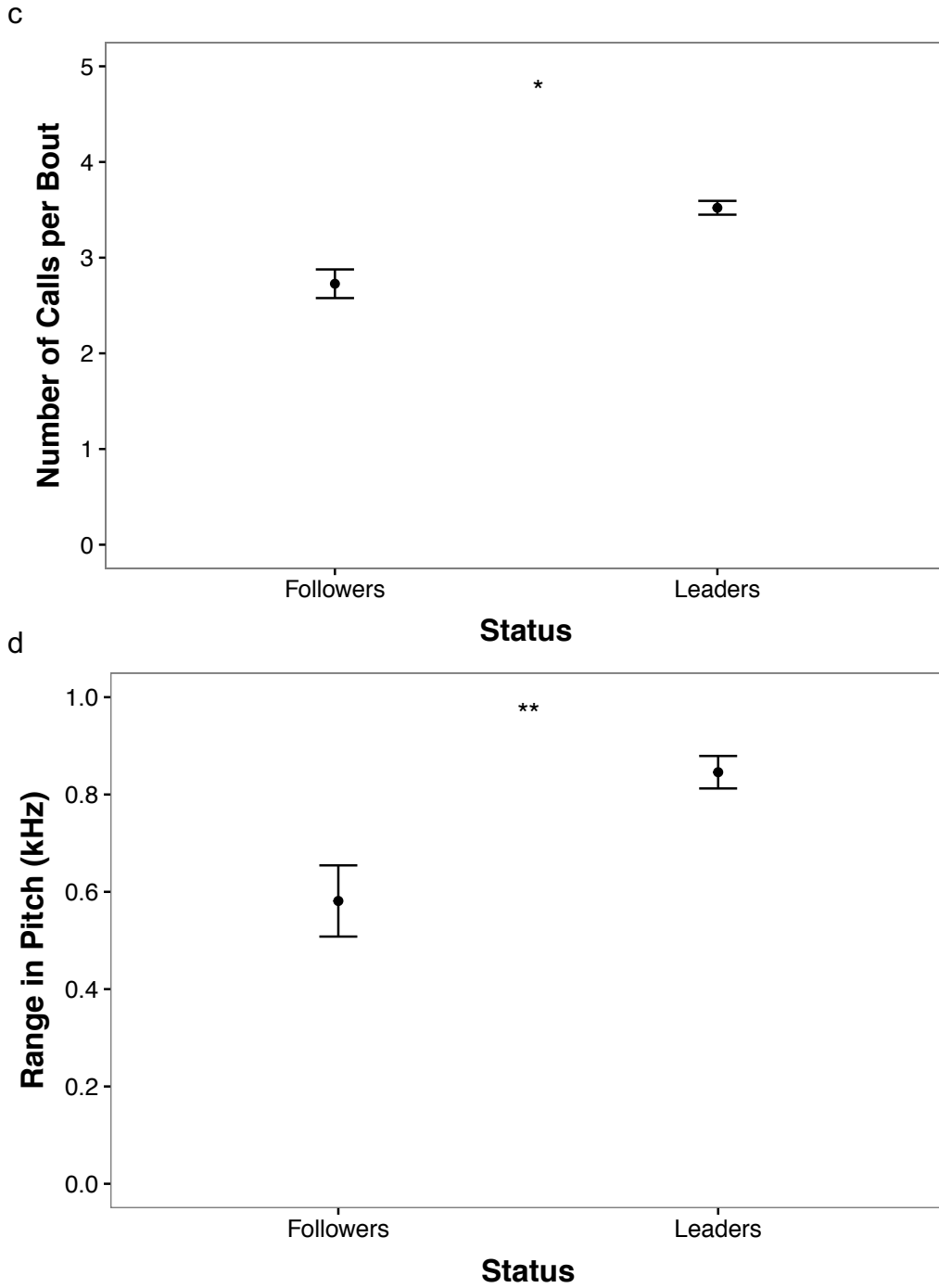
Figure 3.4. Status-based differences (± SEM) in spectral measures (a) and temporal measures (b) expressed as factor scores, the number of calls per bout (± SEM; c), and the range of pitch throughout the bout (± SEM d).** Significant at p<0.001.
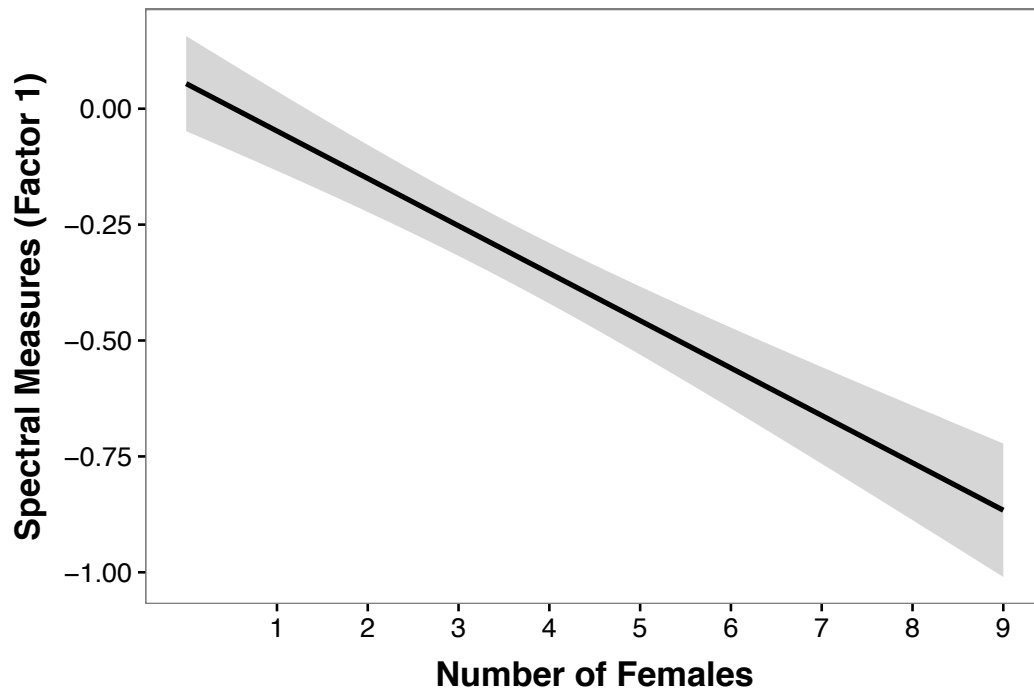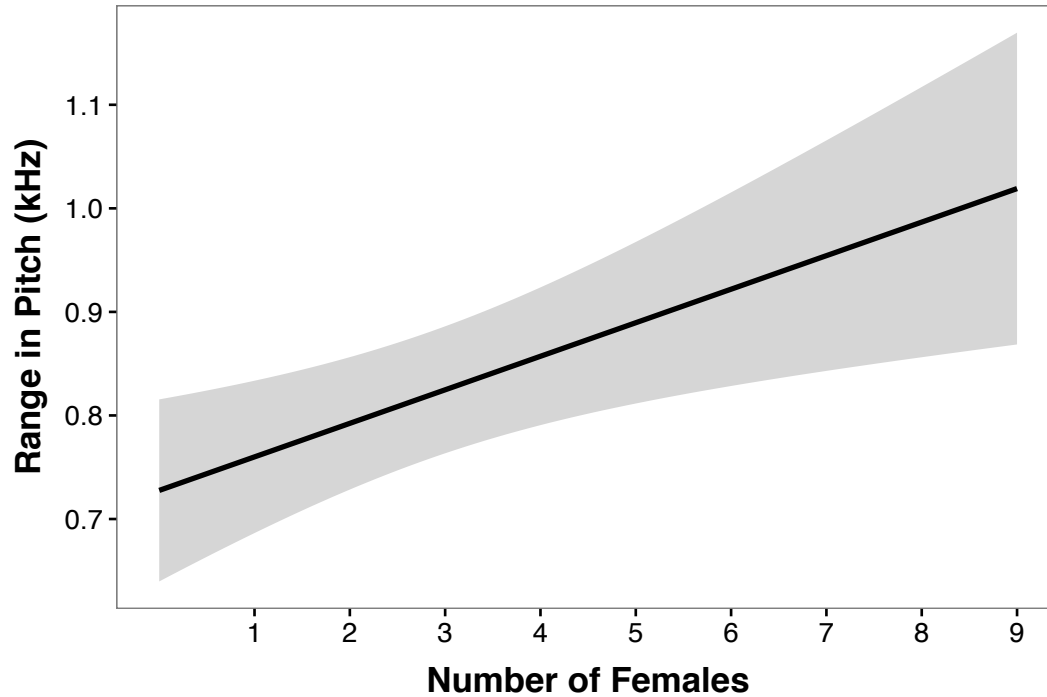
Figure 3.5. Relationship between (a) spectral measures and (b) range in pitch and number of females for leader males.

a.

b.

c.

d.
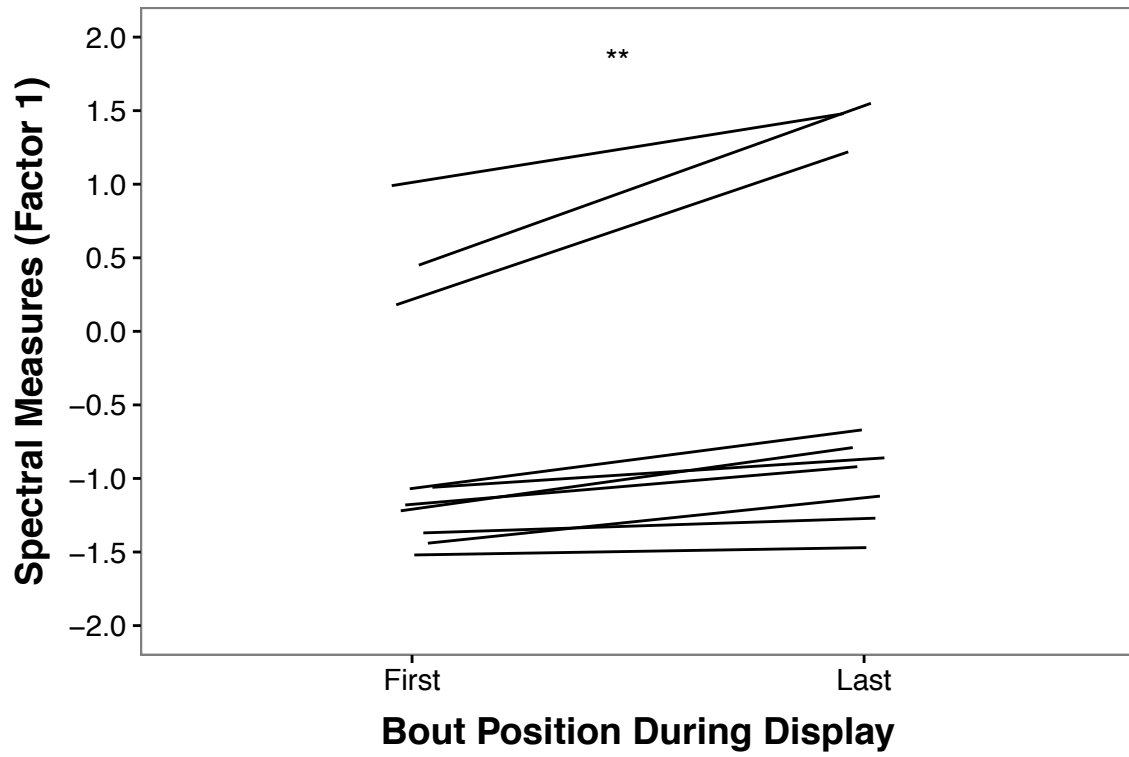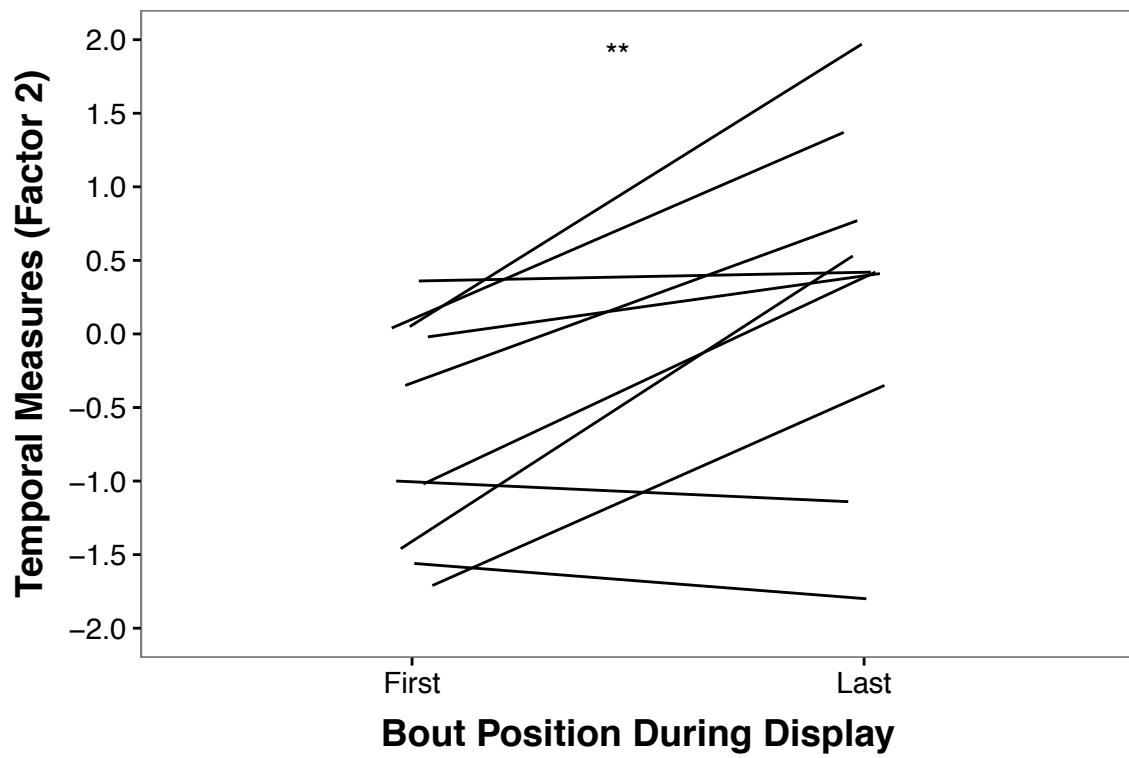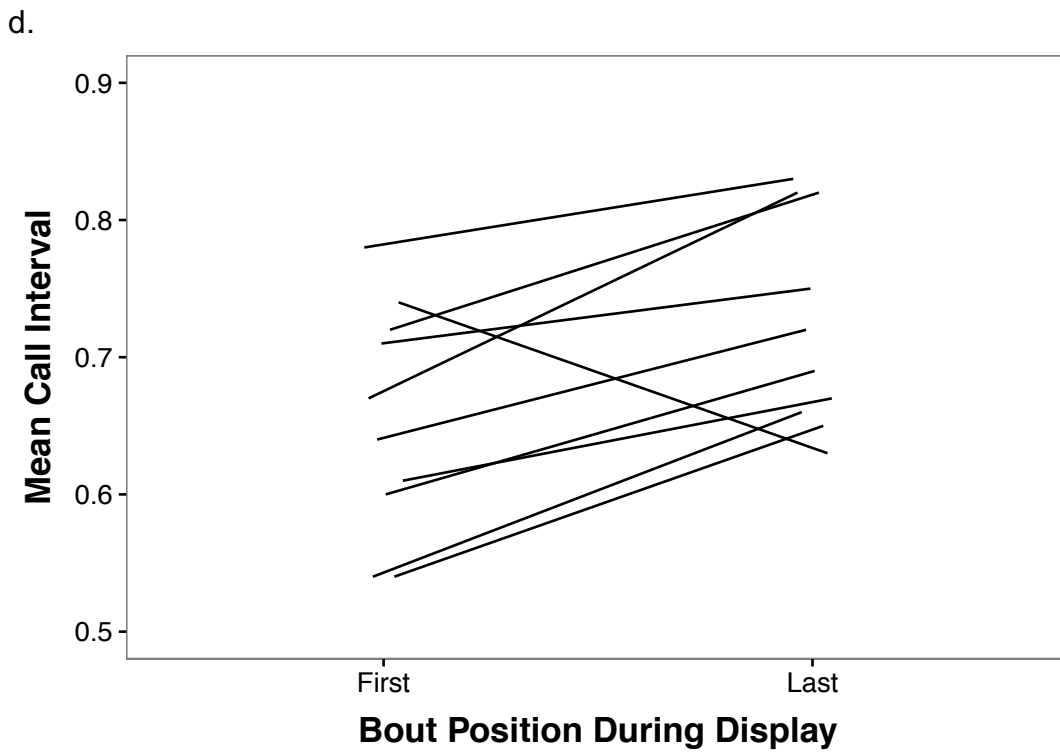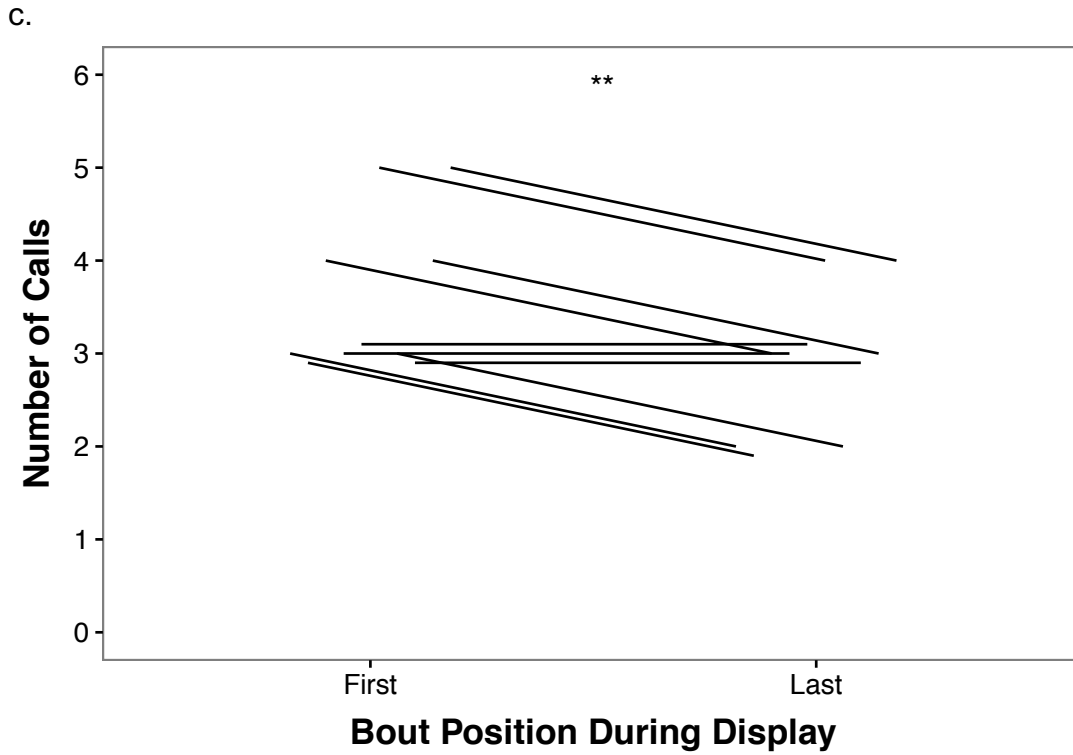
Figure 3.6. Within male differences in spectral measures (a), temporal measures (b), number of calls given per bout (c) and the mean call interval (d) between calls given during the first bout and the last bout of a chase display.

CHAPTER 4

EVIDENCE FOR MUTUAL ASSESSMENT IN A WILD PRIMATE

INTRODUCTION

Limited resources lead animals into contests. Because aggressive contests are costly, game theory predicts that contestants will assess the costs and benefits of a particular contest before escalating[1,2]. Contestants with a high ability to compete (i.e., high resource holding potential – RHP) should escalate the contest, while those with a low ability to compete (low RHP) should withdraw. Despite the simplicity of this prediction, there is enormous debate about how animals make these decisions[3]. It stands to reason that a contestant should gather information about their opponent's condition and compare that to their own (*mutual assessment* [2]). However, many empirical studies find it difficult to reject "simpler" assessment strategies[4] such as *self-assessment* (relying solely on one's own condition[5]), or *opponent-only assessment* (relying solely on a rival's condition[6]). For example, when an inferior contestant withdraws from an aggressive contest with an opponent, the contestant may indeed be using mutual assessment, or they may simply be withdrawing because the damage incurred was too high. Therefore, a "cumulative" *self-assessment* strategy is difficult to distinguish from a "sequential" *mutual assessment* one[4].

Non-contact displays – such as those involving animal signals – avoid this problem entirely[7]. Contestants do not accumulate sufficient costs during displays for a cumulative assessment strategy to be operating. Therefore, measuring receiver responses based on the relative quality of the signaler and the receiver makes for a strong test of mutual assessment. However, within the vast literature documenting receiver responses to putative signals based on the quality of the signaler[8–19], only a handful of studies also examined receiver responses based on the relative quality of the signaler *and the receiver* [7,20,21]. Thus, the current evidence for many signals is only sufficient for identifying opponent-only assessment. In practice, however, it is likely that many of these taxa may be using mutual assessment.

In non-human primates (hereafter, "primates") the evidence for mutual assessment using signals is non-existent for two reasons. First, experimental manipulations are uncommon in primates. In most cases it is not feasible or ethical to stage encounters. Without experimental control, it is difficult to pinpoint the bases of decisions. Second, primates tend to rely on social information to guide their interactions. The use of social information can be quite sophisticated [26], however, interacting based on prior information does not require any form of assessment (other than recognition) at the time of the interaction [24]. For example, with linear dominance hierarchies (common across primates) relative ranks determine social interactions (e.g., an animal ranked 2 has a very different interaction with animal ranked 1 vs. animal 3) [27-29]. However, such differences are unlikely to involve an assessment of the relative Resource Holding Potential

(RHP) of the contestants at the time of the interaction, but rather build on a history of interactions with known individuals. Similarly, in rare cases where experimental manipulations using playback experiments have shown some evidence of attending to the relative RHP of a signaler and receiver [29,30] the responses are almost certainly based on recognition of the individual (not their advertised quality) [26]. Indeed, presumably as a consequence of their reliance on social information, signals of quality (i.e., badges of status) are rare in primates [26]. As yet, we have no evidence that primates use a mutual assessment strategy in the context of animal signals. Here we examined whether a wild primate, the gelada (*Theropithecus gelada*), uses mutual assessment when hearing loud calls from other males.

Geladas present an unusually tractable system for experimentally studying assessment in primates. Geladas have a vocal signal that is used in male-male competition, allowing us to use playback experiments to disentangle various assessment strategies. Geladas are large-bodied, terrestrial primates that live in the high-montane grasslands of Ethiopia[31]. They congregate in a large, fluid, multi-level society composed primarily of harems, or "reproductive units". Reproductive units comprise one harem-holding male ("leader male"), 1–12 related adult females and their offspring, and occasionally one or more subordinate males ("follower males"). Leader males (often joined by follower males) fiercely guard their harems from "bachelor males" that reside in all-male groups at the periphery of the larger aggregations[32]. Importantly, bachelor males gain reproductive access to females primarily by challenging and defeating a

leader male[33]. By contrast, leader males pose no threat to each other[33] and frequently gather into large foraging aggregations[34] for a putative "dilution effect" against predators[35] and/or bachelors[36].

Leader males apparently deter bachelors from challenging them by engaging in highly-ritualized vocal displays that culminate in a series of loud calls[32]. These displays typically begin when a leader male approaches, threatens, and solicits a chase from a group of bachelor males[32]. While only one leader male is chased at a time, these encounters elicit interest from other males and the loud calls themselves are "contagious" (ranging from 2-13 leader males calling in a single display event)[33]. Additionally, each display is often followed by subsequent displays from other leader males, with each male each taking a turn (i.e., soliciting a chase and ending with a bout of loud calls), venturing away from his harem to engage with the bachelors and utter a series of loud calls before returning to his females[33]. Bachelors do not produce loud calls during these displays[33].

Previous research in geladas reported that leader males that display more frequently were less likely to be targeted by bachelors, suggesting that bachelors attend to these displays when assessing rivals[33]. But, in addition to the *quantity* of loud calls produced, recent evidence also suggests that the *quality* of these loud calls is important for rival assessment[37]. Specifically, the males likely to have the highest RHP in gelada society (e.g., prime-aged, high-status males) utter the most calls per bout, produce calls that are the lowest in overall frequency measures, and exhibit the greatest vocal range[37]. Thus, the loud calls

themselves may be honest signals of male RHP, and bachelor males can use

RHP information encoded in these calls for identifying relatively weak males[37].

By contrast, leader males do not assess bachelors but have the potential

to assess *other leader males* using these calls [33,36]. If indeed leader males rely

on a dilution effect to avoid being challenged by bachelor males, then each

leader is safe only if they, themselves, have a higher RHP than the other leader

males around them. Thus, leader males can use RHP information encoded in

these calls for identifying situations when they are surrounded by relatively strong

males.

We used a playback experiment as well as observations of natural

behavior in wild geladas to investigate the rival assessment strategy used by

males. We examined male responses to both experimental and natural loud calls

of varying quality. If gelada males rely only on *self-assessment* in male contests*,*

we predicted that neither leaders nor bachelors would respond differently to low-

and high-quality calls (Fig 1a). If geladas rely on *opponent-only assessment*, we

predicted that all subjects would respond stronger to high-quality calls than low-

quality calls regardless of their own status (Fig 1b; note that the direction of this

response could also be reversed). However, if gelada males rely on *mutual*

assessment in male contests (Fig1c), we predicted that male subjects would

respond to loud calls based on the combined information about themselves (i.e.,

their own status and/or RHP) and information about the quality of the rival (i.e.,

call quality). Specifically, we expected: (1) **bachelor males** to attend more to

low-quality calls (a weak rival) because this represents an easy opportunity for a

takeover; (2) **leader males** to attend more to high quality calls (a situation that makes them more likely to be challenged) – (3) particularly if they themselves have high RHP; (4) **high RHP leader males** to not just attend to high quality calls, but to subsequently advertise their own quality by participating in the display; and (5) **females** to not discriminate between call quality because loud calls are thought to be used in male-male competition rather than female choice.

RESULTS

Do males attend differently to high- and low-quality calls based on their own status?

We conducted a playback experiment on 60 adult geladas (20 females, 20 leader males, and 20 bachelor males) using previously-recorded loud calls obtained during naturally-occurring displays between adult males (7 high-quality bouts and 7 low-quality bouts, to construct 10 playback sets each containing a unique combination of one high- and one low-quality loud call bout from different males). Each subject heard both a high-quality loud call (one caller) and a low-quality loud call (a different caller). We visually recorded each subject's response to each call type (randomized for order of presentation) and examined six response variables (*look duration, approach duration, latency to look, latency to approach, approach distance,* and *time to resume activity*), which were reduced using factor analysis. The factor analysis resulted in two latent factors, (1) an "approach" response and (2) a "look" response, with Eigenvalues > 1, together explaining 90.7% of the total variance. Factor 1 ("approach response") accounted

for 50.7% of the variance and loaded heavily on *approach duration*, *approach distance*, and *latency to approach*. Factor 2 ("look response") accounted for 40.0% of the variance and loaded heavily on *look duration* and *latency to look* (Table 4.1). *Time to resume activity* loaded heavily on both components.

We then used a within-subjects design to examine whether social status determined whether a subject paid attention to one call type over another. Bachelors were more likely to approach (Factor 1) low-quality calls than high-quality calls ($t(1,19)=-2.3$, $p=0.029$; Figure 4.2a); but neither leaders ($t(1,19)=0.12$, $p=0.803$) nor females ($t(1,19)=-1.07$, $p=0.299$) differed in whether they approached either call type. By contrast, leaders were more likely to look (Factor 2) towards high-quality calls than low-quality calls ($t(1,19)=2.1$, $p=0.049$; Figure 4.2b). Yet, neither bachelors ($t(1,19)=1.316$, $p=2.04$) nor females ($t(1,19)=1.21$, $p=0.241$) distinguished between call type in terms of looking time (Figure 4.2b). Females rarely looked towards either one, while bachelors looked a great deal towards both.

We further examined each subject's overall response time (*look duration* + *approach duration*) to allow us to examine whether the subject's social status (leader, bachelor) and/or the call type (low, high) affected the overall strength of a male's response. Bachelors spent more time oriented towards the speaker than leaders ($F(1,38)=4.60$, $p=0.048$), regardless of the call type ($F(1,38)=0.524$, $p=0.473$). Supporting the previous results, we found a significant interaction between social status and call type ($F(1,38)=7.951$, $p=0.008$): leader males spent more time oriented towards loud call bouts of high-quality while bachelor males

spent more time oriented towards loud call bouts of low-quality (Figure 4.3).

Do males attend differently to high- and low-quality calls based on their own quality?

Based on the first question, males responses varied with differences in call quality based on their own categorical differences in status as a leader or bachelor. We additionally wanted to examine whether males further differentiate playback stimuli based on their own "quality" (i.e., using the quality of their own loud calls as a proxy for overall "quality"[37]). The sample for this analysis (N=11) was only a subset of the leader males used for the first analysis (we did not have recordings from all subjects and generally only leader males produce loud calls[33]). Note that because low-quality males rarely produce loud calls, the leader males included in this analysis disproportionately favor males whose loud calls are mid- to high-quality. We predicted that the previous result was due mainly to the high-quality leader males responding to the high-quality call type. We established a *call quality score* for each subject's loud calls in the same way that we determined high- and low-quality calls for the playback experiment.

For each call type (low, high), we compared each subject's overall response time to his own call quality score. In response to the simulated low-quality calls, we found no relationship between the subject's call quality score and his overall response time (r_s= 0.489, p=0.127). However, in response to the simulated high-quality calls, leader males with high call quality scores themselves

responded more strongly than those with low quality scores to the simulated calls (r_s= 0.752, p=0.008; Figure 4.4).

Are males more likely to join a loud call display when they hear calls of similar quality to their own?

The previous two results suggest that we can predict a male's response to the quality of a loud call by using experimental stimuli – bachelor males responded strongly to simulated low-quality calls and leader males responded strongly to simulated high-quality calls. Within leader males, high-quality leaders responded strongest to high-quality calls suggesting that leaders attend to both the quality of the caller and their own quality. Next, we wanted to determine if these same results hold true in natural observations of male contests. Loud call displays often serve as a catalyst for other unit males to join in with loud calls of their own. We predicted that high-quality leader males will be more likely to enter a loud call display when the display includes other males of high quality. To test these predictions, we used behavioral observations and loud call recordings from 20 unit males (16 leader males, 4 follower males) across 291 loud call displays recording 423 loud calls from all 20 males.

We then examined whether male A (subject) was more likely to participate in a display given that male B also displayed (binomial distribution). We included relative call quality (the difference between the call quality scores of both males), caller familiarity (using social network analysis), and leader/follower status in the

models as fixed effects; and we included the identification of both males as random effects.

Males were more likely to display with males of similar call quality scores to their own (β =-0.78, s.e.=0.31, *p*=0.012; Table 2, Figure 4.5), with caller familiarity having no effect (β =0.27, s.e.=0.14, *P*=0.06; Table 4.2).

DISCUSSION

In simulated signal displays, gelada males, but not females, discriminated between loud calls based on the acoustic quality of the signal as well as their own status and quality. Specifically, bachelor males – males that must compete to gain reproductive access to females – exhibited a stronger response to low-quality loud calls, while leader males exhibited a stronger response to high-quality loud calls. Furthermore, within leader males from whom we had loud calls (a sample biased towards mid- to high-RHP males), we found that higher-RHP males themselves (based on their call quality) responded more strongly to the high-quality stimuli than did lower-quality males. Finally, in natural observations, leader males were more likely to join loud call displays when their own calls were of similar quality to the other males involved in the display. In all three cases, males responded (or not) to other males' loud calls based on both their own RHP (or signal quality) and the caller's signal quality. Taken together, these findings support the hypothesis that gelada males use a mutual assessment strategy, rather than a self- or opponent-only one. These data provide the first evidence for

a mutual assessment strategy using signals for any non-human primate.

Although bachelor males attended to both high- and low-quality loud call bouts (Figure 4.2b), they only approached the hidden speaker ("escalated") when they were played the low-quality call (Figure 4.2a). In playback studies, approach behaviors (e.g., approach distance, approach rate, latency to approach) represent more "intense" measures of interest in the signal than looking time alone[38–41]. This is especially true in the study of aggressive signals, where approaching the source of the call is a relatively high-cost response as it implies an interest in engaging the caller [42,43]. In support of this, males that approached the speaker reached (or passed) the source of the call (mean approach distance 32.7m, mean speaker distance 28.9m), and 73% of these approaches were accompanied with visual and vocal threats. When confronted with a potentially weak rival, bachelors may benefit from an escalated response (i.e., an approach) because successful challenges can result in reproductive access to females[33,44,45]. By contrast, when confronted with a potentially strong rival, bachelors may suffer severe (and possibly fatal) costs from an escalated response[33]. Our results suggest that bachelor males assess the quality of leader males by attending to these loud calls, and they use information gleaned from these calls to make decisions about which males to challenge and which to avoid.

By contrast, leader males rarely approached the hidden speaker regardless of call quality (Figure 4.2a), possibly because a strong approach response is especially risky for leader males that leave their females unattended while

bachelor males are in close proximity. However, leader males did spend more time attending to the high-quality calls compared to the low-quality ones (Figure 4.2b), with the strongest responses deriving from the leader males exhibiting the highest-RHP (as measured by their own loud call quality, Figure 4.4). The motivation for leader males to attend to (and, engage in) call displays presumably derives from the need to showcase their own quality in the midst of bachelors. The large aggregations of geladas (sometimes numbering over 1200 individuals) have been hypothesized to create a "dilution effect" against predators[35], but also against bachelors[36]. Indeed, at least one feature of loud call displays (how often a leader male participated in displays[33]) was found to be negatively associated with his likelihood of takeover. Therefore, leader males should broadcast their loud calls when they "compare well" to displaying males around them. In support of this, leader males were more likely to participate in natural loud call displays when their call quality was similar to the males calling around them.

Similar results have been reported for chacma baboons (*Papio ursinus*) where males were more likely to loud call with males of similar social status[27]. However, the male baboons were likely using social knowledge (monitoring other males' ranks and attending to acoustic cues of identity) to assess one another, not signals [27]. By contrast, gelada males – who have remarkably limited acoustic recognition of even males they associate with frequently[46]– attend to encoded cues of quality when making informed decisions about when to engage in loud call displays. Both in gelada and baboon society, males benefit from assessing their own condition in relation to others. However, unlike baboons, the fission-

fusion nature of the gelada social system[47] requires leader males to consistently monitor the quality of *unfamiliar* males. This is especially important in the presence of bachelor males, when a leader male's reproductive tenure is threatened.

Importantly, bachelors, by successfully defeating the resident harem-holding male, become leaders. As males transition from bachelors to leaders, the information an individual pays attention too is likely to change with changes in status. Other primate species have been shown to monitor changes in other individuals' dominance ranks and social relationships over time[48]. In chacma baboons, for example, males track temporary changes in the status of other males' consortship but, once again, the results of this study were likely based on identity information, not signals[49]. In the case of geladas, information acquired from quality signals may be the only way to successfully navigating such large social groups.

Unlike males, gelada females did not differentiate between high- and low-quality calls. Indeed, they rarely attended to either call (Figure 4.a-b). There has been considerable debate as to whether loud calls in primates evolved to attract mates or to deter competitors[23,50]. One of the strengths of this study is that both females and males were tested within the same design. Our results indicate that gelada loud calls evolved as a signal for assessing rivals and not attracting mates.

To date, the vast majority of studies on assessment strategies have focused on solitary organisms in controlled experimental settings. One promising

avenue for future research will be to assess how group dynamics influence assessment strategies in social animals in a natural context[25]. For example, if the composition of social groups is dynamic, we might expect males to rely on information gleaned from signals rather than individual recognition and social knowledge when assessing rivals. More studies, like this one, that combine experiments with natural observations of assessment behavior are necessary to understand the role of assessment strategies in social animals.

METHODS

Study site and subjects

Research was conducted on a population of wild geladas living in the Simien Mountains National Park, Ethiopia from Feb-Dec 2013. The University of Michigan Gelada Research Project has been collecting long-term behavioral and demographic data on this population since January 2006. All males were individually recognizable and habituated to observers on foot (approach distance <3m). Methods include a combination of playback experiments and behavioral observations. We have organized each methods section around three questions that we sought to answer.

Do males attend differently to high- and low-quality calls based on their own status?

We conducted a playback experiment on 60 adult geladas (20 females, 20 leader males, and 20 bachelor males). To increase our sample size, we included

both known and unknown individuals in our experiment. All unknown individuals were identified using morphological features to ensure they were not used in subsequent experiments.

Playback stimuli

Playback stimuli comprised previously-recorded loud calls obtained during naturally-occurring signaling contests between adult males. Loud calls were recorded using a Sennheiser ME-66 directional microphone and a Marantz PMD 660 digital recorder. Loud call bouts were only used as playback stimuli if they were complete (no calls were missed during the recording) and devoid of background noise and interruptions. We audibly and visually inspected calls using Avisoft SASLab Pro (Avisoft Bioacoustics, Berlin, Germany) acoustic software for acoustic disturbances (e.g., background noise). At the time of the experiment, we had 157 loud call bouts from 50 prime-age males that fit this criteria (e.g., free of background noise).

For geladas, loud call bouts generally consist of a series of two-syllable 'ee-yow' calls (2-9 calls per bout). Previously, we found support for the hypothesis that the entire bout (and not just the individual calls within the bout) functions as a quality signal[37]. We selected a total of 14 loud call bouts as playback stimuli: 7 high-quality bouts and 7 low-quality bouts, to construct 10 playback sets, each containing a unique combination of one high- and one low-quality loud call bout from two different males. We determined call quality by comparing calls along two parameters we had previously found to differ with age

and status, fundamental frequency and bout length. We generated spectrogram analysis in Avisoft with a fast Fourier transformation size of 1024 points (frequency range: 22kHZ; frequency resolution: 43Hz time resolution: 2.903ms; 100% frame). We examined the distribution for both parameters and choose bouts that were at the extremes of these distributions.

We later conducted a more detailed analysis on gelada loud calls and revealed that known "high-quality" males (e.g., prime-aged, leader males) utter more calls per bout, produce calls that are lower in overall frequency measures (e.g., fundamental frequency), and exhibit a greater vocal range in pitch within a bout.

Playback design

We presented each subject with one of the playback sets comprising both a high- and a low-quality loud call bout. Because natural occurrences of loud calls in geladas generally occur when leader males encounter bachelor males, experiments were only conducted when both bachelors and leader males were present on a given day. To simulate a natural loud call contest, the calls were played from the direction of the bachelors (when the subject was a unit individual) or from the direction of the units (when the subject was a bachelor male).

For each trial, we placed a Bose Roommate II portable speaker approximately 25-50m (M=28.96m, SD= 7.95m) from the subject. The speaker was hidden behind a physical barrier (i.e., tree, rock, or bush) and completely

obscured from the subject's view. All subjects were observed for 15 minutes prior to the start of the playback experiment; and experiments were only conducted if (1) the subject was sitting (e.g., feeding or resting) for at least 2 minutes prior to the start of each call, and (2) the subject was oriented away from the speaker.

The experiment used a within-subjects design, in which subjects heard both a high-quality loud call bout and a low-quality loud call bout in each trial (to simulate a loud call contest between many males). The second call was played 5 minutes after the first call to allow subjects to return to an initial resting state. Subjects generally returned to an initial resting state within 1 minute after hearing the first call. We played each set of calls (n= 10 unique sets) to 6 subjects each: 2 bachelors, 2 leaders, and 2 females. To combat any order effect, we counter-balanced the order in which the high- and low-quality bouts were played across leaders, bachelors, and females. No subject heard any of the calls in the set prior to his or her experimental trial, and each trial was separated by at least 10 days for individuals in the same band.

Prior to all trials, we noted the identity of the subject, the location of the speaker relative to the subject, the subject's initial state (feeding or resting), the experimental playback set used, and the order of calls heard. During each trial, one observer played the loud calls from a loudspeaker using an MP3 player. A second experimenter with a camera, positioned herself 5-10 m in front of the subject, with the speaker hidden to the left or right of the subject. All subjects were video-recorded continuously from 15 seconds prior to the first call to 5 minutes after the second call. For each individual, we matched his or her state

(feeding or resting) and distance to the speaker between the first and second call – in some cases, moving the speaker to a new hiding spot the appropriate distance away.

For playback trials on unit individuals (leaders and females), we pre-designated two different subjects prior to the start of the trial: a unit male from one unit and a unit female from a different unit at least 40m away. In such cases, we placed the speaker between the two subjects (from the direction of the bachelors) to ensure their visual trajectories towards the stimuli were not overlapping. Each subject was filmed and scored independently. Experimenters were in contact via 2-way radios, and if any of the conditions were not met, we aborted the experiment immediately. We conducted a total of 60 successful playback trials consisting of 20 bachelor males, 20 leader males, and 20 females. An additional 22 trials were aborted prior to completion.

Playback responses

All videos were scored on a computer with a frame-by-frame analysis using Adobe Premier (Adobe Systems, Inc.) by two independent observers. Prior to video analyses, playback videos were cut to contain only the response to one loud call bout within a set. All files were then renamed and randomized such that observers were blind to the identity of the subject (i.e., whether he was a unit male or a bachelor male – it was impossible to hide whether the subject was a female) and the condition (i.e., whether it was a high- or low- quality bout). Reliability for all measurements between the two observers was greater than

95% (M= 97%, SD= 1.2%).

We measured 6 different response variables: (1) duration of time spent looking towards the speaker (*look duration*), (2) duration of time spent moving towards the speaker (*approach duration*), (3) latency of look response (*latency to look*), (4) latency of approach response (*latency to approach*), (5) total distance moved towards the speaker (*approach distance*), and (6) total time to return to initial resting state (*resume activity*).

Look duration measured the time a subject spent orienting toward the speaker while stationary. When a subject oriented toward the speaker while moving towards it, we recorded the response as *approach duration.* For both duration responses, we measured the total duration of all responses until the subject returned to their initial state for up to 1 minute after playback onset. Time to return to initial state was assessed once an individual spent at least 15 seconds feeding or resting without orienting towards the speaker. We did not record responses after subjects returned to their initial state because we felt that such responses were overly influenced by other individuals within the group (unit or bachelor group). We subtracted any time spent looking or moving towards the direction of the speaker during the 15 seconds prior to the onset of the trial. *Latency to look* and/or *latency to approach* were measured as the time from the onset of the playback stimuli until the onset of the subject's first look and/or movement towards the speaker. Due to the high mobility of the group during feeding, if a subject did not look or move within the first minute after the onset of the stimulus, we assigned the subject's latency as 60 seconds. We also recorded

approach distance for all movement toward the speaker in the first minute after the onset of each playback stimulus.

Playback analyses

To remove redundancy between response variables, we reduced response variables into latent factors using Factor Analyses (FA; McGregor 1992) with a varimax rotation with SPSS (v. 22.0.0.0). We accepted all factors with eigenvalues greater than 1.0, which produced two factors (Table 1).

We used these scores to analyze within-subject differences in response to high- and low-quality calls. Prior to these analyses, we checked the distribution of each factor score and, when necessary, transformed the data to approximate a normal distribution. We conducted paired t-tests on the factor scores for bachelors, leaders, and females separately to assess differences in directionality of response within the three groups.

In addition to the paired t-tests on the factor scores, we conducted a mixed-effects analysis of variances to assess status differences in overall duration of a male's response. We additionally calculated a "*overall response time*" for each male by summing the time he spent looking *and* approaching the speaker (*look duration + approach duration*). In this model, we examined the effect of social status (i.e., leader, bachelor) as a between-subject variable and call quality (i.e., high, low) as a repeated measure on *overall response time*.

Do males attend differently to high- and low-quality calls based on their

own quality?

We assigned each male a call quality score by examining 12 acoustic parameters related to frequency (e.g., fundamental frequency) and temporal measures (e.g., call duration). Given our previous results that lower frequency calls are energetically-costly to produce[37], we established a *call quality score* based on the factor analysis (i.e., Factor 1, *spectral measures*). We focused our analysis on the first calls given within a bout (n=122) as these calls are the lowest in frequency measures (and presumably the highest quality). We calculated a mean for the *spectral measure* scores for his calls to establish a call quality score for each male. Because calls that are lower in spectral measures were higher in quality, we multiplied the call quality score by -1, so that a high *call quality score* represents a high-quality call. We then ran two Spearman's rank-order correlations, comparing each male's response time to the high- and low-quality playback stimuli to his own call quality score.

Are males more likely to join a loud call display when they hear calls of similar quality to their own?

We collected all-occurrence behavioral sampling and recorded 423 loud calls across 291 different loud call displays from 20 unit males (16 leaders, 4 followers) across the study period. For all displays, we recorded the identity of all known males that participated in the display as well as the males present in the group that did not participate. We conducted acoustic analyses on all calls in the

same way as described above. Again, we focused our analysis on the first calls

given within a bout (n=122) and established a call quality score for each male.

To control for a subject's "familiarity" with the caller, we used all proximity

data between the subject and the caller in a social network analyses[34]. We

constructed an undirected, weighted network based on male-male association. In

this network, males were represented by nodes and the edge weight was given

by an association index[34.] This index was calculated as:

$$\text{Association index males A,B} = \frac{\text{\# of times male A seen with B}}{\text{minimum \# of times male A or male B seen}}$$

Where the numerator is the total number of times males A and B were

seen together in the same group, divided by the minimum number of times we

observed either A or B in the same group (see[34]). The association index ranges

from 0 (if two individuals were never seen together) to 1 (if they were always

seen together). From this network, we used the Louvain community identification

algorithm to assign males to "cliques" within their social network. Males

associated into two distinct cliques (N=15 and N=21 males respectively) with a

modularity coefficient of 0.011. Males were considered to be "familiar" with each

other if they were assigned to the same clique, and "not familiar" if assigned to

different cliques.

To assess if relative call quality or caller familiarity influenced the

likelihood that a male would participate in these vocal displays, we conducted a

GLMM with a binomial distribution. For each subject, we examined the dyadic

calling relationship with other males. The outcome variable in our model was the

likelihood that male A participated in a display, given that male B also displayed.

This was modeled as the *count of successes,* the number of times male A and

male B displayed together, offset by the *count of failures*, the total number of

times male A or B displayed (but not both), given that both males could have

displayed (e.g., were both present in the group on that day). We included *relative*

call quality and *caller familiarity* in the models as fixed effects. *Relative call*

quality was calculated for each dyad by taking the absolute value of the

difference between the *call quality scores* of both males. The smaller the

difference between the two call quality scores, the closer the males were in

relative call quality. *Caller familiarity* was established for each dyad from the

social network analysis. Males were considered to be "familiar" with each other if

they were assigned to the same clique, and "not familiar" if assigned to different

cliques. We controlled for the identity of both males by including their

identification as random variables in the model. Although the majority of calls

were given by leader males, occasionally subordinate follower males engaged in

these displays. Because leaders are more likely to display than followers, we

controlled for status of both males in the model. We compared the full model to a

null model, which included only the intercept and random effects. The social

network analysis and GLMM were conducted in R 3.2.4 using igraph [51] and lme4

[52] packages respectively.

TABLES

Table 4.1 Loadings from Factor Analysis

Variables	Factor 1 *Approach response*	Factor 2 *Look response*
Look duration (s)	0.17	**0.92**
Look latency (s)	-0.07	**-0.92**
Move duration (s)	**0.97**	0.16
Move latency (s)	**-0.95**	-0.18
Distance moved* (m)	**0.93**	0.19
Resume activity (s)	**0.56**	**0.78**
Eigenvalue	3.92	1.52
Variance	50.70%	40.00%

* distance moved towards speaker (not away)

Table 4.2 Results from GLMM

Predictors	*Beta*	*Se(beta)*	*t-value*	*p-value*
(Intercept)	-2.68	0.52	-5.14	$2.77\text{e-}07$
Difference in call quality score	-0.78	0.31	-2.51	**0.012**
Familiarity	0.27	0.14	1.89	0.060

FIGURES
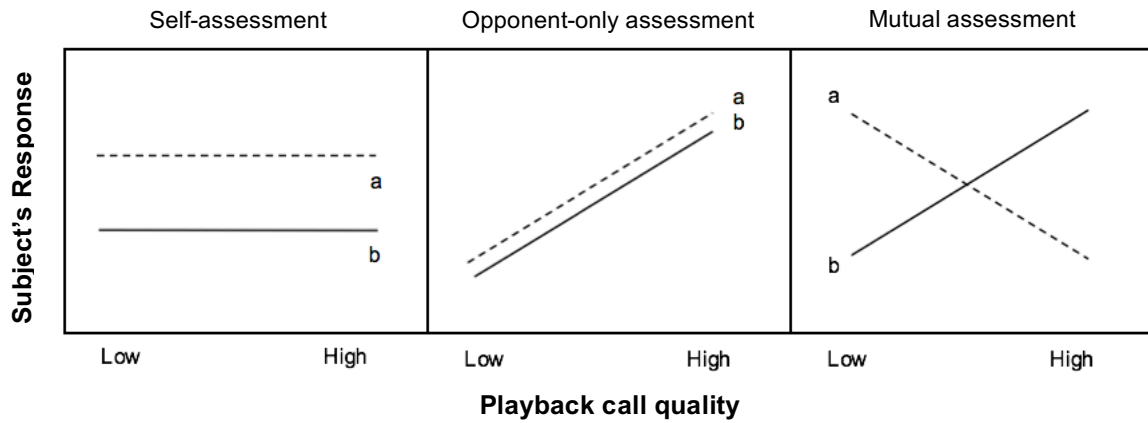
Figure 4.1 Predictions for bachelor male (a) and leader male (b) responses to low- and high-quality simulated loud calls for three assessment strategies: self-assessment, opponent-only assessment, and mutual assessment.
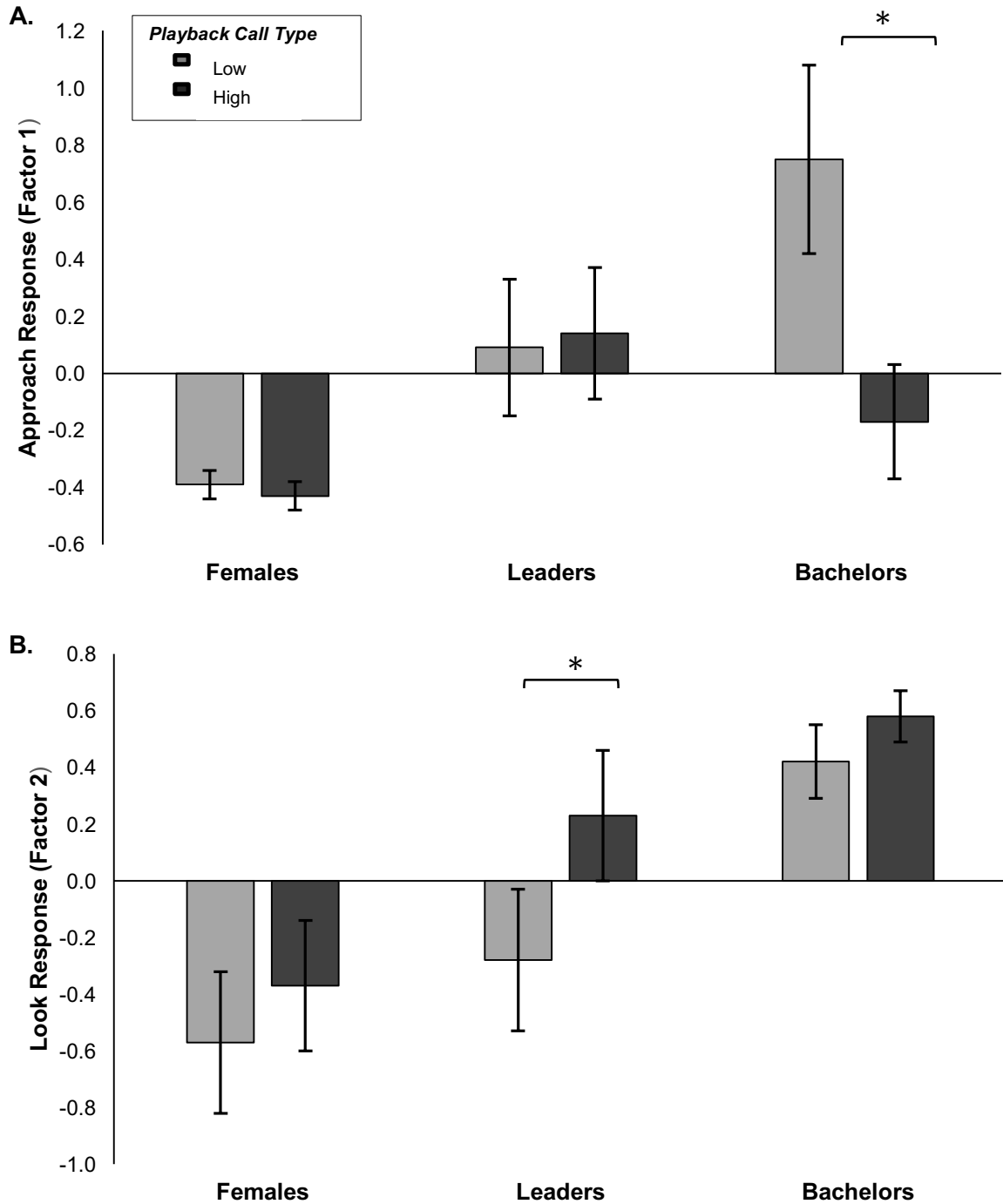
Figure 4.2 Subject responses (Mean of factor scores +SEM) to simulated high and low quality loud calls from bachelors, leaders, and females. (a) Factor 1 is a composite score where larger values indicate a stronger "approach" response. (b) Factor 2 is a composite score where larger values indicate a stronger "look" response. See text for details. An asterisk indicates significance at <0.05.
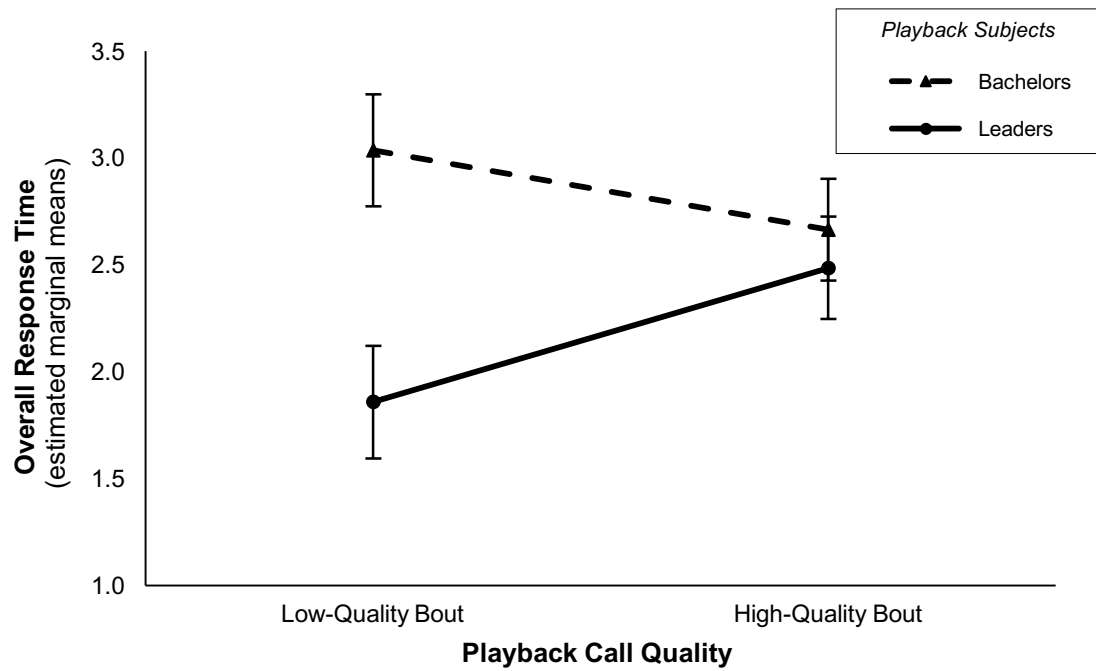
Figure 4.3 Estimated marginal means (+SEM) of "overall response time" (calculated as the sum of looking time and time spent moving toward speaker) to different call types.
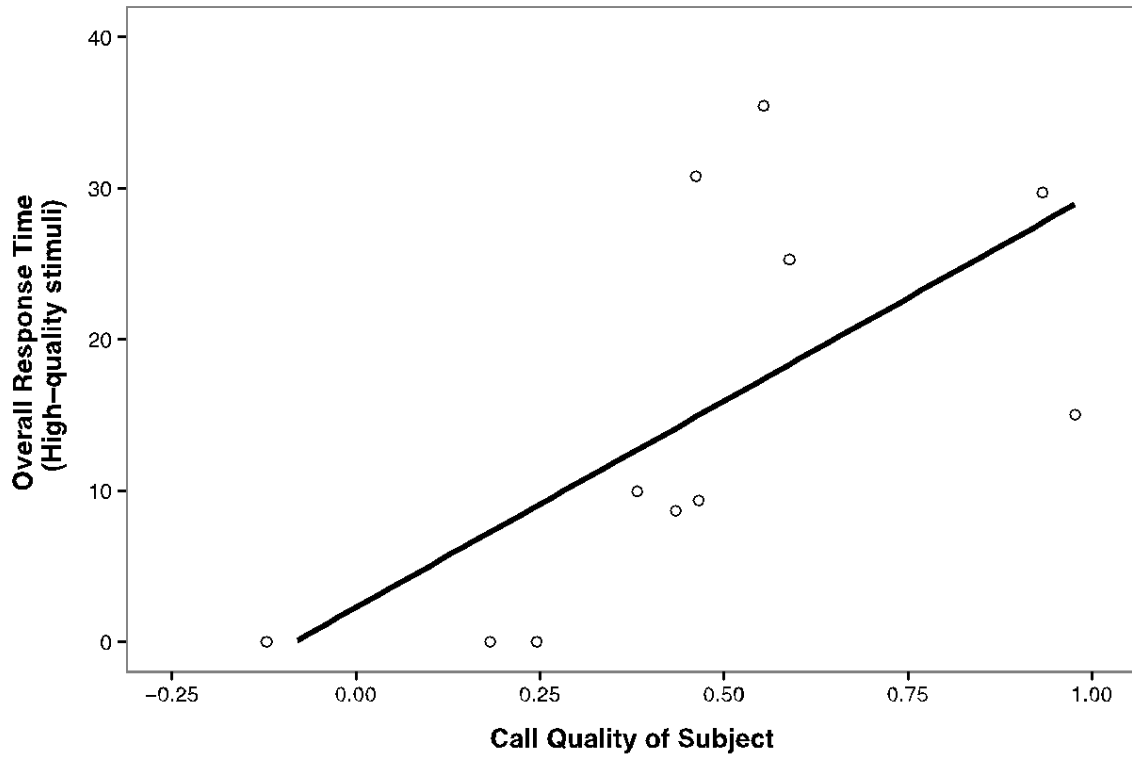
Figure 4.4 Overall response time (s) to the high-quality playback call in relation to the subjects own call quality.
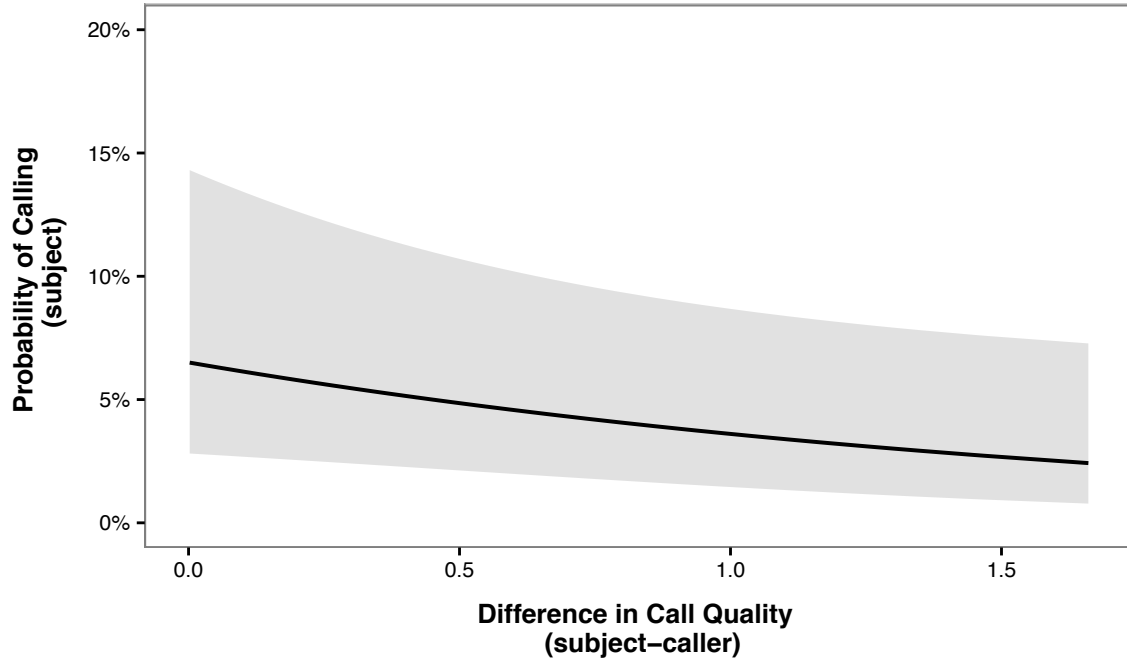
Figure 4.5 The probability that a male subject participated in a display based on the difference in quality between his own loud call and a caller's loud call. Smaller differences in call quality (x-axis) significantly increase the likelihood of participation.

CHAPTER 5

MULTIMODAL SIGNALS IN GELADA MALES

INTRODUCTION

In the last decade, there has been an increasing shift in animal

communication towards a multimodal approach to signaling (Partan & Marler

1999, 2005). Recent research, primarily on frogs (Taylor et al. 2007, 2008, 2011),

birds (Partan et al. 2005; Uy et al. 2009; Uy & Safran 2013; Hick et al. 2016),

insects (Rowe & Guilford 1999; Jetz et al. 2001), and spiders (Hebets & Uetz

2000; Uetz & Roberts 2002; Uetz et al. 2009) have shown that animals often use

diverse signal modalities – such as visual, acoustic, olfactory, and chemical cues

– that may function independently or tandem to signal information (Bradbury &

Vehrencamp 2011; Grether 2011).

Two main hypotheses have been proposed to explain the benefit of

signaling in different modalities. First, multimodal signals may serve as redundant

signals, where different signals carry the same information about the sender

(Partan & Marler 2005; Anderson et al. 2013). Redundant signals may be

particularly advantageous in changing ecological or social environments, with

multiple signals functioning as a "backup" for more accurate information

transmission (Partan & Marler 2005). Second, multimodal signals may function

independently with each signal conveying unique information about the sender

(Hebets & Papaj 2004). For example, one trait may convey information about genetic quality while another trait reliably signals a male's current condition (Candolin 2003). Under either scenario, multimodal signals allow for a more efficient and accurate way to gain information about the condition or quality of the signaler.

Primates are an excellent taxa for studying multimodal signals (Higham et al. 2013). Unusual among mammals, some primates exhibit an extremely vivid and colorful array of visual signals (Setchell & Jean Wickings 2005; Bradley & Mundy 2008; Bergman et al. 2009; Higham 2009). These colorful ornaments appear to function primarily in sexual selection (Gerald 2001). For example, in mandrills (*Mandrillus sphinx)* and macaques (*Macaca mulatta*), females prefer males with redder faces (Setchell & Jean Wickings 2005; Dubuc et al. 2014). Other studies have found a relationship between color and social status (Setchell & Dixson 2001; Marty et al. 2009; Bergman et al. 2009; Grueter et al. 2015), suggesting that these traits may also function in rival assessment. Several lines of evidence suggest that bright colors reliably signal the condition of the sender. For instance, color intensity has been linked to androgen levels (*Mandrillus sphinx*, Setchell et al. 2008), health (Nunn & Altizer 2006), genetic composition (*Mandrillus sphinx*, Setchell et al. 2011), and mating opportunities (*Theropithecus gelada,* Bergman et al. 2009; *Rhinopithecus bieti*, Grueter et al. 2015).

In addition to these visual signals, adult males in many primate species produce loud call vocalizations that are may function to deter rivals or attract mates (Delgado 2006). In chacma baboons (*Papio ursinus*), for example, high-

ranking males produce calls with higher frequency measures, longer temporal

measures, and call at higher rates than low-ranking individuals (Fischer et al.

2004). Similar to color signals, the acoustic properties of these calls are honest

indicators of male condition and have been found to vary with body size in

hamadryas baboons (*Papio hamadryas*. Pfefferle & Fischer 2006), androgen

levels in gibbons species (*Hylobates lar*, Barelli et al. 2013), and dominance rank

(chacma baboons, Kitchen et al. 2003; *Simias concolor*, Erb et al. 2013; geladas,

Benítez et al. 2016).

Despite growing interest in the role of visual and vocal signals in primate

communication (Kappler and van Schaik, 2004), very few studies have examined

the relationship between signals of different modalities in primates (Higham et al.

2013). So few, in fact, that primatologists have been recently called out for

lagging far behind in incorporating a multimodal research approach to the study

of signals (Slocombe et al. 2011; Higham & Hebets 2013; Higham et al. 2013).

Consequently, our understanding of how information from multiple signals is

received, interpreted, and integrated into decision-making in primates remains

poorly understood (Higham et al. 2013). In this chapter, we use a multimodal

approach to investigate the relationship between a visual signal, a vocal signal,

and a behavioral display among males in a terrestrial, Old World monkey, the

gelada (*Theropithecus gelada*).

Geladas live in a multilevel social system comprising of dozens of

reproductive units, which consist primarily of one dominant leader male and 2-13

adult females (Dunbar & Dunbar 1975). As a result, competition between males

for access to these units of females is extremely high (Dunbar & Dunbar 1975; Dunbar 1993; Pappano & Beehner 2014). For bachelor males living in all-male groups, reproduction is contingent on acquiring a unit of a females by successfully targeting and defeating the resident leader male ("takeover"). Fights between bachelors and leaders are extremely costly, and often result in serious injury or death. Because bachelors have many leader males to choose from when deciding which male to challenge, bachelors should assess many possible rivals prior to escalating to an aggressive challenge. Geladas congregate in groups of up 1200 individuals (Dunbar & Dunbar 1975; Kawai 1979; Mori 1979; Dunbar 1984), which makes deciding which leader males to challenge and which to leave alone a particularly difficult task.

We have previously shown that geladas males deter successful challenges from bachelor males by engaging in a physically demanding ritualized display. In Chapter 2, we found that bachelors were more likely to successfully target leader males that displayed less often. This raises an important question. Does a bachelor remember which leader males display more frequently and which ones do not? Given that individual recognition appears to be limited in this species (Bergman 2010), we hypothesize that it is unlikely that bachelor males are keeping track of each leader male and how often they display. An alternative hypothesis is that displays may work in tandem with another signal that accurately reflects male condition or quality (Dunbar 1984).

Gelada males possess two such signals: a loud call given during energetic displays usually towards bachelor males and a red patch of skin on chest and

neck (hereafter, "chest patch"). In chapter 2, we showed that during gelada displays, males produce loud calls that are known to function as "quality" signals with several acoustic features differing between males according to status, age, and stamina (Benítez et al. 2016). Specifically, leader males utter more calls per bout, produce calls that are lower in overall frequency measures, and exhibit a greater vocal range more calls (Benítez et al. 2016). Additionally, in Chapter 2, we demonstrated that the frequency of these displays is an accurate predictor of which males are likely to get taken over (with more frequent displays preventing takeover). Finally, previous research on the gelada chest patch has shown that chest color is associated with a male's' status and condition. Leader males have redder chests than non-reproductive males, and within leader males, those with the largest units have the reddest chests (Bergman et al. 2009). Chest color also appears to be a plastic trait, increasing after physical activity and declining immediately after a male is successfully challenged and overthrown (Bergman & Beehner 2008; Bergman et al. 2009).

Although research on each of these signals suggests that they are sexually selected signals used in male competition, to date, these signals have been studied only independently. Yet, it remains likely that they function together in a multimodal way; either to accentuate the same information about condition/quality, or to highlight different aspects of condition/quality. Here, we investigate the relationship between chest redness, loud call quality, and vocal display rate among leader males in gelada society. First, we test the hypothesis that chest redness and/or loud call quality reflect how often leader males display.

Second, we examine how these signals may function, independently or together, to deter challenges from rivals and influence overall reproductive success.

Among leader males, males with the highest quality calls (and presumably the best quality/condition) should be more likely to advertise by calling. Therefore, first, we predict that males with high-quality calls will display more frequently than males with low-quality calls. Second, we expect a positive relationship between display rate and chest color – with males that display more often having redder chest patches. We know that males exhibit redder chests up to 20 minutes after they engage in physical activity (Bergman et al. 2009). Given that male vocal displays are physically demanding, we expect that males will exhibit redder chests after engaging in a display. In addition, we expect that males that display more often will have the reddest chests even when at rest (baseline). Because loud call quality and chest patch coloration may be linked through male genetic quality or indirectly linked through display behavior, we predict that higher call quality will also be associated with redder chests.

We have also shown that males display more often in the wet season months when food availability is high (Chapter 2). If physical condition is also mediating loud call quality and chest redness, we expect similar variation due to seasonal changes. In other words, a male should give the highest quality calls and exhibit the reddest chests during the months in which he displays the most often (i.e., wet season).

Lastly, for a signal to function in sexual selection, the signal must be related to overall reproductive success (Snowdon 2004). Similar to the analysis

conducted on display rate in Chapter 2 (where we found that males that display less often are more likely to be replaced), here we further investigate whether loud call quality or chest color influences the likelihood of a male being overthrown. Similar to display rate results, we predict that males with high-quality calls or redder chests will be less likely to be targeted by bachelors. We then assess if call quality, display rate, or chest patch color predicts a male's overall reproductive success, as measured by his tenure length and number of offspring sired during that tenure. Gelada males have relatively discrete reproductive windows (i.e., their tenure as a leader male) compared to other primates, and extra unit paternity is close to zero, making it easy to quantify male reproductive output (i.e., number of offspring) (Snyder-Mackler et al. 2012). We predict that males with the highest quality calls, males that display more often, and/or males with the reddest chests will have the longest tenures and sire the most offspring (Figure 5.1, Figure 5.2).

METHODS

Study Site and Subjects

Data were collected from a population of geladas living in the Simien Mountain National Park, Ethiopia. The University of Michigan Gelada Research project has been collecting long-term behavioral and demographic data on this population since January 2006. For this study, we followed a total of 18 leader

males from February 2013-January 2014. All males were individually recognized and habituated to observers on foot.

Display Behavior

We collected all-occurrence behavioral sampling on 279 displays aimed at bachelor males (see Chapter 2). A display event began when one or more male instigated a chase and ended when all males involved returned to normal activity. For each male, we recorded the total the number of times he displayed per month and the number of hours that male spent in the presence of bachelor males. We calculated a monthly display rate for each male as displays per hour spent with bachelor.

Call Quality

In Chapter 3, our acoustic analyses revealed that the "best" males in a gelada society (i.e., males with an unambiguous reproductive advantage – adult males, leader males, "fresh" males in a contest) produced calls with lower frequency measures (i.e., *spectral measures/* Factor 1). Across age, status, and exhaustion, these *spectral measures* showed a consistent pattern of "degradation", and were always higher in known low-quality individuals (i.e., juveniles, follower males, leaders with smaller units, and "fatigued" males) compared to their high-quality counterparts (i.e., adult males, leader males, and fresh males). Given this, we used the *spectral measure* scores derived from the Factor Analysis in Chapter 3 to measure *call quality*

For each male, we created a *call quality score* by averaging his *spectral measure* scores. To control for position of call within a bout and changes due to exhaustion, we focused on the first calls given in the first bout, as these calls are the lowest in acoustic measures (and therefore the highest quality). In total, we calculated call quality scores from 43 calls collected in 2013 from 15 males (3 males did not have acoustic recordings of sufficient quality of analysis). We multiplied the factor score by -1 so that a high call quality score represents a high-quality call.

Chest Patch Color

Photo collection: We analyzed 312 chest photos from 17 leader males from April through November 2013. We collected two types of photos (Figure 5.2). First, to establish a monthly baseline, we photographed males when at rest every 4-5 weeks (n=108 baseline photos / 17 males, mean=6 photos / male). Second, to examine changes in chest color after a male displayed, we took chest photos within 10 minutes of a male engaging in a vocal display (n=48 post display photos / 14 males, mean=3 photos / male).

All photos were taken with a Nikon COOLPIX 8700 digital camera on manual settings for shutter speed and lens aperture. We purposely underexposed photos (by 1-2 f-stops) to guard against "clipping" (Stevens et al., 2007), which occurs when the light levels for any of the RGB (Red, Green, Blue) channels reach the upper limits of the camera (at 255). All photos in this study were taken at the "fine" quality setting, which has a compression ratio of 1:4,

creating a 2-3 MB Joint Photographic Experts Group (JPEG) file per photo. At the time of the photo, we recorded whether the photo was a baseline photo or a post-display photo, the time the photo was taken, the time of the display, and the lighting conditions (full sun, full shade, backlit, or cloud).

Color quantification: We quantified color in the chest patch using a method previously validated for use on geladas (Bergman & Beehner 2008; Bergman et al. 2009). In brief, we took a photo of a male's chest that was fully visible and clear of any obstructions. We then, immediately, took a series of photographs with a X-rite ColorChecker chart in the same position, angle, and lighting as the first photo. Each photo was angled slightly differently to represent both the angles of the left and right side of the chest patch.

Photos were later analyzed in Adobe Photoshop using the inCamera 4.0.1 filter plug-in (a program designed to be used with the X-rite ColorChecker chart). For each set of photos, we chose the best chest patch picture with both sides of the chest clearly exposed. If no one picture showed both sides of the chest clearly, we chose two pictures: one that showed the left side and one that showed the right side clearly. We then compared the angle of the ColorChecker chart pictures to the angles of the chest patch and chose the chart picture that best match the angle of the chest. Using the inCamera plug-in, we created a manual color profile adjusted to the color levels in each square of the ColorChecker chart. We converted the corresponding photo of the male's chest

to the newly created color profile using the same settings recommended by the inCamera plug-in.

For each male, we selected a portion of the chest patch (>200 pixels) on both the left and right side that was free of any obstructions (e.g., blemishes, shadows, scaly skin). We recorded the RGB levels levels using the histogram palette, averaged over selected pixels. As our measure of chest color, we used the ratio of red to green (R/G ratio) and averaged those values for both sides of the chest patch.

Data Analysis

Do males with high-quality calls display at higher rates and/or have redder chests?

To assess if males with high-quality calls displayed more often than males with low-quality calls, we conducted a rank-order Spearman's correlation (due to small sample size) between each male's *call quality score* and his overall display rate (mean monthly display rate). We then examined whether males with high-quality calls had, on average, the reddest chests. We ran two additional Spearman correlations comparing the relationship between (1) call quality and baseline chest redness, and (2) call quality and post-display redness for each male.

Does chest color reflect display rate?

To examine if males exhibited redder chests after displaying, we compared each male's chest color (R/G ratio) when he was at rest (baseline) to his chest color after he displayed (post-display). For the 13 males from which we had both baseline and post-display photos, we compared mean chest color for baseline and post-display chests. We then conducted a paired Wilcoxon signed rank test to determine if a male's' chest color increased within 10 minutes of participating in a vocal display.

To assess if males that displayed more often had the reddest chests, we constructed a linear mixed model (LMM) with mean monthly chest color (R/G ratio, log-transformed) as the dependent variable. Note that monthly means were calculated for baseline and post-display chest photos separately. Predictor variables in the model were monthly display rate (# displays / month / monthly observation time with bachelors), photo type (baseline or post-display), and the interaction between the two. Because age, minimum temperature, and photo light conditions (full sun, full shade, backlit, of cloud) have been previously shown to influence chest color (Bergman & Beehner 2008), we included these in our model as covariates. We controlled for repeated measures from each male by including male ID as a random effect.

We compared univariate models that considered only a single fixed effect to multivariate models that considered a combination of fixed effects and interactions. We compared all candidate models using Akaike information criterion (AICc) and considered the models with the lowest AICc to be the best fit for our data set. We visually inspected each model using a Q-Q plot, histogram of

residuals and scatterplot of fitted versus residual values. For all models, residual values were normally distributed. We performed all statistical analysis using R (v. 3.0.3). All models were run using the lme4 package (v. 1.1-7). We used the MuMIN package (v. 1.12.1) to compare all candidate models and ggplot2 (v. 2.1.0) and sjplot packages (v. 2.0.0) to create figures.

Does call quality or chest patch mirror seasonal changes in display rate?

We conducted three Wilcoxon signed rank test to assess whether produced higher quality calls or redder chests during the wet season months— the months in which displayed most often. During the study period, the wet season ran from June-October. We designated a month as belonging to the wet season if cumulative rainfall for the month was greater than the median rainfall for the year (295.5 mm). For each male from which we had acoustic recording in both the wet and dry season (N=7), we calculated an average call quality score (see above) for each season. We then ran a Wilcoxon paired signed rank test comparing these scores. We conducted a similar analysis on baseline (N=18), post-display (N=11) chest photos, and display rate (to better compare our findings, N=18).

Does signal strength influence reproductive success?

We conducted an exact probability Mann-Whitney U test comparing call quality scores between males that remained leaders (N=10) and males that were overthrown (N=4). We ran a similar analysis on chest color, both baseline and

post display, to assess if males that remained leaders had the reddest chests. For the post-display analysis, we had data on only 3 of the males prior to takeover. We excluded new leader males (males that entered a unit during the study period) from this analysis (N=4).

We then assessed if signal strength predicted a male's reproductive success, as measured by overall tenure length and his estimated number of offspring. For all males that were replaced since this study started in February 2013 (N=11), we know their total tenure length (i.e., the date a male was overthrown minus the date they became a leader male) and the number of offspring sired in unit during a male's tenure. Previously, it was shown for this population that all offspring in a unit are sired by a unit male (the leader or follower) – and remarkably, there was no extra-unit paternity (Snyder-Mackler et al., 2012). Follower males sired up to 17% of the offspring in a unit (Snyder-Mackler et al. 2012). Therefore, for units with no follower male, the leader male was assigned 100% of the paternity; and for units with follower males, the leader male was assigned 83% of the paternity. We then ran six Spearman rho correlations to examine the relationship between each signal (call quality, chest redness, and display rate) on tenure length and number of offspring.

RESULTS

Do males with high-quality calls display at higher rates and/or have redder chests?

We found that males with high-quality calls displayed more often, on average, than males with low quality calls ($r_s=0.627$, n=15, p=0.0164; Figure 5.3). However, we found no relationship between call quality and chest coloration for either baseline ($r_s=0.052$, n=13, p=0.865) or post display ($r_s=-0.046$, n=12, p=0.881) chests.

Does chest color reflect the display frequency?

First, we found that males had redder chests after they displayed when compared to their baseline chest color (Wilcoxon signed-rank test; p= 0.003, Figure 5.4). Second, the model analyses revealed that the best model included only the interaction between photo type (baseline or post display) and display rate on chest color (AICc=-192.2). Specifically, males that displayed more had redder chests but *only* after displaying (interaction, post display x display rate; $\beta=0.893$, SE=0.216, p<0.001 Figure. 5.5). We observed no relationship between baseline chest color and display behavior. Neither display rate ($\beta=-0.167$, SE=0.125, p=0.182), nor photo type ($\beta=0.008$, SE=0.038, p=0.842) were significant predictors when included in either model. Because significant interaction made it difficult to interpret the separate effects of each predictor, we constructed a second model without the interaction term. In this model, only photo type was included in the best model, with post-display chests exhibiting significantly redder coloration than baseline chests ($\beta=0.137$, SE=0.023, p<0.001, Figure. 5.5).

Does call quality or chest patch mirror seasonal changes in display rate?

We found no differences in a males call quality (Wilcoxon signed-rank test; p= 0.813, Figure 5.6a) or baseline chest redness between the wet and dry season months (Wilcoxon signed-rank test; p= 0.346, Figure. 5.6b). However, we did find that males exhibited redder chest after displaying in the wet season than in the dry season months (Wilcoxon signed-rank test; p= 0.021). Again, a paired analysis revealed similar findings to Chapter 2, males displayed more in the wet season months (Wilcoxon signed-rank test; p<0.001, Figure 5.6c).

Does signal strength influence reproductive success?

There was no difference in call quality between males that remained leaders and males that were taken over (Mann Whitney; U=14, SE= 7.063, p=0.454, Figure. 5.7a). However, we found that males with high-quality calls had the longest tenures (r_s=0.735, n=10, p=0.0153) and sired more offspring than males with low-quality calls (r_s=0.769, n=10, p=0.009; Figure. 5.7b). For chest patch color, we found that males that remained leaders had significantly redder chests, but only after displaying, than males that were overthrown (post-display: U=25, SE=0.063, p=0.036, Figure 5.7e; baseline: U=22, SE=0.089, p=0.831). We found no relationship between tenure length and chest redness (baseline, r_s=0.215, n=8, p=0.608; post-display, r_s=-0.214, n=7, p=0.662) or number of offspring and chest redness (baseline, r_s=0.451, n=8, p=0.261; post-display, r_s=-0.180, n=7, p=0.699, Figure 5.7f). We also found no relationship between display

rate and tenure length (r_s=0.192, n=10, p=0.620), or number of offspring (r_s=0.185, n=10, p=0.634, Figure 5.7d).

DISCUSSION

We found that males with high-quality calls display more often, and males that displayed often exhibited the reddest chest after displaying. By attending to either signal, bachelor males can rapidly assess the competitive ability of a rival without relying on the accumulation of social knowledge. But do they? We found that chest patch redness, but not call quality, influenced which males were likely to be overthrown. Yet, males with high-quality calls were more successful at deterring bachelors in the long-term, exhibiting the longest tenures and siring the most offspring. Neither chest color nor display rate, however, predicted a male's overall reproductive success.

At first glance, these results may seem somewhat contradictory. To understand these findings, we need to consider these signals from a bachelor's perspective (Figure 5.8). We know that bachelors attend to information encoded in loud calls and are particularly motivated to investigate the calls of a weaker male (Chapter 4). A male with a low-quality call, would certainly be an easy choice for a takeover. However, a weaker male also represents a less desirable unit, a unit with less females (Chapter 3). For bachelor's, deciding which males to challenge is likely a tradeoff between minimizing the risk of aggression by challenging weak rivals and maximizing reproductive potential by targeting large units. An optimal strategy for a bachelor may not necessarily be to always target

the weakest male but to capitalize on a moment where a high-quality male is at his weakest. It is a bachelor males' best interest, then, to both assess the relative quality of potential rivals and to *monitor* changes in current condition in relatively strong males (e.g., males with larger units).

By attending to both loud calls and chest color, bachelor's could potentially monitor the changes in condition of an unknown rival. We found no significant relationship between call quality and chest color, suggesting that these two traits may signal different aspect of male condition. One prominent hypothesis is that signals that develop over long periods of time are good indicators of long-term condition or genetic quality, whereas flexible signals that reflect present condition may be better indicators of a male's current state (Candolin 2003). For example, temporal measures of male cricket songs reflect current nutritional intake, whereas acoustic frequency is more representative of past growth and juvenile development (Scheuber et al. 2003). Similarly, the acoustic features of gelada loud calls may be a more "fixed" signal that reliably indicates a male's long-term condition (or potential genetic quality) whereas chest patch redness functions primarily as an immediate signal of a male's current condition.

Our previous findings support this hypothesis. In Chapter 3, we found that the acoustic properties of loud calls differed due to age, status, and exhaustion. A male's call quality certainly changes over his lifetime but we argue that this is primarily due to developmental changes, resulting in changes in body size, and following life-history events linked with rapid changes in testosterone. We did find that late-prime leaders had the highest quality calls but we argue that this is a

consequence of males with good calls deterring bachelors for longer (rather than mechanical changes due to age). While the acoustic properties of these calls degraded as a male fatigued, these changes occurred on a small scale, and likely within a vocal range that is constrained primarily by the mechanisms of sound production. For a leader male, his call quality is unlikely to change during his tenure but will change, alongside testosterone and musculature, after he is taken-over. In support of this, we found no evidence that a male's call quality was influenced by seasonal changes, while display rate and post display chest color increased in the wet season months.

On the other hand, chest patch is a dynamic trait that is linked to display behavior. We found that males had redder chests immediately after they displayed when compared to their baseline chest color. In addition, males that displayed more frequently exhibited the reddest chest but *only* after displaying. In primates, red skin coloration is positively association with blood flow and oxygenation (Rhodes et al. 1997). Gelada males that display more regularly, males who are more physically fit, likely exhibit a greater increase in blood flow after they display, which is reflected in the redness of their chest. Studies in humans have shown that men who exercise regularly exhibit higher levels of blood flow after exercising, even when exercising at the same level and intensity as males who do not regularly exercise (Fortney & Vroman 1985). Men who are better able to increase skin blood flow, even at moderate exercise levels, are more efficient and effective at regulating internal temperatures, which allows them to exercise for longer and return to homeostasis sooner (Johnson 1998;

Armstrong & Welsman 2001). In geladas, red chests after a male displays is likely a byproduct of activity, but the intensity of color change accurately reflects a male's current physical state.

When a high-quality leader male is in prime condition, we would expect call quality and chest redness to be highly correlated. However, a male with a high-quality call who exhibits a relatively pale chest after displaying, is a male who is no longer in peak condition. The discrepancy in the strength of these two signals, provides bachelor with valuable information to rapidly assess when a strong male is at his weakest. While attending to just the loud call or the chest patch would provide bachelors with accurate information about the condition of a rival, by attending to both these signals simultaneously, bachelors can monitor changes in the current condition of previously strong competitor.

Other primate species have been shown to monitor changes in others' dominance ranks and social relationships over time (Tomasello & Call 1997; Seyfarth & Cheney 2007), by relying on identity and the accumulation of social knowledge (Bergman & Sheehan 2013). Even in species where auditory or visual signals are present, these signals often function to supplement social information (Bergman & Sheehan 2013). In baboons, for example, males attend to both acoustic features of identity and male condition encoded in loud calls presumably as a way to monitor changes in condition of closely ranked known rivals (Kitchen et al. 2013). Similarly, gelada males attend to information encoded in loud calls when assessing rivals, but in the absence of individual recognition, males require a second signal, the chest patch, to know when a strong male is in poor

condition. Selection may have favored the evolution of multiple signals in geladas as a way for males to accurately assess changes in the condition of unknown males (Bergman 2010; Bergman & Sheehan 2013; Sheehan & Bergman 2015). Geladas may be the exception among primates in relying exclusively on signals, rather than individual recognition, to assess rivals.

The results from the study support the multiple message hypothesis that different signals carry different information about male qualities (Moller & Pomiankowski 1993; Johnstone 1997; Partan & Marler 2005). Specifically, loud calls convey information about long-term condition or quality and chest patch reflects a male's current state. However, a high-quality male in prime condition should give the acoustically strongest call, display the most often, and exhibit the reddest post display chests. When males are in their prime, these cues could also function as "backup" signals for more accurate information transmission (Partan & Marler 2005; Anderson et al. 2013). In zebra finches, for example, under favorable environments, beak redness and song rate are correlated such that males in the best condition sing more often and have redder beaks (Houtman 1992; Collins et al. 1994). However, during periods of food shortage, these traits are not correlated as they respond to changes in condition at different rates (Birkhead et al. 1998). Song rate responded quickly with decreases in body mass indicating a male's current condition whereas beak color, which is a heritable trait, takes significantly longer to change and reflected condition over a longer scale (Birkhead et al. 1998). We found that display rate and chest color declined in the dry season, but call quality did not suggesting that the biggest

discrepancy in call quality and chest color would occur when geladas are nutritionally stressed,

Geladas live in a Afroalpine environment characterized by the gorges and escarpments associated with high plateaux (Iwamoto & Dunbar 1983; Dunbar 1993). Bachelors, which often congregate on the outskirts of gelada bands, are not always in visual contact with units (Pappano et al. 2012). Vocal signals, like the loud call which can carry upwards of several km (and across cliffs) allow bachelors (and leaders) to quickly assess males from a distance (Dunbar 1984). As we have previously shown, eavesdropping on these calls likely influences a bachelor's decision to further investigate the caller (Chapter 4). Yet, gelada environments are also noisy (e.g., high wind speeds) and vocal displays can be particularly chaotic with multiple males calling simultaneously (Dunbar 1984). Under such conditions, acoustic transmission of information may be less reliable than visual signals at close-range (Uy & Safran 2013). The color of a male's chest after displaying may reinforce that a leader male is a strong competitor and should be avoided, or reveal that a male is poor condition and should be targeted. Thus, multimodal signals can function as both a backup signal in ideal conditions, and convey different messages about male quality when a male's condition changes due health, nutrition, or age. Either way, bachelor's benefit from attending to both signals.

Recently there has been a growing interest in incorporating aspects of multimodal signaling into studies of animal signals. There is little evidence, however that multiple signals function in male-male competition (Candolin 2003;

Higham & Hebets 2013). Here, we provide some the first evidence that signals in

different modalities may have evolved as a way for males to accurately assess

and monitor the condition of unknown rivals. In primates, studies of multimodal

signals are very much in their infancy and more studies like this one are needed

to fully understand the role of these signals in framing reproductive choices. An

interesting avenue for future research may be to examine if vocal signals and

badges of status influence decision-making in species with individual recognition.

FIGURES
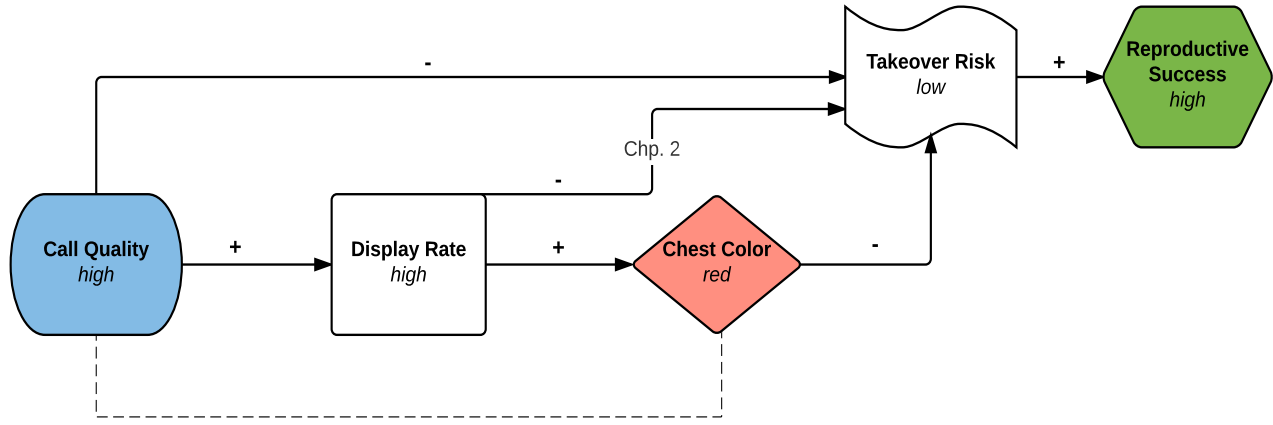
Figure 5.1. Diagram of predicted relationship between vocal and visual signals in gelada males and their potential effects on fitness. +/- signifies an expected positive or negative relationship. For example, males with high quality calls should display more often resulting in redder chests which reduces the risk of being targeted by a bachelor and results in overall greater reproductive success.
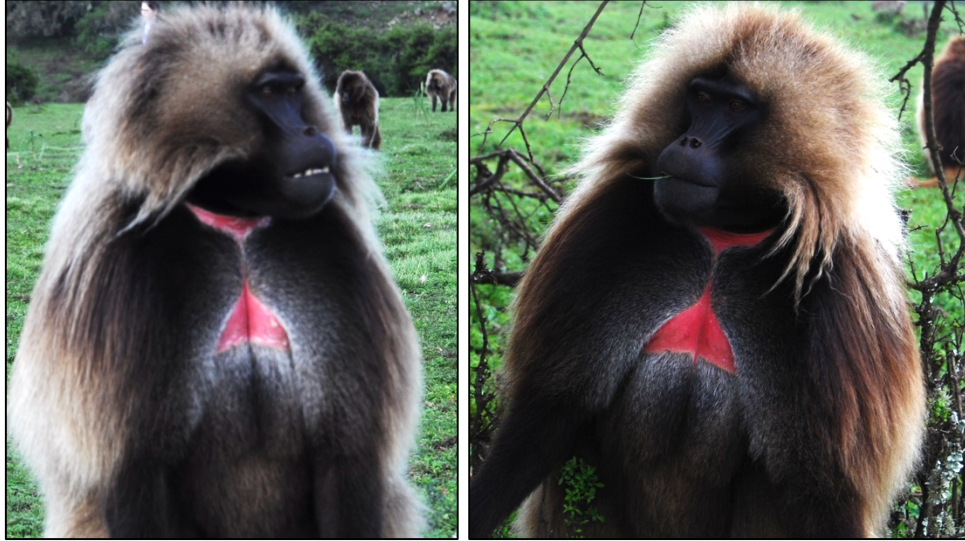
Figure 5.2. Color variability in the same male's chest patch when at rest (left) and after he displayed (right).
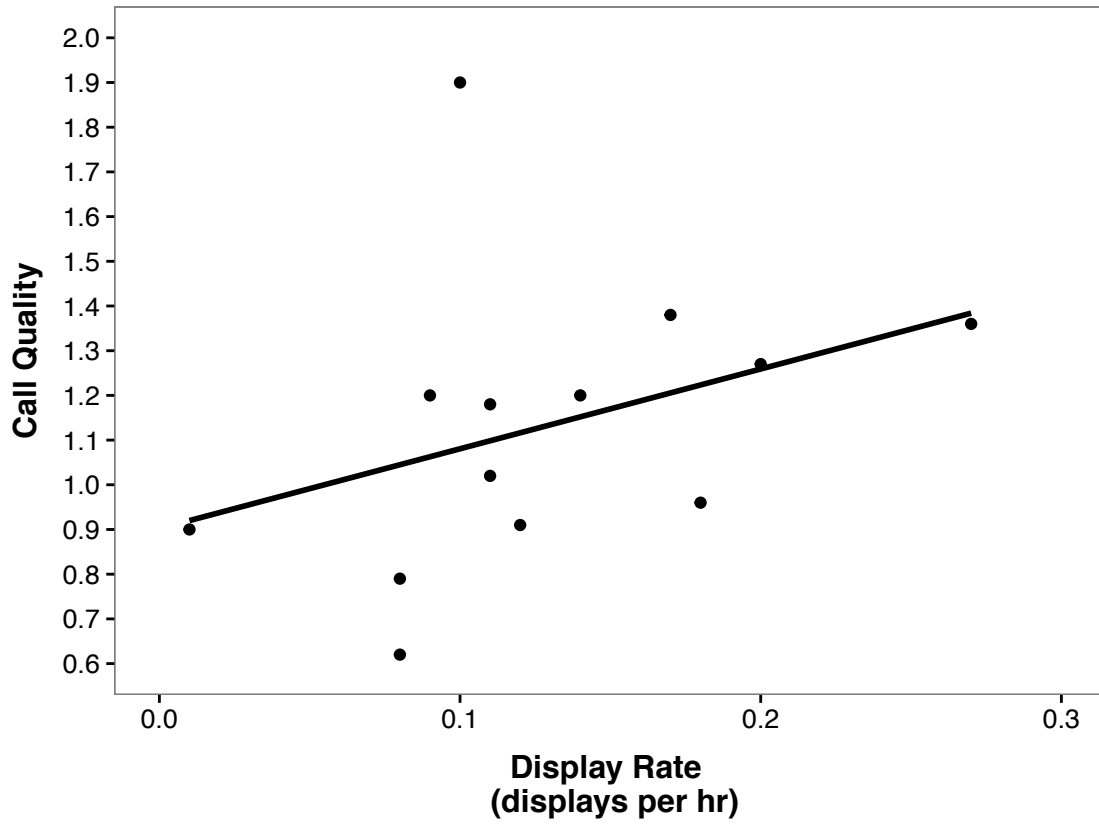
Figure 5.3. Relationship between call quality and display rate.
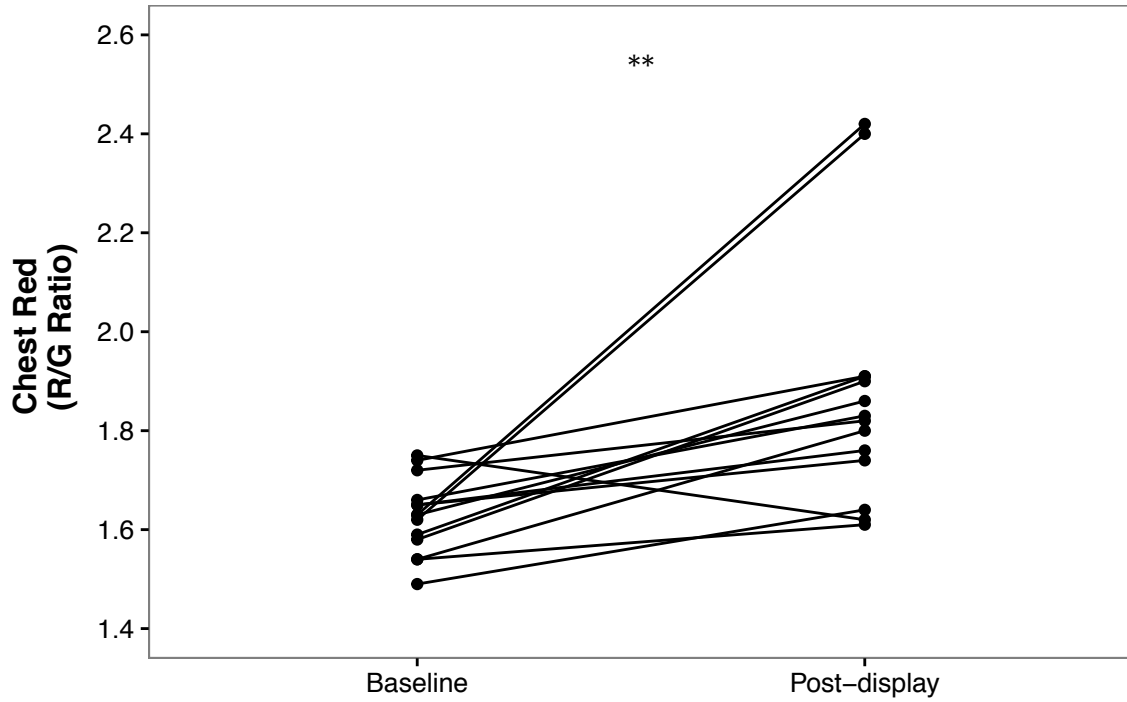
Figure 5.4. Chest color (R/G ratio) for males at rest and after engaging in a display. ** Significant at p<0.01.
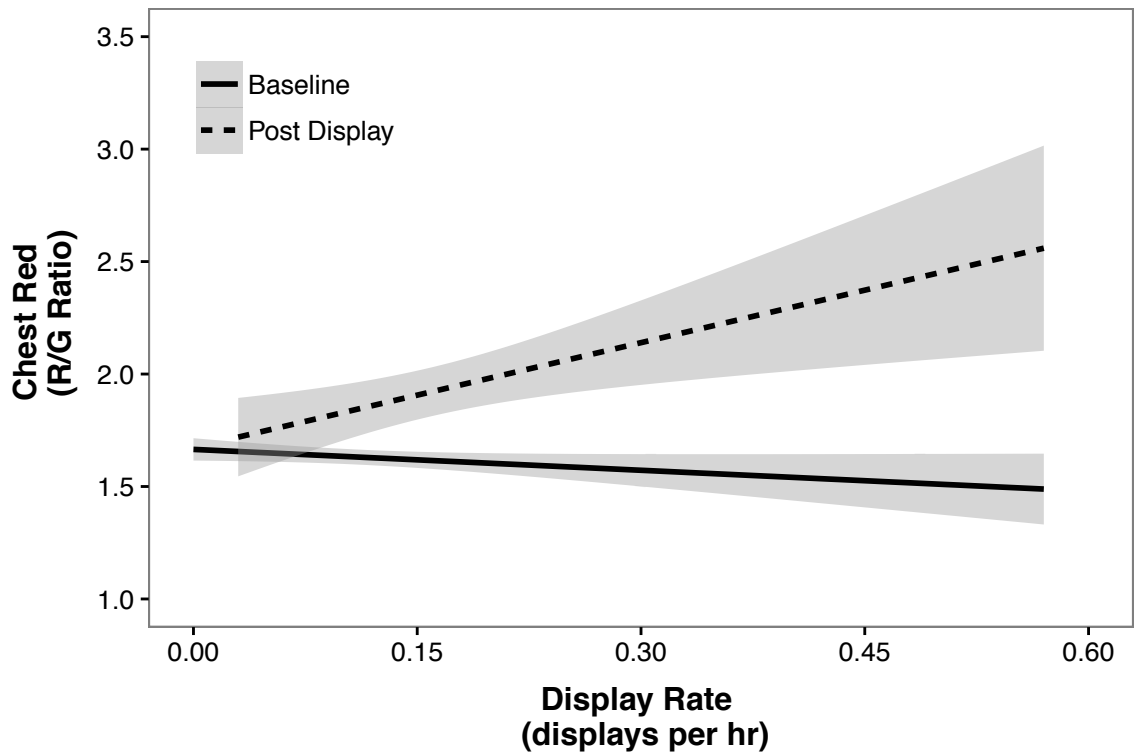
Figure 5.5. Relationship between chest color (R/G ratio ±SEM) and display rate for chest photos taken at rest (baseline) and after a male displayed (post-display)
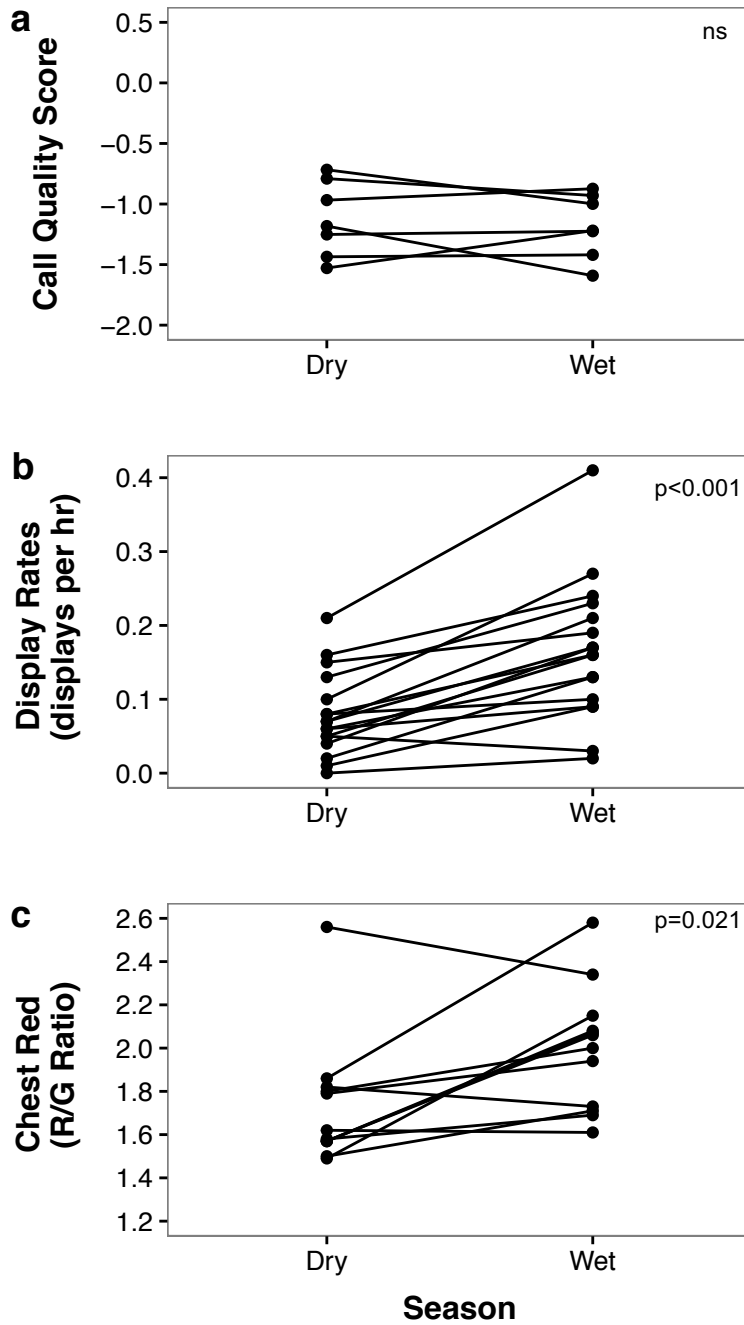
Figure 5.6. Seasonal differences in (a) call quality score, (b) display rate (b), and (c) post-display chest color.
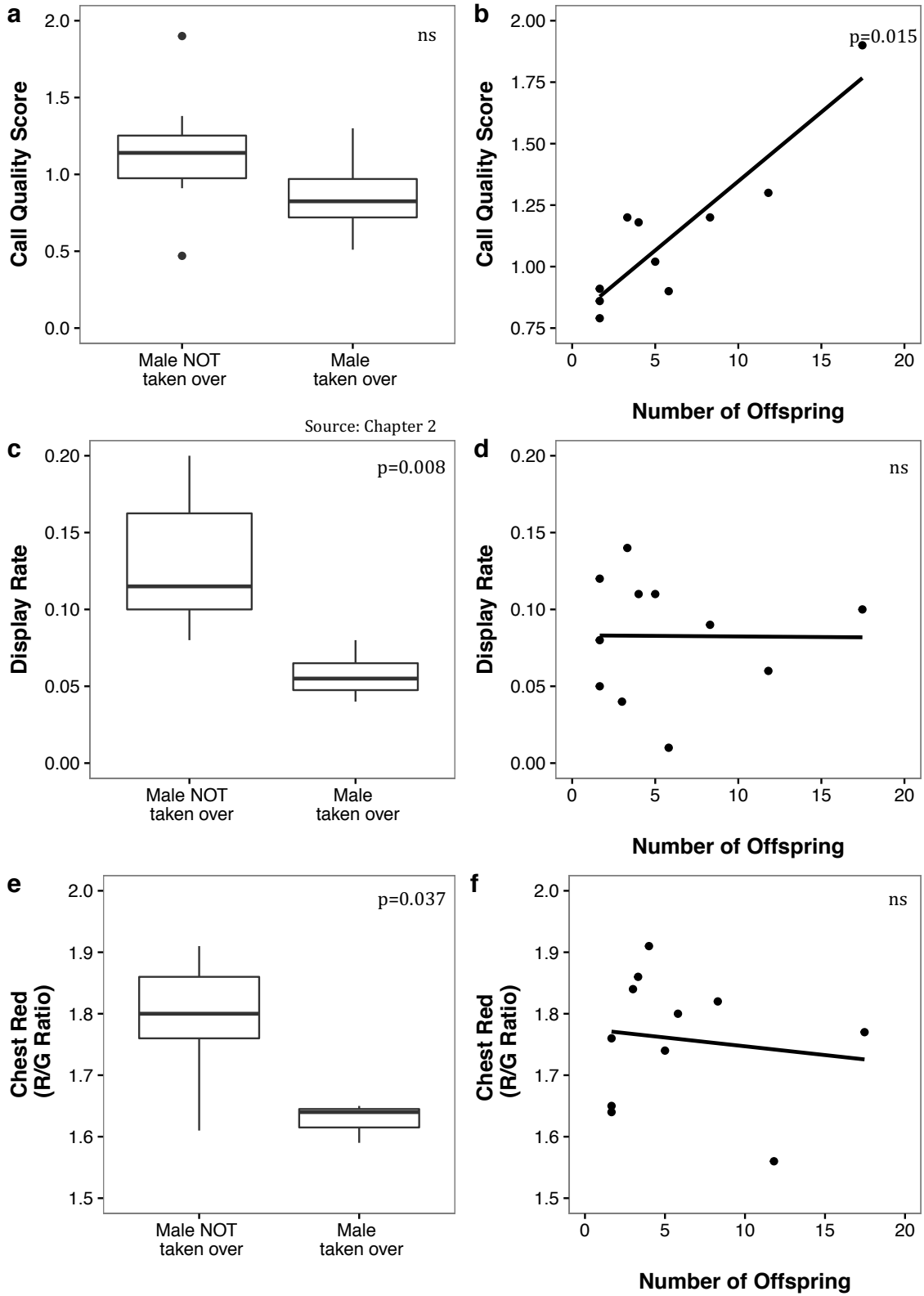
Figure 5.7. Relationship between call quality (a,b), display rate (c,d) , and post-display chest redness (e,f) on likelihood of takeover, and number of offspring sired by a male during his tenure.
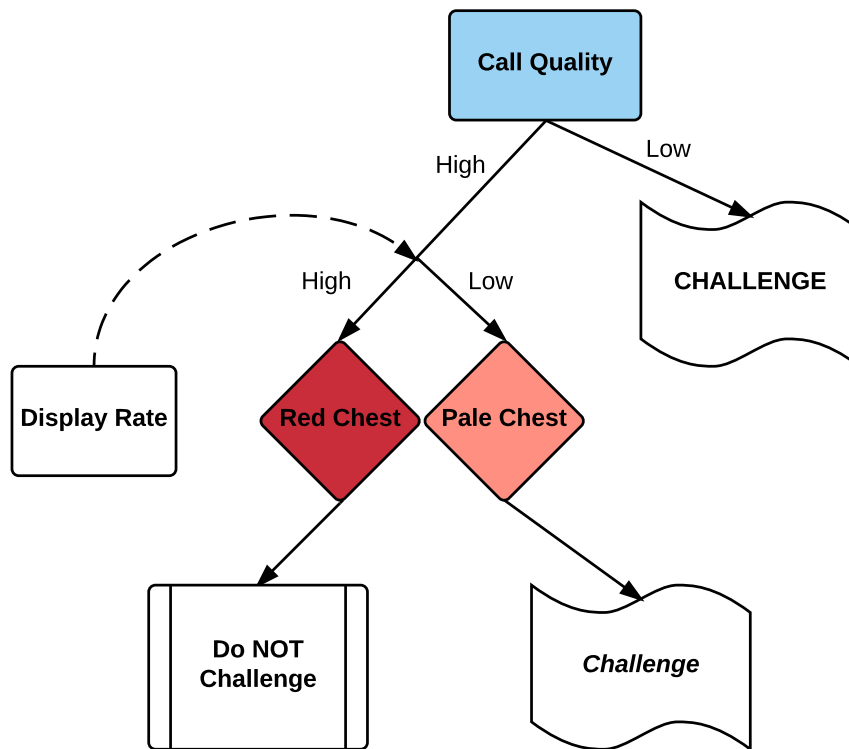
Figure 5.8. Bachelor decision-making flow chart based on signal assessment. Bachelors can attend to just call quality of a rival, a relatively low-risk strategy of targeting the weakest males, or can attend to both call quality and chest patch color during displays to assess when a strong male is at his weakest.

CHAPTER 6

CONCLUSION

Although signals in primates are relatively rare, the unusually large groups found in gelada society may have favored their evolution (Bergman & Sheehan 2013). The research presented here examined one putative signal for male geladas living in the Simien Mountains National Park (SMNP), Ethiopia: the loud call vocalization used in male displays (Dunbar 1984). In order to determine if loud calls are sexually-selected signals it must be established that: (1) signal variation exists across males of different quality, (2) males are able to distinguish between high and low quality males based on these calls, (3) receivers base reproductive decisions on these calls, and (4) males with high quality calls have higher reproductive success (Snowdon 2004). To address these criteria, this research combined acoustic, experimental, hormonal, and behavioral analysis in one of the most comprehensive studies of a sexually-selected signal in a primate.

RESEARCH QUESTIONS

Question 1: Is there variation in loud call production among males of different quality?

Many animals rely on information from vocal displays to assess potential competitors or attract mates. Gelada loud calls are uttered during ritualistic chases with rival males. Given the physically taxing nature of these displays, we examined whether (1) the *rate* of loud call production or (2) the *acoustic properties* of loud calls were energetically constrained and/or mediated by testosterone, and thus, reliable signals of male stamina and competitive ability.

In Chapter 2, we found that the rate at which males engage in these displays functions as an honest indicator of male ability. Leader males displayed more often than follower males, and, among leaders, males that displayed least often were more likely to be replaced. Supporting the hypothesis that these displays are costly to produce, we found that males displayed more often during the wet season months, when food was readily available, despite the fact that male-male competition was highest in the dry season. Furthermore, we found that males with higher testosterone displayed more often than males with low testosterone (controlling for age and status differences). Display rates appeared to mirror seasonal differences in testosterone; males called more during the months when testosterone was highest. These results indicate that displays are used in male-male competition and that males can attend to displays in order to gain honest information about their rivals' overall condition or androgen levels.

In Chapter 3, we found that several acoustic features varied consistently across age, status, and exhaustion, such that males deemed 'higher quality' in gelada society (e.g., prime-aged, high-status) uttered more calls per bout, produced calls that were lower in overall frequency measures, and exhibited a

145

greater vocal range. Results from this study are consistent with the hypothesis that gelada loud calls are quality signals, contributing to the growing evidence that primates may use acoustic information to assess the quality of a rival or a potential mate.

When examined together (Chapter 5), we found a direct relationship between display rate and call quality among dominant leader males. Yet unlike display rate, we found no difference in loud call quality due to seasonal changes. This suggests that loud calls may signal long-term condition or intrinsic quality, while display rate functions as a signal of current condition. We also found that display rate was directly related to the red coloration of a male's chest, a second signal that is unique to geladas. We suspect that these signals work together to deter challenges from rival males (Figure 6.1).

Question 2: Do gelada males discriminate between loud call acoustic properties when assessing potential rivals (high vs. low quality calls)?

Since the acoustic properties of loud calls are honest indicators of a male's physical condition (Benítez et al., 2016), rival males should attend to these calls when making important reproductive decisions about which males to challenge and which to avoid. To test this hypothesis, we conducted a playback experiment where each subject (leaders, bachelors, and females) heard both a high quality call and a low quality call (n=60). We found that males, but not females, discriminate between high and low quality calls (Chapter 4). Moreover, bachelors responded more strongly to low quality calls, while leader males were

146

more attentive to high quality calls. These results suggest that bachelor males have more to gain from engaging weak rivals, and leader males have more to lose from stronger conspecifics. Furthermore, the fact that male, *but not female*, geladas discriminate between loud calls based on acoustic signals of quality is strong evidence that loud calls are used for rival male assessment in this species.

Question 3: Do bachelor males make decisions to challenge leader males based on loud call properties or display frequency?

Importantly, if loud calls are sexually-selected signals then the disparity in acoustic properties of calls and/or the rate at which males call should be the basis for bachelor decision-making. We found several lines of evidence to suggest that bachelors use information from both vocal and visual signals to make decisions. First, in Chapter 3, we found that bachelor males were (a) more likely to approach low-quality calls, and (b) more likely to reach (or pass) the source of the call when they approached the speaker. As is common with playback studies of aggressive calls, approaching the source of the call is a relatively high-cost response as it implies an interest in engaging the caller. Our results suggest that bachelor males assess the quality of leader males by attending to these loud calls, and that they use information from these calls to make decisions about which males to challenge and which to avoid.

However, as discussed in Chapter 4, we did not find that leader males with low-quality calls were more likely to be taken over. Instead we found that

display rate and chest patch color (after a male display) were better indicators of a male's likelihood of being challenged. We suspect that bachelors may be attending to both loud call quality and chest redness as a way to monitor changes in the condition of strong rivals. There is, nevertheless, the possibility that these results are not causal: the best males produce the best signals and are better able to fight off bachelors. Yet the fact that bachelors modify their behavior according to the acoustic quality of these calls suggests that bachelors attend to these calls when making decisions. A next step would be to assess if bachelors can discriminate between males based on the redness of their chests.

We also found evidence that leader males make decisions based on these acoustic signals. Specifically, males were more likely to participate in natural loud call displays when their call quality was similar to the males calling around them. Although primates routinely use individual attributes to classify others relative to themselves, this represents the first direct evidence for mutual assessment in primate signaling contests.

Question 4: Do loud call properties and/or display frequencies predict reproductive success?

Typically, measuring reproductive success in a wild primate requires long-term behavioral data. Yet because geladas have relatively discrete reproductive windows (i.e., tenure as leaders) that last on average two years (Beehner, unpublished data), reproductive success could be measured over the study period. We found that leader males gave the highest quality calls and displayed

more often than follower males. Within leader males, we found that males with the highest quality calls had the largest unit, the longest tenures, and ultimately sired the most offspring. To our knowledge, this is the first study to show a relationship between signal strength and reproductive success in a wild primate. This is surprising considering that, by definition, a sexually-selected signal must be related to reproductive fitness, otherwise "all claims about sexual selection are simply hand waving speculations" (Snowdon 2004, pg. 59).

CONCLUDING REMARKS

I started this thesis with one overarching questions: are gelada loud call displays sexually-selected signals? To answer this question, I had to address four criteria for demonstrating sexual selection in primate communication. These calls have to (1) vary between same-sex individuals, (2) elicit differential responses in conspecifics, (3) influence mating decisions, and 4) impact reproductive success. This dissertation is the first to address all four of these parameters, allowing us to conclude that *yes*, these loud calls are in fact sexually-selected.

Another overarching theme throughout this dissertation is the interplay between sexually-selected signals and social knowledge, two topics that have been independently well-studied but rarely combined in considering non-human primate taxa. Geladas appear to be the exception among primates in relying primarily on quality signals rather than individual recognition when making reproductive choices (Bergman 2010). While this hypothesis requires further

investigation, it is clear that geladas need not attend to social information to make informed decisions about rivals. We speculate that geladas evolved multiple signals, both the loud call and the chest patch, as a way to reliably assess and monitor the fighting abilities of dozens of strangers (Bergman & Sheehan 2013). This may not be the case in baboons and other primate species where loud calls likely function to *supplement,* rather than replace, social knowledge (Bergman & Sheehan 2013).

Understanding how geladas acquire information about conspecifics – specifically unknown rivals and mates – may provide insight to the cognitive abilities needed to successfully navigate large and complex social groups, a social pressure shared by our early ancestors (Elton 2006). Throughout human evolution, group size is thought to have steadily increased with individuals living in small family groups nested within a larger social system – a social system that mirrors that of geladas. Thus, knowledge of individuals for early hominins probably did not extend beyond a small subset of group members. In other words, early hominins (as geladas) may have needed rapid means of assessing rival males in the absence of individual recognition. Offering some support to this hypothesis, the low-pitch voices of men have been proposed to be sexually-selected signals for men (and women) to assess the dominance and quality of their bearers (Puts et al. 2006; Apicella et al. 2007; Tigue et al. 2011). Perhaps at some point during hominin evolution, individuals may have relied more on signals than social knowledge when making reproductive decisions.
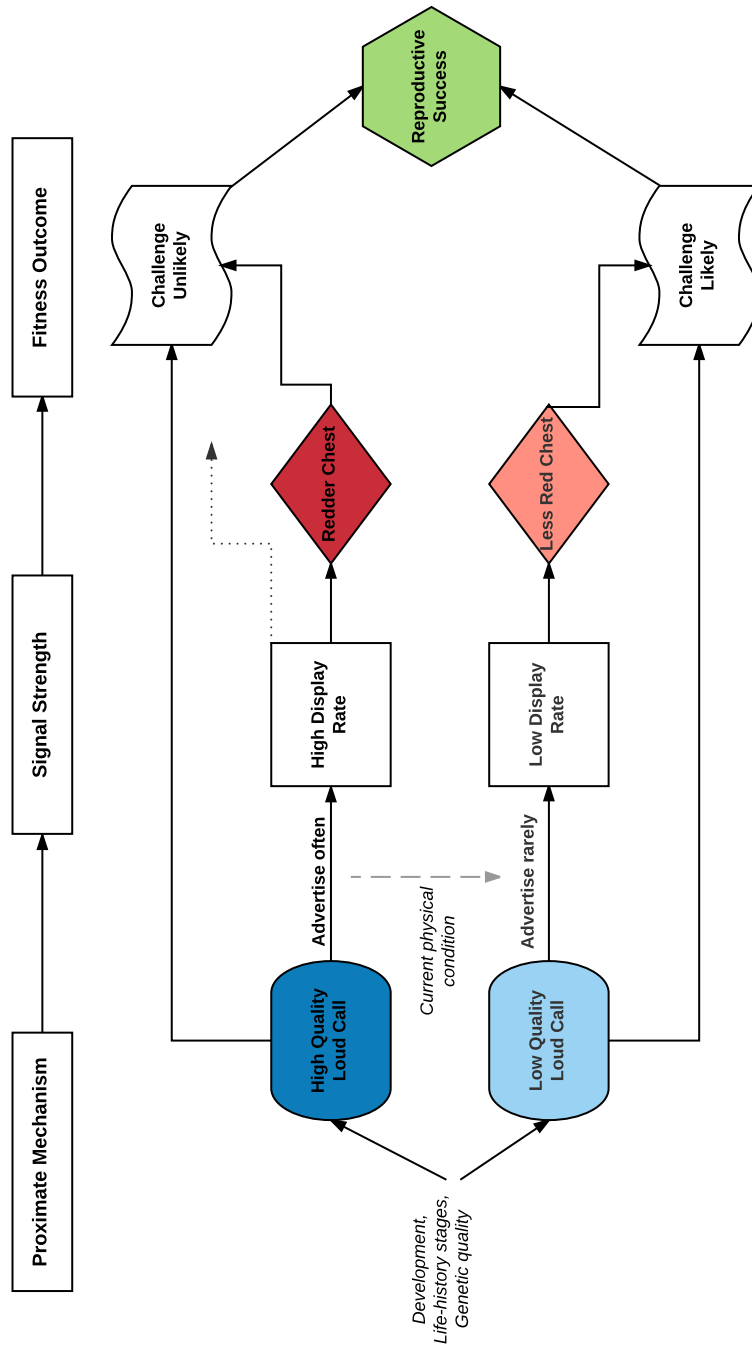
FIGURES

Figure 6.1. Diagram of mechanisms, signal strength, and reproductive fitness for leader males.

REFERENCES

CHAPTER 1

Aich, H., R. Moos-Heilen, and E. Zimmermann. 1990. "Vocalizations of Adult Gelada Baboons (*Theropithecus Gelada*): Acoustic Structure and Behavioural Context." *International Journal of Primatology,* 55, 109–32.

Andersson, M. 1982. "Female Choice Selects for Extreme Tail Length in a Widowbird." *Nature* 299, 818-830.

Andersson, M. B. 1994. *Sexual Selection.* Princeton University Press.

Bee, M. A. 2002. "Territorial Male Bullfrogs (*Rana Catesbeiana*) Do Not Assess Fighting Ability Based on Size-Related Variation in Acoustic Signals." *Behavioral Ecology,* 13, 109-124.

Bergman, T. J. 2010. Experimental evidence for limited vocal recognition in a wild primate: implications for the social complexity hypothesis. *Proceedings. Biological sciences / The Royal Society*, 277, 3045–3053.

Bergman, T. J. & Beehner, J. C. 2008. A simple method for measuring colour in wild animals: validation and use on chest patch colour in geladas (*Theropithecus gelada*). *Biological journal of the Linnean Society. Linnean Society of London*, 94, 231–240.

Bergman, T. J. & Sheehan, M. J. 2013. Social knowledge and signals in primates. *American journal of primatology*, 75, 683–694.

Bergman, T. J., Ho, L. & Beehner, J. C. 2009. Chest Color and Social Status in Male Geladas (*Theropithecus gelada*). *International journal of primatology*, 1–16.

Bradbury, J. W. & Vehrencamp, S. L. 2011. *Principles of Animal Communication.* Macmillan Education.

Clutton-Brock, T. H., & Albon, S. D. (1979). The Roaring of Red Deer and the Evolution of Honest Advertisement. *Behaviour*, *69*(3), 145–170.

Clutton-Brock, T. H., Guinness, F. E., & Albon, S. D. (1982). *Red Deer: Behavior and Ecology of Two Sexes*. University of Chicago Press.

Crook, John Hurrell. 1966. Gelada Baboon Herd Structure and Movement. A Comparative Report. *Symp Zool Soc Lond*, 18, 237-58.

Darwin, C. 1859. *On the Origin of Species*. London: Murray.

Darwin, C. 1871. *The Descent of Man and Selection in Relation To Sex.* London: Murray.

Delgado, R. A. 2006. Sexual selection in the loud calls of male primates: signal content and function. *International journal of primatology*, 27, 5–25.

Delson E. 1993. *Theropithecus* fossils from Africa and India and the taxonomy of the genus. In: Jablonski NG, editor.*Theropithecus*: the rise and fall of a primate genus. Cambridge: Cambridge U Pr. p 157-89.

Dunbar, R. 1984. *Reproductive decisions: an economic analysis of gelada baboon social strategies.* Princeton, New Jersey: Princeton University Press.

Dunbar, R. & Dunbar, P. 1975. Social dynamics of gelada baboons. *Contributions to primatology*, 6, 1–157.

Dunbar, Robin I. M. 1993. "Social Organization of the Gelada." *Theropithecus: The Rise and Fall of a Primate Genus*, 425–39.

Emlen, Stephen T. 1968. "Territoriality in the Bullfrog, *Rana Catesbeiana*." Copeia 1968 (2). American Society of Ichthyologists and Herpetologists (ASIH), Allen Press: 240–43.

Fischer, J., D. M. Kitchen, R. M. Seyfarth, and D. L. Cheney. 2004. "Baboon Loud Calls Advertise Male Quality: Acoustic Features and Their Relation to Rank, Age, and Exhaustion." Behavioral Ecology and Sociobiology 56 (2). Springer: 140–48.

Fusani, L., L. Beani, and F. Dessi-Fulgheri. 1994. "Testosterone Affects the Acoustic Structure of the Male Call in the Grey Partridge (*Perdix Perdix*)." Behaviour, 128 3 (4). Brill: 301–10.

Gerald, M. S. 2001. Primate colour predicts social status and aggressive outcome. *Animal behaviour*, 61, 559–566.

Gustison, M.L., le Roux, A, and Bergman, T.J.. 2012. "Derived Vocalizations of Geladas (*Theropithecus Gelada*) and the Evolution of Vocal Complexity in Primates." *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* 367, 1847–59.

Hall, K. R. L. & DeVore, I. 1965. Baboon social behavior. In: *Primate behavior: field studies of monkeys and apes*, (Ed. by I. DeVore), pp. 53–110. New York: Holt Rinehart Winston.

Howard, Richard D. 1978. "The Evolution of Mating Strategies in Bullfrogs, Rana Catesbeiana." Evolution; International Journal of Organic Evolution 32 (4). [Society for the Study of Evolution, Wiley]: 850–71.

Kawai, M., H. Ohsawa, U. Mori, and R. Dunbar. 1983. "Social Organization of Gelada Baboons: Social Units and Definitions." Primates; Journal of Primatology 24 (1). Springer-Verlag: 13–24.

Kawai, M. 1979. Auditory communication and social relations. *Ecological and Sociological Studies of Gelada Baboons*, 219–241.

Kitchen, D. M., Seyfarth, R. M., Fischer, J. & Cheney, D. L. 2003. Loud calls as indicators of dominance in male baboons (*Papio cynocephalus ursinus)*. *Behavioral ecology and sociobiology*, 53, 374–384.

Kitchen, D. M., Horwich, R. H. & James, R. A. 2004. Subordinate male black howler monkey (*Alouatta pigra*) responses to loud calls: experimental evidence for the effects of intra-group male relationships and age. *Behaviour*, 703–723.

Kitchen, D. M., Cheney, D. L. & Seyfarth, R. M. 2005. Male chacma baboons (*Papio hamadryas ursinus*) discriminate loud call contests between rivals of different relative ranks. *Animal cognition*, 8, 1–6.

Kitchen, D. M., Cheney, D. L., Engh, A. L., Fischer, J., Moscovice, L. R. & Seyfarth, R. M. 2013. Male baboon responses to experimental manipulations of loud wahoo calls: testing an honest signal of fighting ability. *Behavioral ecology and sociobiology*, 67, 1825–1835.

Le Boeuf, Burney J. 1974. "Male-Male Competition and Reproductive Success in Elephant Seals." American Zoologist 14 (1). The Oxford University Press: 163–76.

Linhart, Pavel, and Roman Fuchs. 2015/5. "Song Pitch Indicates Body Size and Correlates with Males' Response to Playback in a Songbird." Animal Behaviour 103: 91–98.

Maynard Smith, J. & Price, G. R. 1973. The Logic of Animal Conflict. *Nature*, 246, 15.

Maynard Smith, J. 1982. Evolution and the Theory of Games. Cambridge University Press.

Mitani, J. C. 1985. Sexual selection and adult male orangutan long calls. *Animal behaviour*, 33, 272–283.

Mitani, J. C. 1985. Location-specific Responses of Gibbons (*Hylobates muelleri*) to Male Songs. *Zeitschrift für Tierpsychologie*,

Mitani, J. C. 1988. Male Gibbon (*Hylobates agilis*) Singing Behavior: Natural History, Song Variations and Function. *Ethology: formerly Zeitschrift fur Tierpsychologie*, 79, 177–194.

Mitani, J. C. & Nishida, T. 1993. Contexts and social correlates of long-distance calling by male chimpanzees. *Animal behaviour*, 45, 735–746.

Mitani, J. C. & Stuht, J. 1998. The evolution of nonhuman primate loud calls: Acoustic adaptation for long-distance transmission. *Primates; journal of primatology*, 39, 171–182.

Pappano, D. J., & Beehner, J. C. (2014). Harem-holding males do not rise to the challenge: androgens respond to social but not to seasonal challenges in wild geladas. *Royal Society open science*, *1*(1), 140081.

Raemaekers, J. J., Raemaekers, P. M. & Haimoff, E. H. 1984. Loud Calls of the Gibbon (*Hylobates Lar)*: Repertoire, Organisation and Context. *Behaviour*, 91, 146–189.

Reby, D., & McComb, K. (2003). Anatomical constraints generate honesty: acoustic cues to age and weight in the roars of red deer stags. *Animal behaviour*, *65*(3), 519–530.

Rendall, Drew, Michael J. Owren, and Michael J. Ryan. 2009/8. "What Do Animal Signals Mean?" Animal Behaviour 78 (2): 233–40.

Sekulic, R. 1982. The Function of Howling in Red Howler Monkeys (*Alouatta Seniculus*). *Behaviour*, 81, 38–54.

Setchell, J. M. & Dixson, A. F. 2001. Changes in the secondary sexual adornments of male mandrills (*Mandrillus sphinx*) are associated with gain and loss of alpha status. *Hormones and behavior*, 39, 177–184.

Setchell, J. M. & Kappeler, P. M. 2003. Selection in Relation to Sex in Primates. In: *Advances in the Study of Behavior*, Vol Volume 33 pp. 87–173. Academic Press.

Snowdon, C. T. 2004. Sexual selection and communication. In: *Sexual selection in primates*, (Ed. by P. Kappeler & C. van Shaik), pp. 57–70. Cambridge: Cambridge University Press.

Snyder-Mackler, N., Beehner, J. C. & Bergman, T. J. 2012. Defining Higher Levels in the Multilevel Societies of Geladas (*Theropithecus gelada*). *International journal of primatology*, 33, 1054–1068.

Sullivan, B. K. & Kwiatkowski, M. A. 2007. Courtship displays in anurans and lizards: theoretical and empirical contributions to our understanding of costs and selection on males due to female choice. *Functional ecology*, 21, 666–675.

Teichroeb, J. A. & Sicotte, P. 2010. The Function of Male Agonistic Displays in Ursine Colobus Monkeys *(Colobus vellerosus*): Male Competition, Female Mate Choice or Sexual Coercion? *Ethology: formerly Zeitschrift fur Tierpsychologie*, 116, 366–380.

Tenaza, R. R. 1976. Songs, choruses and countersinging of Kloss' gibbons (*Hylobates klossii*) in Siberut Island, Indonesia. *Zeitschrift fur Tierpsychologie*, 40, 37–52.

Tomasello, M. & Call, J. 1997. *Primate Cognition.* Oxford University Press.

Utami, S. & Mitra Setia, T. 1995. Behavioral Changes in Wild Male and Female Sumatran Orangutans (*Pongo pygmaeus abelii*) During and Following a Resident Male Take-Over. In: *The Neglected Ape*, (Ed. by R. D. Nadler, B. F. M. Galdikas, L. K. Sheeran, & N. Rosen), pp. 183–190. Springer US.

Van Belle, S., Estrada, A. & Garber, P. A. 2014. The function of loud calls in black howler monkeys (*Alouatta pigr*a): food, mate, or infant defense? *American journal of primatology*, 76, 1196–1206.

Vehrencamp, S. L. 2000. Handicap, index, and conventional signal elements of bird song. *Animal signals: Signalling and signal design in animal communication*, 277–300.

Vehrencamp, Sandra L., Jack W. Bradbury, and Robert M. Gibson. 1989. "The Energetic Cost of Display in Male Sage Grouse." Animal Behaviour 38 (5). Elsevier: 885–96.

Waser, P. M. 1975. Experimental playbacks show vocal mediation of intergroup avoidance in a forest monkey. *Nature*,

Waser, P. M. 1977. Individual Recognition, Intragroup Cohesion and Intergroup Spacing: Evidence From Sound Playback To Forest Monkeys. *Behaviour*, 60, 28–74.

Whitehead, J. M. 1989. The Effect of the Location of a Simulated Intruder On Responses To Long-Distance Vocalizations of Mantled Howling Monkeys, *Alouatta Palliata Palliata*. *Behaviour*, 108, 73–103.

Wich, S. A. & Nunn, C. L. 2002. Do male" long-distance calls" function in mate defense? A comparative study of long-distance calls in primates. *Behavioral ecology and sociobiology*,

Zahavi, A. 1975. "Mate Selection-a Selection for a Handicap." Journal of Theoretical Biology 53 (1): 205–14.

Zahavi, A., A. Zahavi, N. Ely, M. P. Ely, and A. Balaban. 1999. The Handicap Principle: A Missing Piece of Darwin's Puzzle. Oxford University Press.

Zimmermann, E. 1995. Loud Calls in Nocturnal Prosimians: Structure, Evolution and Ontogeny. In: *Current Topics in Primate Vocal Communication*, (Ed. by E. Zimmermann, J. D. Newman, & U. Jürgens), pp. 47–72. Springer US.

CHAPTER 2

Adkins-Regan, E. (1981). Effect of sex steroids on the reproductive behavior of castrated male ring doves (*Streptopelia sp.*). *Physiology & behavior*, *26*(4), 561–565.

Andersson, M. B. (1994). *Sexual Selection*. Princeton University Press.

Barelli, C., Mundry, R., Heistermann, M., & Hammerschmidt, K. (2013). Cues to androgens and quality in male gibbon songs. *PloS one*, *8*(12), e82748.

Barfield, R. J. (1971). Activation of sexual and aggressive behavior by androgen implanted into the male ring dove brain. *Endocrinology*, *89*(6), 1470–1476.

Beehner, J. C., Bergman, T. J., Cheney, D. L., Seyfarth, R. M., & Whitten, P. L. (2006). Testosterone predicts future dominance rank and mating activity among male chacma baboons. *Behavioral ecology and sociobiology*, *59*(4), 469–479.

Beehner, J. C., Gesquiere, L., Seyfarth, R. M., Cheney, D. L., Alberts, S. C., & Altmann, J. (2009). Testosterone related to age and life-history stages in male baboons and geladas. *Hormones and behavior*, *56*(4), 472–480.

Beehner, J. C., Gesquiere, L., Seyfarth, R. M., Cheney, D. L., Alberts, S. C., & Altmann, J. (2015). Corrigendum to Testosterone related to age and life-history stages in male baboons and geladas [Horm. Behav. 56/4 (2009) 472--480]. *Hormones and behavior*.

Beehner, J. C., & McCann, C. (2008). Seasonal and altitudinal effects on glucocorticoid metabolites in a wild primate (*Theropithecus gelada*). *Physiology & behavior*, *95*(3), 508–514.

Beehner, J. C., & Whitten, P. L. (2004). Modifications of a field method for fecal steroid analysis in baboons. *Physiology & behavior*, *82*(2-3), 269–277.

Berg, A., Alvaro, B., & Greenfield, M. D. (2005). Sexual selection in insect choruses: Influences of call power and relative timing. *Journal of insect behavior*, *18*(1), 59–75.

Bergman, T. J. (2010). Experimental evidence for limited vocal recognition in a wild primate: implications for the social complexity hypothesis. *Proceedings. Biological sciences / The Royal Society*, *277*(1696), 3045–3053.

Bergman, T. J., Beehner, J. C., Cheney, D. L., Seyfarth, R. M., & Whitten, P. L. (2006). Interactions in male baboons: the importance of both males' testosterone. *Behavioral ecology and sociobiology*, *59*(4), 480–489.

Braude, S., Tang-Martinez, Z., & Taylor, G. T. (1999). Stress, testosterone, and the immunoredistribution hypothesis. *Behavioral ecology: official journal of the International Society for Behavioral Ecology*, *10*(3), 345–350.

Buchanan, K. L., Evans, M. R., Goldsmith, A. R., Bryant, D. M., & Rowe, L. V. (2001). Testosterone influences basal metabolic rate in male house sparrows: a new cost of dominance signalling? *Proceedings. Biological sciences / The Royal Society*, *268*(1474), 1337–1344.

Clutton-Brock, T. H., & Albon, S. D. (1979). The Roaring of Red Deer and the Evolution of Honest Advertisement. *Behaviour*, *69*(3), 145–170.

Clutton-Brock, T. H., Guinness, F. E., & Albon, S. D. (1982). *Red Deer: Behavior and Ecology of Two Sexes*. University of Chicago Press.

Cowlishaw, G. (1996). Sexual Selection and Information Content in Gibbon Song Bouts. *Ethology*, *102*(2), 272–284.

Crocker, D. E., Houser, D. S., & Webb, P. M. (2012). Impact of body reserves on energy expenditure, water flux, and mating success in breeding male northern elephant seals. *Physiological and biochemical zoology: PBZ, 85*(1), 11–20.

Davies, N. B., & Halliday, T. R. (1978). Deep croaks and fighting assessment in toads *Bufo bufo*, *274*(5672), 683–685.

Delaney, K. J., Andrew Roberts, J., & Uetz, G. W. (2007). Male signaling behavior and sexual selection in a wolf spider (*Araneae lycosidae*): a test for dual functions. *Behavioral ecology and sociobiology*, *62*(1), 67–75.

Delgado, R. A. (2006). Sexual selection in the loud calls of male primates: signal content and function. *International journal of primatology*, *27*(1), 5–25.

Dixson, A. F. (1980). Androgens and aggressive behavior in primates: A review. *Aggressive behavior*, *6*(1), 37–67.

Dunbar, R. (1984). Reproductive decisions. *An economic analysis of gelada baboon social strategies*. Princeton, NJ: Princeton University Press.

Dunbar, R., & Dunbar, P. (1975). Social dynamics of gelada baboons. *Contributions to primatology*, *6*, 1–157.

Dunbar, R., & Bose, U. (1991). Adaptation to grass-eating in gelada baboons. *Primates; journal of primatology*, *32*(1), 1–7.

Emerson, S. B., & Hess, D. L. (2001). Glucocorticoids, androgens, testis mass, and the energetics of vocalization in breeding male frogs. *Hormones and behavior*, *39*(1), 59–69.

Emery Thompson, M., & Knott, C. D. (2008). Urinary C-peptide of insulin as a non-invasive marker of energy balance in wild orangutans. *Hormones and behavior*, *53*(4), 526–535.

Erb, W. M., Ziegler, T., Lestari, N. S., & Hammerschmidt, K. (2016). Are simakobu (*Simias concolor*) loud calls energetically costly signals? *American journal of physical anthropology*. doi:10.1002/ajpa.23005

Fischer, J., Kitchen, D. M., Seyfarth, R. M., & Cheney, D. L. (2004). Baboon loud calls advertise male quality: acoustic features and their relation to rank, age, and exhaustion. *Behavioral ecology and sociobiology*, *56*(2), 140–148.

Folstad, I., & Karter, A. J. (1992). Parasites, Bright Males, and the Immunocompetence Handicap. *The American naturalist*, *139*(3), 603–622.

Fusani, L. (2008). Testosterone control of male courtship in birds. *Hormones and behavior*, *54*(2), 227–233.

Gentner, T. Q., & Hulse, S. H. (2000). Female European starling preference and choice for variation in conspecific male song. *Animal behaviour*, *59*(2), 443–458.

Gerhardt, H. C. (2000). Female preference functions based on call duration in the gray tree frog (*Hyla versicolor*). *Behavioral ecology: official journal of the International Society for Behavioral Ecology*, *11*(6), 663–669.

Godfrey, J. D., & Bryant, D. M. (2000). State-dependent behaviour and energy expenditure: an experimental study of European robins on winter territories. *The Journal of animal ecology*, *69*(2), 301–313.

Gottlander, K. (1987). Variation in the song rate of the male pied flycatcher *Ficedula hypoleuca*: causes and consequences. *Animal behaviour*, *35*(4), 1037–1043.

Grafen, A. (1990). Biological signals as handicaps. *Journal of theoretical biology*, *144*(4), 517–546.

Gray, D. A., & Eckhardt, G. (2001). Is cricket courtship song condition dependent? *Animal behaviour*, *62*(5), 871–877.

Halliday, T. R. (1987). Physiological constraints on sexual selection. *Sexual selection: testing the alternatives*, 247–264.

Hall, K. R. L., & DeVore, I. (1965). Baboon social behavior. In I. Devore (Ed.), *Primate behavior: field studies of monkeys and apes* (pp. 53–110). New York: Hold Rinehart Winstor.

Harris, T. R., Fitch, W. T., Goldstein, L. M., & Fashing, P. J. (2006). Black and White Colobus Monkey (*Colobus guereza*) Roars as a Source of Both Honest and Exaggerated Information About Body Mass. *Ethology*, *112*(9), 911–920.

Hill, R. A. (2006). Thermal constraints on activity scheduling and habitat choice in baboons. *American journal of physical anthropology*, *129*(2), 242–249.

Hill, W. C. O. (1970). *Primates: Papio, Mandrillus, Theropithecus : Comparative Anatomy and Taxonomy*.

Humfeld, S. C. (2013). Condition-dependent signaling and adoption of mating tactics in an amphibian with energetic displays. *Behavioral ecology: official journal of the International Society for Behavioral Ecology*, *24*(4), 859–870.

Hunter, C. P. (2001). *Ecological determinants of gelada ranging patterns (Theropithecus gelada)*. University of Liverpool.

Iwamoto, T. (1993). Food digestion and energetic conditions in *Theropithecus gelada*. In N. G. Jablonski & N. G. Jablonski (Eds.), *Theropithecus* (pp. 453–464). Cambridge: Cambridge University Press.

Iwamoto, T., & Dunbar, R. I. M. (1983). Thermoregulation, Habitat Quality and the Behavioural Ecology of Gelada Baboons. *The Journal of animal ecology*, *52*(2), 357–366.

Kacelnik, A. (1979). The foraging efficiency of great tits (*Parus major L.*) in relation to light intensity. *Animal behaviour*, *27*, 237–241.

Kawai, M. (1979). Auditory communication and social relations. *Ecological and Sociological Studies of Gelada Baboons*, 219–241.

Kitchen, D. M., Cheney, D. L., Engh, A. L., Fischer, J., Moscovice, L. R., & Seyfarth, R. M. (2013). Male baboon responses to experimental manipulations of loud wahoo calls: testing an honest signal of fighting ability. *Behavioral ecology and sociobiology*, *67*(11), 1825–1835.

Kitchen, D. M., Seyfarth, R. M., Fischer, J., & Cheney, D. L. (2003). Loud calls as indicators of dominance in male baboons (*Papio cynocephalus ursinus*). *Behavioral ecology and sociobiology*, *53*(6), 374–384.

Kotiaho, J. S., Alatalo, R. V., Mappes, J., Nielsen, M. G., Parri, S., & Rivero, A. (1998). Energetic costs of size and sexual signalling in a wolf spider. *Proceedings of the Royal Society of London B: Biological Sciences*, *265*(1411), 2203–2209.

Mace, R. (2008). The relationship between daily routines of singing and foraging: an experiment on captive Great Tits *Parus major*. *The Ibis*, *131*(3), 415–420.

Marler, C. A., & Moore, M. C. (1988). Evolutionary costs of aggression revealed by testosterone manipulations in free-living male lizards. *Behavioral ecology and sociobiology*, *23*(1), 21–26.

Marler, C. A., & Ryan, M. J. (1996). Energetic constraints and steroid hormone correlates of male calling behaviour in the túngara frog. *Journal of zoology*, *240*(3), 397–410.

Mau, M., Südekum, K.-H., Johann, A., Sliwa, A., & Kaiser, T. M. (2009). Saliva of the graminivorous *Theropithecus gelada* lacks proline-rich proteins and tannin-binding capacity. *American journal of primatology*, *71*(8), 663–669.

Mcelligott, A. G., O'neill, K. P., & Hayden, T. J. (1999). Cumulative long-term investment in vocalization and mating success of fallow bucks, *Dama dama*. *Animal behaviour*, *57*(5), 1159–1167.

Mitani, J. C. (1988). Male Gibbon (*Hylobates agilis*) Singing Behavior: Natural History, Song Variations and Function. *Ethology*, *79*(3), 177–194.

Mitani, J. C., & Nishida, T. (1993). Contexts and social correlates of long-distance calling by male chimpanzees. *Animal behaviour*, *45*(4), 735–746.

Mori, U. (1979). Ecological and sociological studies of gelada baboons. Development of sociability and social status. *Contributions to primatology*, *16*, 125–154.

Mowles, S. L., & Jepson, N. M. (2015). Physiological Costs of Repetitive Courtship Displays in Cockroaches Handicap Locomotor Performance. *PloS one*, *10*(11), e0143664.

Muller, M. N., & Wrangham, R. W. (2004). Dominance, aggression and testosterone in wild chimpanzees: a test of the "challenge hypothesis." *Animal behaviour*, *67*(1), 113–123.

Neumann, C., Assahad, G., Hammerschmidt, K., Perwitasari-Farajallah, D., & Engelhardt, A. (2010). Loud calls in male crested macaques, *Macaca nigra*: a signal of dominance in a tolerant species. *Animal behaviour*, *79*(1), 187–193.

Ohsawa, H., & Dunbar, R. I. M. (1984). Variations in the demographic structure and dynamics of gelada baboon populations. *Behavioral ecology and sociobiology*, *15*(3), 231–240. Accessed 29 June 2016

Pappano, D. J., & Beehner, J. C. (2014). Harem-holding males do not rise to the challenge: androgens respond to social but not to seasonal challenges in wild geladas. *Royal Society open science*, *1*(1), 140081.

Pappano, D. J., Roberts, E. K., & Beehner, J. C. (2010). Testing extraction and storage parameters for a fecal hormone method. *American journal of primatology*, *72*(11), 934–941.

Payne, R., & Pagel, M. (1997). Why do animals repeat displays? *Animal behaviour*, *54*(1), 109–119.

Pérez-Rodriguez, L., Blas, J., Viñuela, J., Marchant, T. A., & Bortolotti, G. R. (2006). Condition and androgen levels: are condition-dependent and testosterone-mediated traits two sides of the same coin? *Animal behaviour*, *72*(1), 97–103.

Prestwich, K. N. (1994). The energetics of acoustic signaling in anurans and insects. *American zoologist*, *34*(6), 625–643.

Prohl, H. (2003). Variation in male calling behaviour and relation to male mating success in the strawberry poison frog (*Dendrobates pumilio*). *Ethology*, *109*(4), 273–290.

Raemaekers, J. J., Raemaekers, P. M., & Haimoff, E. H. (1984). Loud calls of the gibbon (*Hylobates lar*): Repertoire, organisation and context. *Behaviour*, *91*(1), 146–189.

Reby, D., & McComb, K. (2003). Anatomical constraints generate honesty: acoustic cues to age and weight in the roars of red deer stags. *Animal behaviour*, *65*(3), 519–530.

Reid, M. L. (1987). Costliness and reliability in the singing vigour of Ipswich sparrows. *Animal behaviour*, *35*(6), 1735–1743.

Rintamaki, P.T., Eevi, K., Alatalo, R. V., & Arne, L. (1999). Why do black grouse males perform on lek sites outside the breeding season? *Journal of avian biology*, *30*(4), 359.

Robbins, M. M. (2003). Behavioral aspects of sexual selection in mountain gorillas. In *Sexual Selection & Reproductive Competition in Primates: New Perspectives and Directions* (pp. 477–501). American Society of Primatologists.

Ryan, M. J. (1988). Energy, calling, and selection. *American zoologist*, *28*(3), 885–898.

Schwartz, J. J., Buchanan, B. W., & Carl Gerhardt, H. (2001). Female mate choice in the gray treefrog (*Hyla versicolor*) in three experimental environments. *Behavioral ecology and sociobiology*, *49*(6), 443–455.

Sicotte, P. (2002). The function of male aggressive displays towards females in mountain gorillas. *Primates; journal of primatology*, *43*(4), 277–289.

Snowdon, C. T. (2004). Sexual selection and communication. In K. can Schaik (Ed.), *Sexual Selection in Primates* (pp. 57–70). Cambridge University Press.

Steenbeek, R., & Assink, P. (1998). Individual Differences in Long-Distance Calls of Male Wild Thomas Langurs *(Presbytis thomasi)*. *Folia primatologica; international journal of primatology*, *69*(2), 77–80.

Teichroeb, J. A., & Sicotte, P. (2010). The function of male agonistic displays in ursine colobus monkeys (*Colobus vellerosus*): Male competition, female mate choice or sexual Coercion? *Ethology*, *116*(4), 366–380.

Terrien, J., & Jeremy, T. (2011). Behavioral thermoregulation in mammals: a review. *Frontiers in bioscience: a journal and virtual library*, *16*(1), 1428.

Vehrencamp, S. L. (2000). Handicap, index, and conventional signal elements of bird song. *Animal signals: Signalling and signal design in animal communication*, 277–300.

Vehrencamp, S. L., Bradbury, J. W., & Gibson, R. M. (1989). The energetic cost of display in male sage grouse. *Animal behaviour*, *38*(5), 885–896.

Wagner, W. E., & Hoback, W. W. (1999). Nutritional effects on male calling behaviour in the variable field cricket. *Animal behaviour*, *57*(1), 89–95.

Wagner, W. E., Jr. (1989). Graded aggressive signals in Blanchard's cricket frog: vocal responses to opponent proximity and size. *Animal behaviour*, *38*(6), 1025–1038.

Ward, S., Speakman, J. R., & Slater, P. J. B. (2003). The energy cost of song in the canary, *Serinus canaria*. *Animal behaviour*, *66*(5), 893–902.

Waser, P. M. (1977). Individual recognition, intragroup cohesion and intergroup spacing: Evidence from sound playback to forest monkeys. *Behaviour*, *60*(1), 28–74.

Whitten, A. J. (1982). The ecology of singing in Kloss gibbons (*Hylobates klossii*) on Siberut Island, Indonesia. *International journal of primatology*, *3*(1), 33–51.

Wich, S. A., Assink, P. R., Becher, F., & Sterck, E. H. M. (2002). Playbacks of loud calls to wild Thomas langurs (primates; *Presbytis thomasi*): the effect of familiarity. *Behaviour*, *139*(1), 79–87.

Wich, S. A., Van der Post, D. J., Heistermann, M., Möhle, U., Van Hooff, J., & Sterck, E. H. M. (2003). Life-phase related changes in male loud call characteristics and testosterone levels in wild Thomas langurs. *International journal of primatology*, *24*(6), 1251–1265.

Wingfield, J. C., Ball, G. F., Dufty, A. M., Hegner, R. E., & Ramenofsky, M. (1987). Testosterone and Aggression in Birds. *American scientist*, *75*(6), 602–608.

Wingfield, J. C., Hegner, R. E., Dufty, A. M., Jr, & Ball, G. F. (1990). The" challenge hypothesis": theoretical implications for patterns of testosterone secretion, mating systems, and breeding strategies. *The American naturalist*, 829–846.

Zahavi, A. (1975). Mate selection-a selection for a handicap. *Journal of theoretical biology*, *53*(1), 205–214.

CHAPTER 3

Aich, H., Moos-Heilen, R., & Zimmermann, E. (1990). Vocalizations of adult gelada baboons (*Theropithecus gelada*): Acoustic structure and behavioural context. *Folia Primatologica; International Journal of Primatology*, *55*(3), 109-32.

Andersson, M. B. (1994). *Sexual selection.* Princeton, NJ. Princeton University Press.

Barelli, C., Mundry, R., Heistermann, M., & Hammerschmidt, K. (2013). Cues to androgens and quality in male gibbon songs. *PloS One*, *8*(12), e82748.

Bates, D., Maechler, M., Bolker, B., Walker, S., Christensen, R. H. B., Singmann, H., et al. (2015). *Package lme4*. [http://lme4.r-forge.r-project.org/]

Beehner, J. C., Gesquiere, L., Seyfarth, R. M., Cheney, D. L., Alberts, S. C., & Altmann, J. (2015). Corrigendum to "Testosterone related to age and life-history stages in male baboons and geladas" [Horm. Behav. 56/4 (2009) 472--480]. *Hormones and Behavior.*

Bergman, T. J. (2010). Experimental evidence for limited vocal recognition in a wild primate: Implications for the social complexity hypothesis. Proceedings of the Royal Society of London B: Biological Sciences, *277*, 3045-53.

Bergman, T. J. & Sheehan, M. J. (2013). Social knowledge and signals in primates. *American Journal of Primatology*, *75*, 683-694.

Bouchet, H., Blois-Heulin, C., Pellier, A. S., Zuberbühler, K., & Lemasson, A. (2012). Acoustic variability and individual distinctiveness in the vocal repertoire of red-capped mangabeys (*Cercocebus torquatus*). *Journal of Comparative Psychology*, *126*, 45-56.

Caselli, C. B., Mennill, D. J., Bicca-Marques, J. C., & Setz, E. Z. (2014). Vocal behavior of black-fronted titi monkeys (*Callicebus nigrifrons*): Acoustic properties and behavioral contexts of loud calls. *American Journal of Primatology,* 76, 788-800.

Davies, B. & Halliday, R. (1978). Deep croaks and fighting assessment in toads *Bufo bufo*. *Nature*, *274*, 683-685.

Delgado, R. A. (2006). Sexual selection in the loud calls of male primates: Signal content and function. *International Journal of Primatology*, *27*(1), 5-25.

Dunbar, R. I. M. & Dunbar, P. (1975). Social dynamics of gelada baboons. In H. Kuhn, W. P. Luckett, C. R. Noback, A. H. Schultz, D. Starck & F. S. Szalay (Eds.), Contributions to primatology. Basel: S. Karger.

Dunbar RIM. 1983 Structure of gelada baboon reproductive units. II. Social relationships between reproductive females. Animal Behaviour, 31, 556-564.

Dunbar, R. I. M. (1984). *Reproductive decisions: An economic analysis of gelada baboon social strategies.* Princeton, NJ: Princeton University Press.

Erb, W. M., Hodges, J. K., & Hammerschmidt, K. (2013). Individual, contextual, and age-related acoustic variation in simakobu (*Simias concolor*) loud calls. *PloS One*, *8*, e83131.

Ey, E., Pfefferle, D., & Fischer, J. (2007). Do age- and sex-related variations reliably reflect body size in non-human primate vocalizations? A review. *Primates; Journal of Primatology*, *48*, 253-67.

Fischer, J., Hammerschmidt, K., Cheney, D. L., & Seyfarth, R. M. (2002). Acoustic features of male baboon loud calls: Influences of context, age, and individuality. *The Journal of the Acoustical Society of America*, *111*, 1465-1474.

Fischer, J., Kitchen, D. M., Seyfarth, R. M., & Cheney, D. L. (2004). Baboon loud calls advertise male quality: Acoustic features and their relation to rank, age, and exhaustion. *Behavioral Ecology and Sociobiology*, 140-148.

Fischer, J., Noser, R., & Hammerschmidt, K. (2013). Bioacoustic field research: A primer to acoustic analyses and playback experiments with primates. *American Journal of Primatology,* 75:643–663.

Fitch, W. T. (1997). Vocal tract length and formant frequency dispersion correlate with body size in rhesus macaques. *The Journal of the Acoustical Society of America*, *102*, 1213-1222.

Fitch, W. T. & Hauser, M. D. (1995). Vocal production in nonhuman primates: Acoustics, physiology, and functional constraints on "honest" advertisement. *American Journal of Primatology*, *37*, 191-219.

Hall, K. R. L., & DeVore, I. (1965). Baboon social behavior. In I. DeVore (Ed.), *Primate Behavior: Field Studies of Monkeys and Apes* (pp. 53-110). New York: Holt, Rinehart and Winston.

Gerhardt, H. C., Tanner, S. D., Corrigan, C. M., & Walton, H. C. (2000). Female preference functions based on call duration in the gray tree frog (*Hyla versicolor*). *Behavioral Ecology*, *11*, 663-669.

Holt, M. M., Noren, D. P., Dunkin, R. C., & Williams, T. M. (2015). Vocal performance affects metabolic rate in dolphins: Implications for animals communicating in noisy environments. *The Journal of Experimental Biology*, *218*, 1647-54.

Inoue, M. (1988). Age gradations in vocalization and body weight in Japanese monkeys (*Macaca fuscata*). *Folia Primatologica*, *51*, 76-86.

Jaquiéry, J., Broquet, T., Aguilar, C., Evanno, G., & Perrin, N. (2009). Good genes drive female choice for mating partners in the lek-breeding European treefrog. *Evolution; International Journal of Organic Evolution,* 64, 108-115*.*

Kawai, M., Ohsawa, H., Mori, U., & Dunbar, R. (1983). Social organization of gelada baboons: Social units and definitions. *Primates; Journal of Primatology*, *24*, 13-24.

Kitchen, D. M., Seyfarth, R. M., Fischer, J., & Cheney, D. L. (2003). Loud calls as indicators of dominance in male baboons (*Papio cynocephalus ursinus*). *Behavioral Ecology and Sociobiology*, *53*, 374-384.

le Roux & Bergman (2012). Indirect rival assessment in a social primate, *Theropithecus gelada*. *Animal Behaviour*, *83*, 249-255.

McComb, K. 1991. Female choice for high roaring rates in red deer, *Cervus elaphus*. Animal Behaviour, 41, 79-88.

Méndez-Cárdenas, M., Randrianambinina, B., Rabesandratana, A., Rasoloharijaona, S., & Zimmermann, E. (2008). Geographic variation in loud calls of sportive lemurs (*lepilemur ssp.*) And their implications for conservation. *American Journal of Primatology*, *70*, 828-838.

Meise, K., Keller, C., Cowlishaw, G., & Fischer, J. (2011). Sources of acoustic variation: Implications for production specificity and call categorization in chacma baboon (*Papio ursinus*) grunts. *The Journal of the Acoustical Society of America*, *129*, 1631-41.

Mori, U. (1979a). Social structure of gelada baboons. In M. Kawai (Ed.), Ecological and sociological studies of gelada baboons (Vol. 16, pp. 243-247). Basel: S. Karger.

Mori, U. (1979b). Unit formation and the emergence of a new leader. In M. Kawai (Ed.), Ecological and sociological studies of gelada baboons (Vol. 16, pp. 155-181). Basel: S. Karger.

Mougeot, F., Irvine, J. R., Seivwright, L., Redpath, S. M., & Piertney, S. (2004). Testosterone, immunocompetence, and honest sexual signaling in male red grouse. *Behavioral Ecology*, *15*, 930-937.

Mundry, R. & Fischer, J. (1998). Use of statistical programs for nonparametric tests of small samples often leads to incorrect p values: Examples from animal behaviour. *Animal Behaviour*, *56*, 256-259.

Mundry, R. & Sommer, C. (2007). Discriminant function analysis with nonindependent data: Consequences and an alternative. *Animal Behaviour*, *74*, 965-976.

Neumann, C., Assahad, G., Hammerschmidt, K., Perwitasari-Farajallah, D., & Engelhardt, A. (2010). Loud calls in male crested macaques, *Macaca nigra*: A signal of dominance in a tolerant species. *Animal Behaviour*, *79*, 187-193.

Pfefferle, D. & Fischer, J. (2006). Sounds and size: Identification of acoustic variables that reflect body size in hamadryas baboons, *Papio hamadryas*. *Animal Behaviour*, *72*, 43-51.

Reby, D., McComb, K., Cargnelutti, B., Darwin, C., Fitch, W. T., & Clutton-Brock, T. (2005). Red deer stags use formants as assessment cues during intrasexual agonistic interactions. *Proceedings of the Royal Society of London B: Biological Sciences*, *272*(1566), 941-947.

Riede, T., Arcadi, A. C., & Owren, M. J. (2007). Nonlinear acoustics in the pant hoots of common chimpanzees (*Pan troglodytes*): Vocalizing at the edge. *The Journal of the Acoustical Society of America*, *121*, 1758-1767.

Snyder-Mackler, N., Alberts, S. C., & Bergman, T. J. (2014). The socio-genetics of a complex society: Female gelada relatedness patterns mirror association patterns in a multilevel society. *Molecular Ecology*, *23*, 6179-6191.

Spillmann, B., Dunkel, L. P., Van Noordwijk, M. A., Amda, R. N., Lameira, A. R., Wich, S. A., et al. (2010). Acoustic properties of long calls given by flanged male orang-utans (*Pongo pygmaeus wurmbii*) reflect both individual identity and context. *Ethology*, *116*, 385-395.

Thomas, R. J. (2002). The costs of singing in nightingales. *Animal Behaviour*, *63*, 959-966.

Titze, I. R. & Riede, T. (2010). A cervid vocal fold model suggests greater glottal efficiency in calling at high frequencies. *PLoS Computational Biology*, *6*, e1000897.

Tomasello, M. & Call, J. (1997). *Primate cognition.* New York: Oxford University Press.

Vehrencamp, S. (2000). Handicap, index, and conventional signal elements of bird song. In Y. Espmark, T. Amundsen & G. Rosenqvist (Eds.), *Animal signals: Signalling and signal design in animal communication* (pp. 227-300). Trondheim, Norway: Tapir Academic Press.

Wagner, W. E. 1992. Deceptive or honest signalling of fighting ability? A test of alternative hypotheses for the function of changes in call dominant frequency by male cricket frogs. Animal Behaviour, 44, 449-462.

Ward, S., Speakman, J. R., & Slater, P. J. (2003). The energy cost of song in the canary, *Serinus canaria*. *Animal Behaviour*, *66*, 893-902.

Wich, S. A., Van der Post, D. J., Heistermann, M., Möhle, U., Van Hooff, J., & Sterck, E. H. M. (2003). Life-phase related changes in male loud call characteristics and testosterone levels in wild Thomas langurs. *International Journal of Primatology*, *24*, 1251-1265.

Zahavi, A. (1975). Mate selection--a selection for a handicap. *Journal of Theoretical Biology*, *53*, 205-214.

CHAPTER 4 (Formatted for Nature Communications)

1. Maynard Smith, J. & Price, G. R. The Logic of Animal Conflict. *Nature* **246,** 15 (1973).

2. Enquist, M. & Leimar, O. Evolution of fighting behaviour: Decision rules and assessment of relative strength. *J. Theor. Biol.* **102,** 387–410 (1983).

3. Briffa, M. & Elwood, R. W. Difficulties remain in distinguishing between mutual and self-assessment in animal contests. *Anim. Behav.* **77,** 759–762 (2009).

4. Elwood, R. W. & Arnott, G. Understanding how animals fight with Lloyd Morgan's canon. *Anim. Behav.* **84,** 1095–1102 (2012).

5. Taylor, P. W. & Elwood, R. W. The mismeasure of animal contests. *Anim. Behav.* **65,** 1195–1202 (2003).

6. Rillich, J., Schildberger, K. & Stevenson, P. A. Assessment strategy of fighting crickets revealed by manipulating information exchange. *Anim. Behav.* **74,** 823–836 (2007).

7. Tibbetts, E. A., Mettler, A. & Levy, S. Mutual assessment via visual status signals in *Polistes dominulus* wasps. *Biol. Lett.* **6,** 10–13 (2010).

8. Davies, N. B. & Halliday, T. R. Deep croaks and fighting assessment in toads *Bufo bufo*. **274,** 683–685 (1978).

9. Arak, A. Male-male competition and mate choice in anuran amphibians. *Mate choice* 181–210 (1983).

10. Given, M. F. Vocalizations and Acoustic Interactions of the Carpenter Frog*, Rana virgatipes*. *Herpetologica* **43,** 467–481 (1987).

11. Wagner, W. E., Jr. Graded aggressive signals in Blanchard's cricket frog: vocal responses to opponent proximity and size. *Anim. Behav.* **38,** 1025–1038 (1989).

12. Leonard, M. L. & Horn, A. G. Crowing in relation to status in roosters. *Anim. Behav.* **49,** 1283–1290 (1995).

13. Slabbekoorn, H. & ten Cate, C. Stronger territorial responses to frequency modulated coos in collared doves. *Anim. Behav.* **54,** 955–965 (1997).

14. Burt, J. M., Campbell, S. E. & Beecher, M. D. Song type matching as threat: a test using interactive playback. *Anim. Behav.* **62,** 1163–1170 (2001).

15. Behr, O. & von Helversen, O. Bat serenades—complex courtship songs of the sac-winged bat (*Saccopteryx bilineata*). *Behav. Ecol. Sociobiol.* **56,** 106–115 (2004).

16. Clutton-Brock, T. H. & Albon, S. D. The Roaring of Red Deer and the Evolution of Honest Advertisement. *Behaviour* **69,** 145–170 (1979).

17. Reby, D. *et al.* Red deer stags use formants as assessment cues during intrasexual agonistic interactions. *Proc. Biol. Sci.* **272,** 941–947 (2005).

18. Casey, C., Charrier, I., Mathevon, N. & Reichmuth, C. Rival assessment among northern elephant seals: evidence of associative learning during male–male contests. *Open Science* **2,** 150228 (2015).

19. Kitchen, D. M. *et al.* Male baboon responses to experimental manipulations of loud wahoo calls: testing an honest signal of fighting ability. *Behav. Ecol. Sociobiol.* **67,** 1825–1835 (2013).

20. Egge, A. R., Brandt, Y. & Swallow, J. G. Sequential analysis of aggressive interactions in the stalk-eyed fly *Teleopsis dalmanni*. *Behav. Ecol. Sociobiol.* **65,** 369–379 (2010).

21. Taylor, A. M., Reby, D. & McComb, K. Size communication in domestic dog, *Canis familiaris*, growls. *Anim. Behav.* **79,** 205–210 (2010).

22. Setchell, J. M. & Kappeler, P. M. in *Advances in the Study of Behavior* **Volume 33,** 87–173 (Academic Press, 2003).

23. Snowdon, C. T. in *Sexual selection in primates* (eds. Kappeler, P. & van Shaik, C.) 57–70 (Cambridge University Press, 2004).

24. Bergman, T. J. & Sheehan, M. J. Social knowledge and signals in primates. *Am. J. Primatol.* **75,** 683–694 (2013).

25. Sheehan, M. J. & Bergman, T. J. Is there an evolutionary trade-off between quality signaling and social recognition? *Behav. Ecol.* **27**, 2-13 (2016).

26. Tomasello, M. & Call, J. *Primate Cognition*. (Oxford University Press, 1997).

27. Kitchen, D. M., Cheney, D. L. & Seyfarth, R. M. Male chacma baboons (*Papio hamadryas ursinus*) discriminate loud call contests between rivals of different relative ranks. *Anim. Cogn.* **8,** 1–6 (2005).

28. Kitchen, D. M., Seyfarth, R. M., Fischer, J. & Cheney, D. L. Loud calls as indicators of dominance in male baboons (*Papio cynocephalus ursinus*). *Behav. Ecol. Sociobiol.* **53,** 374–384 (2003).

29. Bergman, T. J., Beehner, J. C., Cheney, D. L. & Seyfarth, R. M. Hierarchical classification by rank and kinship in baboons. *Science* **302,** 1234–1236 (2003).

30. Bergman, T. J., Beehner, J. C., Cheney, D. L., Seyfarth, R. M. & Whitten, P. L. Interactions in male baboons: the importance of both males testosterone. *Behav. Ecol. Sociobiol.* **59,** 480–489 (2006).

31. Kawai, M. Ecological and Sociological Studies of Gelada Baboon. Auditory communication and social relations. *Contrib. Primatol.* **16***,* 219–241 (1979).

32. Dunbar, R. & Dunbar, P. Social dynamics of gelada baboons. *Contrib. Primatol.* **6,** 1–157 (1975).

33. Dunbar, R. *Reproductive decisions: An Economic Analysis of Gelada Baboon Social Strategies*. 96–105 (Princeton University Press, 1984).

34. Snyder-Mackler, N., Beehner, J. C. & Bergman, T. J. Defining Higher Levels in the Multilevel Societies of Geladas (*Theropithecus gelada*). *Int. J. Primatol.* **33,** 1054–1068 (2012).

35. Crook, J. H. Gelada baboon herd structure and movement. A comparative report. *Symp Zool Soc Lond* 237–258 (1966).

36. Pappano, D. J., Snyder-Mackler, N., Bergman, T. J. & Beehner, J. C. Social 'predators' within a multilevel primate society. *Anim. Behav.* **84,** 653–658 (2012).

37. Benítez, M. E., le Roux, A., Fischer, J., Beehner, J. C. & Bergman, T. J. Acoustic and temporal variation in gelada loud calls advertise male quality. *Int. J. Primatol.* (accepted).

38. Pfefferle, D., Heistermann, M., Hodges, J. K. & Fischer, J. Male Barbary macaques eavesdrop on mating outcome: a playback study. *Anim. Behav.* **75,** 1885–1891 (2008).

39. Fischer, J., Noser, R. & Hammerschmidt, K. Bioacoustic field research: a primer to acoustic analyses and playback experiments with primates. *Am. J. Primatol.* **75,** 643–663 (2013).

40. Schmidt, R., Kunc, H. P., Amrhein, V. & Naguib, M. Aggressive responses to broadband trills are related to subsequent pairing success in nightingales. *Behav. Ecol.* **19,** 635–641 (2008).

41. Naguib, M. in *Animal Communication Networks* (eds. McGregor, P. K. & McGregor, P. K.) 300–319 (Cambridge University Press, 2005).

42. Wiewandt, T. A. Vocalization, Aggressive Behavior, and Territoriality in the Bullfrog, *Rana catesbeiana*. *Copeia* **1969,** 276–285 (1969).

43. Vehrencamp, S. L. Is song-type matching a conventional signal of aggressive intentions? *Proc. Biol. Sci.* **268,** 1637–1642 (2001).

44. Mori, U. Ecological and sociological studies of gelada baboons. Development of sociability and social status. *Contrib. Primatol.* **16,** 125–154 (1979).

45. Pappano, D. J. & Beehner, J. C. Harem-holding males do not rise to the challenge: androgens respond to social but not to seasonal challenges in wild geladas. *R Soc Open Sci* **1,** 140081 (2014).

46. Bergman, T. J. Experimental evidence for limited vocal recognition in a wild primate: implications for the social complexity hypothesis. *Proc. Biol. Sci.* **277,** 3045–3053 (2010).

47. Dunbar, R. I. M. Social organization of the gelada. in *Theropithecus: The rise and fall of a primate genus* (ed. Jablonski, N.) 425–439 (Cambridge University Press, 1993).

48. Seyfarth, R. M. & Cheney, D. L. Baboon Metaphysics: The Evolution of a Social Mind. (2007).

49. Crockford, C., Wittig, R. M., Seyfarth, R. M. & Cheney, D. L. Baboons eavesdrop to deduce mating opportunities. *Anim. Behav.* **73,** 885–890 (2007).

50. Delgado, R. A. Sexual selection in the loud calls of male primates: signal content and function. *Int. J. Primatol.* **27,** 5–25 (2006).

51. Csardi, G. & Nepusz, T. The igraph software package for complex network research. *InterJournal, Complex Systems* **1695,** 1–9 (2006).

52. Bates, D., Mächler, M., Bolker, B. & Walker, S. Fitting Linear Mixed-Effects Models using lme4. *arXiv [stat.CO]* (2014).

CHAPTER 5

Anderson, R. C., DuBois, A. L., Piech, D. K., Searcy, W. A. & Nowicki, S. 2013. Male response to an aggressive visual signal, the wing wave display, in swamp sparrows. *Behavioral ecology and sociobiology*, 67, 593–600.

Armstrong, N. & Welsman, J. 2001. Peak oxygen uptake in relation to growth and maturation in 11-to 17--year-old humans. *European journal of applied physiology*, 85, 546–551.

Barelli, C., Mundry, R., Heistermann, M. & Hammerschmidt, K. 2013. Cues to androgens and quality in male gibbon songs. *PloS one*, 8, e82748.

Benítez, M. E., le Roux, A., Fischer, J., Beehner, J. C. & Bergman, T. J. 2016. Acoustic and temporal variation in gelada loud calls advertise male quality. *International Journal of Primatology*,

Bergman, T. J. 2010. Experimental evidence for limited vocal recognition in a wild primate: implications for the social complexity hypothesis. *Proceedings. Biological sciences / The Royal Society*, 277, 3045–3053.

Bergman, T. J. & Beehner, J. C. 2008. A simple method for measuring colour in wild animals: validation and use on chest patch colour in geladas *(Theropithecus gelada)*. *Biological journal of the Linnean Society. Linnean Society of London*, 94, 231–240.

Bergman, T. J. & Sheehan, M. J. 2013. Social knowledge and signals in primates. *American journal of primatology*, 75, 683–694.

Bergman, T. J., Ho, L. & Beehner, J. C. 2009. Chest Color and Social Status in Male Geladas (Theropithecus gelada). *International journal of primatology*, 1–16.

Birkhead, T. R., Fletcher, F. & Pellatt, E. J. 1998. Sexual selection in the zebra finch *Taeniopygia guttata* : condition, sex traits and immune capacity. *Behavioral ecology and sociobiology*, 44, 179–191.

Bradbury, J. W. & Vehrencamp, S. L. 2011. *Principles of Animal Communication.* Macmillan Education.

Bradley, B. J. & Mundy, N. I. 2008. The primate palette: The evolution of primate coloration. *Evolutionary anthropology*, 17, 97–111.

Candolin, U. 2003. The use of multiple cues in mate choice. *Biological reviews of the Cambridge Philosophical Society*, 78, 575–595.

Collins, S. A., Hubbard, C. & Houtman, A. M. 1994. Female mate choice in the zebra finch—the effect of male beak colour and male song. *Behavioral ecology and sociobiology*, 35, 21–25.

Delgado, R. A. 2006. Sexual selection in the loud calls of male primates: signal content and function. *International journal of primatology*, 27, 5–25.

Dubuc, C., Allen, W. L., Maestripieri, D. & Higham, J. P. 2014. Is male rhesus macaque red color ornamentation attractive to females? *Behavioral ecology and sociobiology*, 68, 1215–1224.

Dunbar, R. 1984. *Reproductive decisions: an economic analysis of gelada baboon social strategies.* Princeton, New Jersey: Princeton University Press.

Dunbar, R. I. M. 1993. Social organization of the gelada. *Theropithecus: The rise and fall of a primate genus*, 425–439.

Dunbar, R. & Dunbar, P. 1975. Social dynamics of gelada baboons. *Contributions to primatology*, 6, 1–157.

Erb, W. M., Hodges, J. K. & Hammerschmidt, K. 2013. Individual, Contextual, and Age-Related Acoustic Variation in Simakobu (*Simias concolor)* Loud Calls. *PloS one*, 8, e83131.

Fischer, J., Kitchen, D. M., Seyfarth, R. M. & Cheney, D. L. 2004. Baboon loud calls advertise male quality: acoustic features and their relation to rank, age, and exhaustion. *Behavioral ecology and sociobiology*, 56, 140–148.

Fortney, S. M. & Vroman, N. B. 1985. Exercise, performance and temperature control: temperature regulation during exercise and implications for sports performance and training. *Sports medicine* , 2, 8–20.

Gerald, M. S. 2001. Primate colour predicts social status and aggressive outcome. *Animal behaviour*, 61, 559–566.

Grether, G. F. 2011. The neuroecology of competitor recognition. *Integrative and comparative biology*, 51, 807–818.

Grueter, C. C., Zhu, P., Allen, W. L., Higham, J. P., Ren, B. & Li, M. 2015. Sexually selected lip colour indicates male group-holding status in the mating season in a multi-level primate society. *Royal Society open science*, 2, 150490.

Hebets, E. A. & Papaj, D. R. 2004. Complex signal function: developing a framework of testable hypotheses. *Behavioral ecology and sociobiology*, 57, 197–214.

Hebets, E. A. & Uetz, G. W. 2000. Leg ornamentation and the efficacy of courtship display in four species of wolf spider *(Araneae: Lycosidae)*. *Behavioral ecology and sociobiology*, 47, 280–286.

Hick, K. G., Doucet, S. M. & Mennill, D. J. 2016. Tropical wrens rely more on acoustic signals than visual signals for inter- and intraspecific discrimination. *Animal behaviour*, 118, 153–163.

Higham, J. P. 2009. Primate Coloration: An Introduction to the Special Issue. *International journal of primatology*, 30, 749–751.

Higham, J. P. & Hebets, E. A. 2013. An introduction to multimodal communication. *Behavioral ecology and sociobiology*, 67, 1381–1388.

Higham, J. P., Pfefferle, D., Heistermann, M., Maestripieri, D. & Stevens, M. 2013. Signaling in multiple modalities in male rhesus macaques: sex skin coloration and barks in relation to androgen levels, social status, and mating behavior. *Behavioral ecology and sociobiology*, 67, 1457–1469.

Houtman, A. M. 1992. Female Zebra Finches Choose Extra-Pair Copulations with Genetically Attractive Males. *Proceedings of the Royal Society of London B: Biological Sciences*, 249, 3–6.

Iwamoto, T. & Dunbar, R. 1983. Thermoregulation, Habitat Quality and the Behavioural Ecology of Gelada Baboons. *The Journal of animal ecology*, 52, 357–366.

Jetz, W., Rowe, C. & Guilford, T. 2001. Non-warning odors trigger innate color aversions—as long as they are novel. *Behavioral ecology: official journal of the International Society for Behavioral Ecology*, 12, 134–139.

Johnson, J. M. 1998. Physical training and the control of skin blood flow. *Medicine and science in sports and exercise*, 30, 382–386.

Johnstone, R. A. 1997. The evolution of animal signals. *Behavioural ecology: An evolutionary approach*, 155–178.

Kitchen, D. M., Seyfarth, R. M., Fischer, J. & Cheney, D. L. 2003. Loud calls as indicators of dominance in male baboons (*Papio cynocephalus ursinus*). *Behavioral ecology and sociobiology*, 53, 374–384.

Kitchen, D. M. M., Cheney, D. L. L., Engh, A. L. L., Fischer, J., Moscovice, L. R. R. & Seyfarth, R. M. M. 2013. Male baboon responses to experimental manipulations of loud wahoo calls: testing an honest signal of fighting ability. *Behavioral ecology and sociobiology*, 67, 1825–1835.

Marty, J. S., Higham, J. P., Gadsby, E. L. & Ross, C. 2009. Dominance, coloration, and social and sexual behavior in male drills *Mandrillus leucophaeus. International journal of primatology*, 30, 807–823.

Moller, A. P. & Pomiankowski, A. 1993. Why have birds got multiple sexual ornaments? *Behavioral ecology and sociobiology*, 32, 167–176.

Nunn, C. & Altizer, S. M. 2006. *Infectious Diseases in Primates: Behavior, Ecology and Evolution.* OUP Oxford.

Pappano, D. J. & Beehner, J. C. 2014. Harem-holding males do not rise to the challenge: androgens respond to social but not to seasonal challenges in wild geladas. *Royal Society open science*, 1, 140081.

Pappano, D. J., Snyder-Mackler, N., Bergman, T. J. & Beehner, J. C. 2012. Social "predators" within a multilevel primate society. *Animal behaviour*, 84, 653–658.

Partan, S. & Marler, P. 1999. Communication goes multimodal. *Science*, 283, 1272–1273.

Partan, S. R. & Marler, P. 2005. Issues in the classification of multimodal communication signals. *The American naturalist*, 166, 231–245.

Partan, S., Yelda, S., Price, V. & Shimizu, T. 2005. Female pigeons, Columba livia, respond to multisensory audio/video playbacks of male courtship behaviour. *Animal behaviour*, 70, 957–966.

Pfefferle, D. & Fischer, J. 2006. Sounds and size: identification of acoustic variables that reflect body size in hamadryas baboons, Papio hamadryas. *Animal behaviour*, 72, 43–51.

Rhodes, L., Argersinger, M. E., Gantert, L. T., Friscino, B. H., Hom, G., Pikounis, B., Hess, D. L. & Rhodes, W. L. 1997. Effects of administration of testosterone, dihydrotestosterone, oestrogen and fadrozole, an aromatase inhibitor, on sex skin colour in intact male rhesus macaques. *Journal of reproduction and fertility*, 111, 51–57.

Rowe, C. & Guilford, T. 1999. The Evolution of Multimodal Warning Displays. *Evolutionary ecology*, 13, 655–671.

Scheuber, H., Jacot, A. & Brinkhof, M. W. G. 2003/4. Condition dependence of a multicomponent sexual signal in the field cricket *Gryllus campestris. Animal behaviour*, 65, 721–727.

Setchell, J. M. & Dixson, A. F. 2001. Changes in the secondary sexual adornments of male mandrills (*Mandrillus sphinx)* are associated with gain and loss of alpha status. *Hormones and behavior*, 39, 177–184.

Setchell, J. M. & Jean Wickings, E. 2005. Dominance, Status Signals and Coloration in Male Mandrills (*Mandrillus sphinx*). *Ethology: formerly Zeitschrift fur Tierpsychologie*, 111, 25–50.

Setchell, J. M., Smith, T., Wickings, E. J. & Knapp, L. A. 2008. Social correlates of testosterone and ornamentation in male mandrills. *Hormones and behavior*, 54, 365–372.

Seyfarth, R. M. & Cheney, D. L. 2007. Baboon Metaphysics: The Evolution of a Social Mind.

Sheehan, M. J. & Bergman, T. J. 2015. Is there an evolutionary trade-off between quality signaling and social recognition? *Behavioral ecology: official journal of the International Society for Behavioral Ecology*,

Slocombe, K. E., Waller, B. M. & Liebal, K. 2011/5. The language void: the need for multimodality in primate communication research. *Animal behaviour*, 81, 919–924.

Taylor, R. C., Buchanan, B. W. & Doherty, J. L. 2007. Sexual selection in the squirrel treefrog *Hyla squirella*: the role of multimodal cue assessment in female choice. *Animal behaviour*, 74, 1753–1763.

Taylor, R. C., Klein, B. A., Stein, J. & Ryan, M. J. 2008. Faux frogs: multimodal signalling and the value of robotics in animal behaviour. *Animal behaviour*, 76, 1089–1097.

Taylor, R. C., Klein, B. A., Stein, J. & Ryan, M. J. 2011. Multimodal signal variation in space and time: how important is matching a signal with its signaler? *The Journal of experimental biology*, 214, 815–820.

Tomasello, M. & Call, J. 1997. *Primate Cognition.* Oxford University Press.

Uetz, G. W. & Roberts, J. A. 2002. Multisensory cues and multimodal communication in spiders: insights from video/audio playback studies. *Brain, behavior and evolution*, 59, 222–230.

Uetz, G. W., Roberts, J. A. & Taylor, P. W. 2009. Multimodal communication and mate choice in wolf spiders: female response to multimodal versus unimodal signals. *Animal behaviour*, 78, 299–305.

Uy, J. A. C. & Safran, R. J. 2013. Variation in the temporal and spatial use of signals and its implications for multimodal communication. *Behavioral ecology and sociobiology*, 67, 1499–1511.

Uy, J. A. C., Moyle, R. G. & Filardi, C. E. 2009. Plumage and song differences mediate species recognition between incipient flycatcher species of the Solomon Islands. *Evolution; international journal of organic evolution*, 63, 153–164.

CHAPTER 6

Apicella, C. L., Feinberg, D. R. & Marlowe, F. W. 2007. Voice pitch predicts reproductive success in male hunter-gatherers. *Biology letters*, 3, 682–684.

Bergman, T. J. 2010. Experimental evidence for limited vocal recognition in a wild primate: implications for the social complexity hypothesis. *Proceedings. Biological sciences / The Royal Society*, 277, 3045–3053.

Bergman, T. J. & Sheehan, M. J. 2013. Social knowledge and signals in primates. *American journal of primatology*, 75, 683–694.

Dunbar, R. 1984. *Reproductive decisions: an economic analysis of gelada baboon social strategies.* Princeton, New Jersey: Princeton University Press.

Elton, S. 2006. Forty years on and still going strong: the use of hominin-cercopithecid comparisons in palaeoanthropology. *The journal of the Royal Anthropological Institute*,

Puts, D. A., Gaulin, S. J. C. & Verdolini, K. 2006. Dominance and the evolution of sexual dimorphism in human voice pitch. *Evolution and human behavior: official journal of the Human Behavior and Evolution Society*, 27, 283–296.

Snowdon, C. T. 2004. Sexual selection and communication. In: *Sexual selection in primates*, (Ed. by P. Kappeler & C. van Shaik), pp. 57–70. Cambridge: Cambridge University Press.

Tigue, C. C., Borak, D. J., O'Connor, J. J. M., Schandl, C. & Feinberg, D. R. 2011. Voice pitch influences voting behavior. *Evolution and human behavior: official journal of the Human Behavior and Evolution Society*,