Social and Ecological Challenges in Female Geladas:
A Test of the Vocal Grooming Hypothesis

by

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DEDICATION

For my mother, Joanne M. Tinsley

Who nourished my early love of the natural world and for telling stories.

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ABSTRACT

Maintaining social bonds is an important and time-consuming part of primate life. Strong social bonds provide individuals with fitness benefits, yet grooming – the primary way in which primates socialize – requires a significant investment of time and energy. Vocalizations, in contrast, could furnish a different and efficient means of socializing, a strategy that may have been adopted by humans in their use of language. The hypothesis that calls serve to cement social bonds, known as the vocal grooming hypothesis, has yet to be tested empirically.

This research presents a thorough test of the vocal grooming hypothesis in a highly social and exceptionally vocal primate, the gelada (*Theropithecus gelada*). Among geladas, an herbivorous primate that must spend much of their day feeding, time budgets are extremely strained. In this dissertation, I address each of the following components of the vocal grooming hypothesis: (1) I identify when and why social time is most constrained for female geladas; (2) I assess the impact of these constraints on individual reproductive fitness; (3) I identify when and how vocalizations are used as potential substitutes for grooming. To do so, I combine longitudinal behavioral and demographic data with extensive hormonal sampling, allowing me to capture variation across seasons, social contexts, and individuals.

This research has 4 main findings that further our understanding of the role of vocalizations in primate social behavior. First, I identify two distinct kinds of social relationships that female geladas maintain: primary social partners and secondary social partners. Second, I demonstrate that both ecological and social factors can shape female reproductive timing. Third, I demonstrate that the optimal unit size for female gelada reproductive performance is larger than the number of grooming partners an individual female can maintain. Finally, I provide evidence that a specific kind of vocalization, the affiliative grunt or contact call, is used primarily between secondary social partners and is used more frequently when social time is most constrained. These results provide support for the idea that vocalizations may substitute for grooming. Specifically, I highlight how vocal grooming allows females to socialize with more individuals than they can through grooming alone, perhaps contributing to the stability of optimally-sized units.

CHAPTER 1

INTRODUCTION & BACKGROUND

INTRODUCTION

One of the most provocative hypotheses about the origins of human language is that language evolved as a social tool, allowing us to live with – and keep tabs on – many other people (Aiello and Dunbar 1993; Dunbar 1996). Dunbar argues that *gossip*, in particular, works to solidify human social relationships, much in the way that grooming has been shown to maintain social bonds in many non-human primate species. He calls this form of communication ‘vocal grooming’. Inspiration for his theory came from observations of wild geladas (*Theropithecus gelada*) living in Ethiopia, an Old World monkey that seems to share our own species’ ‘gift of gab’. However, the hypothesis that vocalizations serve to cement social bonds in nonhuman primates has yet to be tested empirically. This dissertation investigates the vocal grooming hypothesis in a highly social, and exceptionally vocal primate, the gelada. Among geladas – an herbivorous primate that must spend much of their day feeding – time budgets may be especially strained, due in part to the extra challenges of living at altitude (Dunbar 1984). Perhaps as a result, geladas (like humans) have adopted vocal forms of social grooming as an effective and efficient way to bond with multiple partners.

Maintaining social bonds is an important part of primate life. In at least two species of baboons (sister taxa to geladas), females with strong social bonds have more offspring and live longer than those with only weak social ties (Silk et al. 2009; Silk et al. 2010). Moreover, ‘stress hormones’ (i.e., glucocorticoids) are lower in female baboons that maintain stable grooming networks (Crockford et al. 2008). In these studies, however, female bonds were measured directly using *grooming exchanges*. In contrast, the vocal grooming hypothesis predicts that social bonds will be evident from *vocal exchanges*. Grooming is a time-consuming behavior, and under certain circumstances individuals may be limited in the amount of time they can devote to it. In geladas, for example, ecological challenges (due to time spent foraging) and social challenges (due to large numbers of social partners) could both impede upon social time. In this dissertation, I first characterize the ecological and social challenges geladas face and assess how these challenges shape individual fitness. I then consider whether vocalizations help individuals maintain social bonds in spite of these ecological and social challenges.

A thorough test of the vocal grooming hypothesis requires three components, each of which I address in this dissertation. First, it requires identifying potential constraints on social time. Second, it requires assessing the impact of these constraints on individual reproductive fitness. Finally, it requires identifying when and how vocalizations are used: do vocalizations substitute for grooming, and if so, how? To meet these criteria, I combine longitudinal behavioral and demographic data with extensive hormonal sampling, allowing me to capture variation across seasons, social contexts, and individual characteristics.

GELADAS (*Theropithecus gelada*)

There are several reasons why geladas are an ideal test species for this investigation. First, as the only gramnivorous primate, geladas face unique challenges in balancing their nutritional and social needs, which is only further complicated by living in a highly seasonal environment (Beehner and McCann 2008). For female mammals, reproductive success (and, ultimately, lifetime fitness) is tightly linked to energy balance, which itself is a function of energy intake and energy expenditure (reviewed in Di Bitetti and Janson 2000; Brockman and van Schaik 2005; Janson and Verdolin 2005). Geladas face ecological challenges that impact both sides of this equation: green grass is abundant for only 5 months every year (Jul-Nov; Jarvey et al. 2018) and temperatures can dip below freezing between June and January (Iwamoto and Dunbar 1983; Beehner and McCann 2008). In mammals, periods of low food availability can impact patterns of female reproduction (e.g., Dubost and Henry 2017) and can result in infertility, miscarriages, and infant deaths (Beehner et al. 2006). In addition, thermoregulatory demands due to exposure to both extreme heat or extreme cold can also hinder female reproduction (e.g., Fernandez-Duque et al. 2002; Xiang and Sayers 2009; Polo and Colmenares 2016). Throughout this dissertation I return to these two main ecological challenges and explore how they impact female reproduction, activity budgets, and social behavior.

Second, gelada social structure is quite complex: geladas live in multilevel societies, which consist of aggregations of many one-male units. These core units vary in size (from 1-13 adult female kin: Dunbar 1984; le Roux et al. 2011). Because of this variance, some females – who together form the ‘glue’ of the unit – have more potential social partners than others. Females in large units may be more constrained in the amount of time they can spend socializing or in the number of individuals they can socialize with. Additionally, or alternatively, females with increased nutritional demands may also suffer higher social costs. Dunbar and Dunbar (1988) suggest that when females spend more time foraging they restrict their grooming to only their primary, or closest, social partners. However, being able to maintain both primary *and* secondary social partners has important social consequences for unit social cohesion. For example, in baboons, group fissions are more likely to occur when groups are too large (Henzi et al. 1997). Interestingly, the next level of social organization above that of the unit is the team – an aggregation of units that associate more than 90% of the time (Snyder-Mackler et al. 2012). These teams may represent recently fissioned ‘daughter’ units, which still maintain some kind of connection, perhaps through vocal contact. The cohesion of the gelada unit, and the maintenance of different kinds of social relationships within the unit, is one of the main social challenges I address in this dissertation.

Third, the social environment can also impact female reproduction and fitness. For example, one salient social threat to female reproduction is infanticide by males (reviewed in Agrell et al. 1998). Infanticide occurs when non-sire males kill the dependent offspring of females to expedite reproductive cycling and mating receptivity in the mother (Hrdy 1974; Sugiyama 1984). Infanticide by new males during takeovers (when a bachelor male challenges and overthrows and unit leader male to gain reproductive access to unit females, Pappano and Beehner 2014; Teichroeb and Jack 2017) is the leading cause of infant mortality in this population (incoming males kill more than half of the infants of lactating females, Beehner and Bergman 2008). Takeovers are also associated with male-mediated pregnancy termination (i.e., the Bruce effect, Bruce 1959; Roberts et al. 2012), and represent stressful social events that disrupt female social lives and reproductive trajectories. Therefore, male takeovers, and their subsequent effects, represent the second main social challenge that I address that significantly shapes female fitness.

Finally, like humans, geladas are highly vocal, and the complexity of their vocal repertoire mirrors the complexity of their social system (Gustison et al. 2012). Of their remarkably varied and distinctive vocalizations, the most prominent is a ‘contact grunt’. In baboons, similar calls are used to maintain group cohesion and to reconcile after fights (Cheney et al. 1995; Cheney and Seyfarth 1997; Silk et al. 2016). However, the function of contact grunts in female geladas is not yet known. These vocalizations could represent a more efficient strategy for maintaining social cohesion.

STUDY SITE & SUBJECTS

The data presented in this dissertation come from a population of wild geladas living in the Simien Mountains National Park (SMNP), Ethiopia (13.3064 N, 38.2641 E). The SMNP is listed as a UNESCO World Heritage Site (1978) and comprises 170 km^2 of Afroalpine habitat (3200-4500 m.a.s.l.). The environment features open grassland plateaus and sparse remnant forests, bordered by steep cliff precipices that descend into lush valleys. With the high altitude comes highly variable temperatures, which can range from below freezing at night to up to 25˚C during the day (Iwamoto & Dunbar 1983). Both temperature and rainfall also vary across the year, resulting in three distinct seasons: a “cold-rainy” season (Jun-Sep, when the region receives 80% of annual precipitation and experiences the lowest maximum temperatures), a “cold-dry” season (Oct-Jan, which features the highest green grass availability and lowest minimum temperatures), and a “hot-dry” season (Feb-May, when high maximum temperatures and little to no rain transform the mountains into a dry, dusty landscape).

The total population size of geladas living in the park was previously estimated at 2460 (Beehner et al. 2007). Drs. Jacinta Beehner and Thore Bergman habituated a subset of this population in 2006 and established what is today known as the Simien Mountains Gelada Research Project (SMGRP, formerly the University of Michigan Gelada Research Project). Since its inception, the SMGRP has actively studied around 200 geladas at any given time and study subjects are individually recognized and habituated to the presence of observers on foot.

My research primarily draws on longitudinal data on female geladas from 2006-2014 (*N* = 189 adult females in 33 reproductive units; 792 female-years of observation time). Specifically, I focus on female life history parameters (i.e., births, maturations, deaths), behavioral data (i.e., grooming, dominance interactions, and vocalizations), climatological patterns (i.e., variation in rainfall and temperature), and endocrinology (i.e., fecal glucocorticoid hormone metabolites).

RESEARCH QUESTIONS & CHAPTERS

In this thesis, I broadly examine why primates live in social groups, and what strategies allow them to manage the costs associated with group-living. Specifically, I answer 3 main questions that together lay the groundwork for an empirical test of the vocal grooming hypothesis in a wild primate. I address these questions in four separate chapters that are either published (Chapters 2 & 3) or in preparation for submission for peer review (Chapters 4 & 5). Although I am the first author on all chapters, each represents a collaborative effort with several coauthors including my advisor, Dr. Jacinta Beehner. Therefore, throughout the remainder of the dissertation I use the pronoun “we” instead of “I” to denote this collaborative effort. I briefly describe each research question and chapter below.

Question 1: Do female geladas have preferred social partners?

In **Chapter 2**, we present a general characterization of female social bonds – identifying whether individuals form preferential relationships, and the extent to which characteristics of the dyad predict the strength of the relationship. For group-living animals, sociality represents a trade-off that carries fitness consequences: it offers predation protection (Pulliam 1973; Van Schaik 1983; Sterck et al. 1997; Caro 2005; Beauchamp 2008) but can also heighten levels of feeding competition (Janson and Goldsmith 1995; Chapman and Chapman 2000; Majolo et al. 2008; Grove 2012;

Markham et al. 2015; Markham and Gesquiere 2017). Forming bonds with a few close partners can mitigate some of this stress (Uchino et al. 1999; Hennessy et al. 2006; Hennessy et al. 2009), presumably by providing social structure (reducing uncertainty) and establishing alliances (reducing the costs of feeding competition). In humans and non-human primates, social bonds reduce stress, improve overall health, and increase lifespan (House et al. 1988; Christenfeld et al. 1997; Glynn et al. 1999; Silk et al. 2009; Silk et al. 2010). In at least two species of baboons (sister taxa to geladas), females with strong social bonds have more offspring and live longer than those with weak social ties (Silk et al. 2003; Silk et al. 2009; Silk et al. 2010). Further, bonds provide important social capital: preferred social partners are more likely to intervene in an ongoing dispute to aid their ally (Silk et al. 2004). Moreover, ‘stress hormones’ (i.e., glucocorticoids) are significantly lower in female baboons that maintain stable grooming networks with preferred partners (Crockford et al. 2008) and skyrocket following the loss of one of these partners (Engh et al. 2006).

Primates do not typically form social bonds with all group members indiscriminately. Rather, they form preferences based on individual characteristics, such as sex, kinship, and/or dominance rank (e.g., Silk et al. 1999; Mitani 2009; Thompson and Norconk 2011). In this chapter, we ask whether the social bonds of female geladas follow the typical cercopithecine pattern, where the strongest bonds are found between close kin and are dictated by an individual’s position in the dominance hierarchy. To test this, we used behavioral and genetic sampling to examine whether dominance rank and/or genetic relatedness mediated female social bonds. We found that female geladas, much like their close relatives the baboons, form the strongest social bonds with their closest kin, and with females who share a similar dominance rank. However, while rank disparity predicted grooming rates, it did not predict whether females maintained proximity (i.e., were nearest neighbors). This suggests that, in contrast to data from other cercopithecines, spatial proximity among females may be less indicative of strong social bonds for geladas, a species that routinely exhibits a high degree of spatial overlap with extra-unit individuals.

Identifying the features of gelada social relationships is important for later predicting whether, and how, vocal grooming may play a role in gelada social life. For example, in **Chapter 5** we ask whether the factors that predict the strongest social bonds – relatedness and rank disparity – also predict the frequency of vocal contact.

Question 2: How do ecological and social factors impact female reproductive performance?

We address this second question across two chapters. First, in **Chapter 3** we consider how ecological and social factors shape female energetic demands and impact the timing of female reproduction. When it comes to reproduction, female geladas face two main challenges: a highly seasonal environment, with fluctuations in both temperature and rainfall, and stochastic events – male takeovers – that ‘reset’ a female’s reproduction via both infanticide and neuroendocrine mediation (e.g., the Bruce effect; Roberts et al. 2012). We consider how these two challenges influence stress hormone profiles, the timing of reproduction, and infant survival. Specifically, we first assess how seasonal variation in the afro-alpine ecosystem (considering both temperature and rainfall) shape patterns of female reproductive seasonality. Second, we assess how male takeovers exert independent effects on female reproduction.

We found that, although female geladas can give birth year-round, they still exhibited a seasonal birth peak every year following the rainy season. The timing of this birth peak coincided with conceptions that would have occurred in the middle of the hot-dry season, when food sources are scarce but temperatures are high. This time of year also featured the lowest female glucocorticoid metabolites, or stress hormones, suggesting that females, like males (Beehner and McCann 2008) are cold-stressed. We also identified a second, separate birth peak that only occurred in females that had experienced a takeover during the peak takeover season (Feb-Apr). This second peak was likely the result of males "resetting" the reproductive trajectories of unit females following the takeover (e.g., due to infanticide and/or the Bruce effect). Finally, we did not identify any effect of birth timing on infant death, suggesting that if there are costs associated with giving birth at a certain time of year, they are likely paid upfront (i.e., due to infertility).

In **Chapter 4** we focus on the social environment. Specifically, we ask whether there is an optimal unit size for female fitness. Geladas live in units of variable size (1-12 females) and we have evidence that units tend to fission after they reach about 9-10 adult females. In this chapter, we first present a novel method for quantifying female fitness that allowed us to assess the reproductive consequences of unit size. We demonstrate that females in mid-sized units have the highest reproductive performance and lower mortality rates than females in small units. We next explore potential causal factors – both ecological and social – that could explain these patterns. Both ecological and social challenges contributed to why mid-sized units are optimal for female fitness. First, although geladas are folivores, we find evidence that they may still compete over food, as females in both smaller and larger units spend the most time foraging. Second, as in **Chapter 3**, male takeovers played a pivotal role in shaping female reproduction: takeovers, and their subsequent effects, were more frequent in larger units, and infant death was highest in both small and large units than in mid-sized units.

Together, **Chapter 3** and **Chapter 4** set up a number of hypotheses about the kinds of social and ecological challenges female geladas face, and specifically about when they may be especially time-constrained. In **Chapter 5** we use these findings to inform our predictions about when geladas might use vocalizations as an efficient social tool.

Question 3: What is the function of the gelada contact call?

In **Chapter 5** we address the intriguing hypothesis first proposed by (Dunbar 1996), that vocal contact may help maintain social bonds when time budgets are constrained. Given that geladas are highly vocal, highly social, and live in a seasonal environment, they represent the ideal species in which to test the vocal grooming hypothesis.

Chapter 5 presents a first test of the vocal grooming hypothesis in a wild primate. This hypothesis posits that vocalizations can supplement grooming when social time is constrained. Specifically, we investigate the function of the female gelada contact call, or call exchange. To do so, we address (1) the behavioral context(s) in which females vocalized, (2) how seasonal and individual variation predicted the frequency of call exchanges, and (3) how seasonal and individual variation predicted the number of call exchange partners an individual had. For each question, we compared the features of vocal contact with those associated with grooming and proximity maintenance. We present evidence that geladas use call exchanges to substitute for grooming, but that they also use calls to interact with secondary social partners, in addition to their primary grooming partners.

SIGNIFICANCE OF RESEARCH

The vocal grooming hypothesis (Aiello and Dunbar 1993; Dunbar 1996) proposes one possible route for the evolution of human language, and places non-human primate vocalizations and language on a continuum based on their shared social function. If our earliest ancestors evolved the capacity for language in response to increasing social challenges, then we would expect to see a greater reliance on vocal contact in primate species faced with similar social demands. For many primates, the demands of social life take many forms, including maintaining group cohesion, managing the stressors of living in close proximity with conspecifics, coordinating social activities with partners, and budgeting social time. Identifying the different ways that primates address these challenges can help us understand how our own social strategies, including language, evolved.

CHAPTER 2

KINSHIP AND DOMINANCE RANK INFLUENCE THE STRENGTH OF SOCIAL BONDS IN FEMALE GELADAS

INTRODUCTION

Primates form highly differentiated social relationships with one another, which may be hostile, indifferent, or affiliative, depending on the individuals involved. As we begin to uncover the many benefits associated with close affiliative relationships (e.g., Brent et al. 2011; Crockford et al. 2008; Schülke et al. 2010; Silk et al. 2009, 2010), it becomes increasingly important to identify the factors that determine why individuals form bonds with some group-mates, but not others. For example, many female cercopithecines focus on 1-3 *primary*, or preferred relationships, spending any extra social time on *secondary* or “casual” relationships (Crockford et al. 2008; Dunbar & Dunbar 1988; Engh et al. 2006; Nakamichi & Shizawa 2003; Range & Noë 2002; Silk et al. 2012). Based on the assumption that social bonds are adaptive, much research has been focused on identifying the criteria by which females select their preferred social partners. Maintaining a bond with another individual involves a high degree of cooperation, and these relationships are essentially social contracts that are susceptible to cheating. Therefore, mechanisms must be in place to minimize the risk of destabilization (Dunbar and Shultz 2010). It is therefore not surprising that among female-philopatric species, the most consistent factors that emerge are (1) dominance rank (Range & Noë 2002; Seyfarth 1976, 1977), (2) kinship (Chapais 2001; Silk et al. 1999, 2010), or (3) both (Bernstein & Ehardt 1985; Perry et al. 2008; Schino 2001; Schülke et al. 2013; Silk et al. 2006a, 2006b).

First, dominance rank has the potential to shape female social relationships. Socioecological theory predicts that female primates should form strict, linear dominance hierarchies and differentiated social bonds when within-group competition for resources is high and between-group competition is low (Sterck et al. 1997; Wrangham 1980; van Schaik 1989). If dominant females are the most valuable allies during agonistic encounters, then competition for powerful partners should result in a consistent pattern: high-ranking females monopolize access to high-ranking partners, mid-ranking females monopolize access to mid-ranking partners, and the lowest-ranking females are left to form alliances with each other (Seyfarth 1977). Although this hypothesis (Seyfarth's model) specifically predicts that grooming is directed up the dominance hierarchy, the outcome is such that females end up grooming individuals that are adjacent in rank. In other words, the *rank disparity* between two females should predict the strength of the bond between them. Indeed, many studies have supported this hypothesis, demonstrating strong bonds among females with adjacent ranks (e.g., *Cercocebus torquatus*: Range & Noë 2002; *Macaca mulatta*: de Waal 1991; *M. radiata*: Silk 1982; *Papio cynocephalus*: Silk et al. 2006a; *P. ursinus*: Silk et al. 2010; reviewed in Kapsalis 2003).

Second, inclusive fitness benefits may favor individuals that bias affiliative behavior towards close kin (Hamilton 1964). Therefore, kinship may represent an alternative (or additional) predictor of female social relationships. To date, researchers have focused mainly on the effects of *maternal* kinship on social bonds, which, unlike paternal kinship, can be identified through behavioral observations and long-term pedigrees. Moreover, not only are maternal relationships detectable to observers in the absence of genetic data, they may also be readily recognized by the subjects themselves, presumably through social overlap facilitated by a matriarch (Silk 2002). Maternal kinship is known to structure female social relationships in many primate species (*Cebus capuchinus*: Perry et al. 2008; *Cercopithecus solatus*: Charpentier et al. 2008; *M. mulatta*: Schülke et al. 2013; *P. cynocephalus*: Silk et al. 2006a; *P. ursinus*: Silk et al. 2010; reviewed in Chapais and Berman 2004). For example, female Japanese macaques (*M. fuscata*) preferentially form close relationships with females that fall within a threshold level of maternal relatedness, approximating a kinship "rule of thumb" (e.g., individuals should preferentially affiliate with individuals that are at least their half-sibling, Chapais et al. 1997). A handful of studies also suggest that paternal kinship may be important for female relationships. For example, in rhesus macaques (Schülke et al. 2013; Widdig et al. 2002) and yellow baboons (Smith et al. 2003; Silk et al. 2006a) genetic data suggest that relatedness along both maternal and paternal lines may predict the degree of social affiliation. However, paternal kinship has been shown to have only a moderate effect on bond strength in most primates, showing only a slightly stronger effect than bonds between non-kin (Schülke et al. 2013; Silk et al. 2006a).

Despite widespread support for the effects of rank and kinship, the vast majority of these studies have been conducted on cercopithecines living in large, multi-male, multi-female groups, making it difficult to extrapolate these findings to other primate species. These groups typically include both related and unrelated females and exhibit despotic, linear dominance hierarchies (Cords 2012). In one of the few studies of female bonds in a non-cercopithecine primate (white-faced capuchins, Perry et al. 2008), both dominance rank and kinship were primary determinants of social relationships, yet, like cercopithecines, female white-faced capuchins are matrilocal and their dominance hierarchies are matrilineal (Fedigan 1993, Jack and Fedigan 2004, Perry 1996, Perry et al. 2008). Not surprisingly, kinship plays a negligible role for social bonds among species characterized by female dispersal, where few if any kin are available (e.g., chimpanzees, *Pan troglodytes,* Langergraber et al. 2009). What remains uncertain is the extent to which dominance and kinship influence female social relationships in matrilocal species that diverge from the typical cercopithecine model in their social structure. Here, we explore whether dominance rank and kinship predict female social bonds in a wild population of geladas (*Theropithecus gelada*) – a species that differs from other cercopithecines in that they have: (1) an unusual modular social system, (2) low food competition, and (3) extraordinarily high levels of social tolerance.

First, the modular social system of geladas is composed of small core units (i.e., *one-male units*) comprised of closely-related females, one dominant male, and 1-5 subordinate males (Snyder-Mackler et al. 2012a). These units are socially closed, meaning that grooming and other affiliative behaviors have never been observed between females of different units (with the rare exception of recently fissioned units; Bergman and Beehner, unpublished data). In sharp contrast with the cercopithecine model, where females can associate with both kin and non-kin group mates, gelada females have only kin from which to choose social partners. In such situations, does the presence of kin-only groups strengthen or weaken the importance of kin-biased social behavior?

Second, although female geladas have a linear, stable, and maternally-inherited dominance hierarchy, interactions among females are characterized by lower levels of aggression and a less strict hierarchy than other cercopithecines (le Roux et al. 2011). These differences may reflect the characteristics of the gelada dietary staple, grass, a food resource that is not clumped, defensible, or in short supply (Dunbar 1977; Dunbar 1992; Iwamoto 1979). Socioecological theory predicts that such a diet should result in a more egalitarian society with less emphasis on female competition (Sterck et al. 1997). Indeed, gelada hierarchies may be more tolerant than those reported for other cercopithecines (Dunbar and Bose 1991; Fashing et al. 2010). Consequently, dominance rank might not structure social relationships in geladas in quite the same way.

Third, geladas show unusually high levels of tolerance for extra-group individuals, including animals they may not recognize (Bergman 2010). Gelada core units group together to form large aggregations approaching 1,200 individuals, but the specific units within any one aggregation can fluctuate across seasons and even throughout the day

(Snyder-Mackler et al. 2012a). Furthermore, at any given time, geladas from one unit can demonstrate a high degree of spatial overlap with individuals from other units (Snyder-Mackler et al. 2012a). Thus, although gelada reproductive units are socially-closed (i.e., affiliative interactions are restricted to within the unit), they are by no means spatially-closed (i.e., females are often in close proximity to extra-unit individuals). Previous studies examining social bonds in primates have demonstrated that close proximity is a useful proxy for identifying a close relationship between two animals. For example, in chacma baboons (*P. ursinus*), females with strong social bonds frequently forage close together and individuals that co-feed have the strongest grooming relationships (King et al. 2011). However, this may not be the case for geladas where selection has favored larger aggregations than is typical among ceropithecines. Thus, even though closely bonded females are likely to be in close proximity, all females in close proximity may not necessarily be bonded.

Here, we examine whether the strength of social bonds between two females can be predicted by how close they are in rank and/or kinship. Although early field studies on geladas demonstrated that females preferred social partners that were both close kin and close in rank to themselves (Dunbar and Dunbar 1977; Dunbar 1979; Dunbar 1984), these studies relied on presumed lineal relationships (i.e., mother-daughter) for evidence of kinship rather than genetics. Furthermore, the effects of dominance rank and kinship were not addressed separately and these two variables are likely to be highly correlated. In this study, we seek to contribute to and corroborate these early findings in the following ways: (1) We employ genetic analyses that allow us to examine all levels of relatedness, not just relatedness along maternal lines; (2) We use multivariate statistics to examine the effects of rank and kinship (and their interaction) on the formation of social bonds; (3) Finally, because proximity may be less indicative of close social bonds in geladas, we examine how grooming and proximity each contribute to female bonds.

METHODS

Study site and subjects

Data for this study come from 22 reproductive units within a community of wild geladas living in the Sankaber area of the Simien Mountains National Park, Ethiopia. The entire community of geladas has been under observation as part of the long-term University of Michigan Gelada Research Project since Jan 2006 and the geladas are fully habituated to human observers on foot. The average number of adult females per unit in this population is 5.24 +/- 0.09 the standard error of the mean (hereafter, SEM), with a maximum size of 11 and a minimum of 1 during this study period. Adult males and females of the same unit are always found together, and because geladas are matrilocal, mothers and daughters are always in the same unit. Female geladas in this population spend, on average, 4.92 min/hr grooming (+/- 0.28 SEM, with a range from 0.36-21.43 min/hr) and groom with an average of 3.6 adult female partners (+/- 0.15 SEM, with a range from 1-8 partners).

Behavioral data collection

We studied all adult females in 22 units (N=124 females). We assessed relationships according to dyad – that is, by the frequency of interactions between any two females within the same unit. The 124 females correspond to 416 within-unit dyads (hereafter, *coresident dyads*: Silk et al. 2006a).

The data presented here represent a 4-year subset of the long-term data set (Jan 2009-Dec 2012). Using 15-minute focal animal samples (Altmann 1974), we recorded all social behaviors involving adult females, focusing on dominance interactions (i.e., visual threats, vocal threats, physical aggression, submission, and vocal submission) and grooming, for a total of 1,653 hours of focal observation. In addition, at 5-min intervals within each focal sample we recorded the identity of the nearest within-unit adult female and their distance (in meters) from our focal subject. Finally, because dominance interactions are relatively rare events (Dunbar & Bose 1991; Fashing et al. 2010), we supplemented data collection with additional observations of dominance interactions (i.e., all approach-retreat interactions, both with and without aggression) collected *ad libitum* throughout the day.

Dominance ranks

We assigned dominance ranks to adult females within units using the Elo-rating system (Albers & de Vries 2001; Neumann et al. 2010) – a system originally developed to rank chess players (Elo 1961; 1978). This system is thought to model the process by which dominance is generated within a group (Albers & de Vries 2001). Specifically, after each contest, the winner’s rating increases (and the loser’s rating decreases) based on the expected probability of that individual winning the interaction. For example, if a higher-ranking female (i.e., one with a higher Elo-rating) wins an interaction with a lower-ranking female, her Elo-rating will increase (and the lower-ranking female’s will decrease) marginally. If, on the other hand, a lower-ranking female dominates a higher-ranking female, each female’s Elo-rating will change to a greater extent. The Elo-rating system offers several advantages over other ranking methods because the rankings: (1) are independent of the number of individuals (which varies across groups and through time), (2) easily accommodate the entry and exit of females across time (due to maturation and death), and (3) are particularly useful for our purposes because they distinguish between adjacently-ranked individuals that are closely-matched from those that are clearly delineated.

We calculated Elo-ratings for each female based on all dominance interactions with other coresident females during the study period. We set the initial Elo-rating for each female (i.e., the ranking each female gets when they “enter” the unit) at 1000. The number of points an individual gains or loses during an encounter (*k*) was set at 100 and weighted for each interaction by the expected probability of that individual winning or losing (Note: because geladas have a relatively stable dominance hierarchy, altering these initial parameters did not change any of our results). We then calculated a mean Elo-rating (i.e., rank) for each female over the study period. Because the unit of analysis for this study is a female dyad, we subsequently calculated the difference in the Elo-ratings for the two females in the dyad (hereafter, *rank disparity*), which we then used in all subsequent analyses.

Strength of social bonds

To determine the strength of social bonds between females, we used a common method for calculating a composite sociality index (CSI: Silk et al. 2006a) that uses the frequencies of grooming behavior and time in proximity for each female in a dyad. We standardized by unit averages rather than the study population average because the gelada unit is a closed social group, and other studies normalize their social measures to this level (e.g., standardize within each baboon troop rather than across the whole population: Silk et al. 2006a). Moreover, females in different units have access to a different number of potential social partners due to the wide variation in unit sizes. The CSI is the mean of the adjusted frequencies of grooming and proximity such that:

$$CSI = \frac{\left(\frac{G_{ab}}{G_u}\right)+\left(\frac{P_{ab}}{P_u}\right)}{2}$$

where G_{ab} is the total time (in seconds) that each female in a dyad spent grooming with the other (ignoring directionality), controlled by total observation time; G_u is the mean grooming frequency for all dyads in the unit; P_{ab} is the proportion of point samples where each female in a dyad was each other's nearest neighbor and within 5 meters of each other (as per Silk et al. 2006a), controlled by total observation time; and P_u is the mean proximity frequency for all dyads in the unit. High CSI values indicate dyads with strong bonds (i.e., stronger than the mean for the unit).

Additionally, we calculated separate indexes for the individual components of the CSI (grooming and proximity) to examine whether each was equally likely to predict social bonds (given that even unknown geladas can have a high degree of spatial overlap). We used the following formula for the *grooming index*:

$$grooming\ index = \frac{G_{ab}}{G_u}$$

Because our proximity data also included times when females were grooming, we subtracted the proportion of time a dyad spent grooming from the proportion of point samples when they were nearest neighbors to calculate a *proximity index*:

$$proximity\ index = \frac{P_{ab} - G_{ab}}{P_u - G_u}$$

Genetics

We collected fecal samples from all females (1-4 samples/female) and stored them in RNAlater for subsequent DNA extraction and genotyping (for methods of storage and extraction see Snyder-Mackler et al. 2012b). We genotyped samples using polymerase chain reactions (PCR) at 23 human derived MapPairs microsatellite loci (20 described in Snyder-Mackler et al. 2012b, as well as D4s243, D11s2002, D10s1432), which were found to be variable in this gelada population (average number of alleles/loci = 5.91).

We successfully genotyped all individuals at the majority of all 23 loci (average percentage of loci typed per individual = 95%). To estimate relatedness, we used Wang's pairwise relatedness estimator in all analyses (r_w: Wang 2002), which provided the most accurate estimate of relatedness between individuals of known pedigree in our population (e.g., for parent-offspring dyads r_w should be 0.50).

Data analyses

First, to examine the relationship between social bonds, rank disparity, and relatedness, we used three linear mixed models. Each model used a different outcome variable: the combined index (CSI), the grooming index, or the proximity index. We do not include female age or the separate contributions of maternal and paternal kinship because, at present, the majority of adult females in our population have estimated ages and unknown mothers and fathers. All outcome indexes were log-transformed to approximate a normal distribution (Fig. 2.4). Each model considered only the dyads with sociality measures greater than zero, so the total number of dyads per model varied accordingly: CSI model (*N*=406); grooming model (*N* =277); proximity model (*N* =391). Because a significant number of dyads were never observed to groom at all (*N*=129), we also ran a binary GLMM (groomed vs. never groomed) to determine how relatedness and rank disparity predicted whether individuals groomed at all. We could not model proximity and CSI in this manner because very few within-unit dyads were never found in proximity to one another. As random effects for each model, we entered the unit and the identities of each female in the dyad. As fixed effects in each model, we entered the degree of relatedness and the rank disparity between the two females. We were able to include both rank disparity and relatedness as predictors in the models because the correlation between the two was low (r=-0.10, p=0.036), suggesting that females that are closely related are not always close in rank (as measured by Elo). We compared the univariate models (i.e., only rank disparity or relatedness as a predictor) to the additive and interactive models using Akaike's Information Criterion (AIC) to find the model that best fit the data. All models were fit using the lmer function of the R package lme4 (Sarkar & Bates 2009; R package version 0.999999-2; R version 3.0.1, R Foundation for Statistical Computing, R Development Core Team 2013).

Second, we examined each individual female's primary and secondary social partners. Previous analyses have defined 'preferred' partners as those that fall into the top 10% of the CSI distribution (which typically derives from one social group: e.g., Silk et al. 2006a). However, because we are comparing females from multiple groups that vary greatly in size and range of CSI scores, we labeled females as *primary social partners* if their dyadic CSI score was both the highest CSI score for one female and the first or second highest CSI score for the other female. By this definition, primary social partners do not necessarily reflect the highest dyadic CSI scores of the unit, but rather the highest scores for those individual females. We labeled females as *secondary social partners* if their dyadic CSI score was both the second highest CSI score for one female and the second or third highest CSI for the other female. All other female dyads were labeled as *non-bonded.* We then compared these categorical levels of preferred partners across rank disparity and relatedness using a permutation test. In each simulation, we randomly assigned the category (i.e., primary, secondary or non-bonded) for a dyad and calculated the average difference in relatedness and rank disparity between these categories in the permuted data (i.e., primary vs. secondary, secondary vs. nonbonded, and primary vs. nonbonded). We then counted the proportion of the 10,000 simulations in which the simulated difference in relatedness (or rank disparity) between each category was greater than the observed difference.

RESULTS

Composite sociality index (CSI)

In the CSI models, the best-fit model included rank disparity, relatedness, and an interaction between the two (ΔAIC > 4.8; Table 2.1), although in the univariate models, rank disparity and relatedness each significantly predicted CSI scores as well. First, the CSIs were highest among dyads that were closely related ($t=8.18$, $p<0.0001$; Fig. 2.1). Second, among females that were more closely related, the bonds were significantly stronger between females that were closer in rank (interaction between rank and relatedness: $t=-2.61$, $p<0.01$; Fig. 2.1). Finally, there was no significant effect of rank disparity on CSI in the interaction model ($t=-0.152$, $p>0.8$; Fig. 3.1).

However, CSI scores were highly variable, even at high relatedness and low rank disparity (e.g., the scatter in the points at the far right of Fig. 2.2a for relatedness and the left side of Fig. 2.2b for rank disparity). To further understand this variation, we examined whether partner preference (e.g., primary, secondary) was related to specific characteristics of the social partner. Indeed, we found that there were significant differences in both rank disparity and relatedness among primary, secondary, and non-bonded social partners. Females that were primary social partners were more closely related than females that were secondary social partners ($p<0.0001$) and non-bonded ($p<0.0001$), and secondary partners were more closely related than non-bonded partners ($p=0.0027$; Fig 2a). Finally, primary social partners were significantly closer in rank than both secondary ($p=0.0016$) and non-bonded dyads ($p<0.0001$), while secondary social partners were not significantly closer in rank than non-bonded partners ($p=0.2677$; Fig. 2.2b).

Grooming and proximity indexes

In our analyses of the individual components of the CSI (grooming and proximity), we found that relatedness was the sole significant predictor of whether or not a dyad groomed at all during the study period ($\beta=4.36$, se=0.83, $p<2*10^{-7}$). However, as in the CSI model, the best model for the adjusted rate of grooming included an interaction between rank disparity and relatedness ($\Delta AIC > 3.96$; Fig. 2.3a). Relatedness and the interaction between rank disparity and relatedness significantly predicted the amount of grooming among dyads (Table 2.1); closely related females groomed more in general ($t=5.36$, $p<0.0001$), but this effect was highest if these females were also close in rank ($t=-2.43$, $p<0.02$).

When we examined the proximity index, we found that the univariate model with relatedness as the sole predictor was better at predicting which females were found in proximity than the additive or interactive models ($\Delta AIC = 0.63$; Fig. 2.3b). Specifically, females in close proximity were more closely related ($t=6.697$, $p<0.0001$; Table 2.1).

Therefore, relatedness was a significant predictor for both grooming and proximity, but rank disparity was only a significant predictor for grooming, and not proximity. While closely related females that were close in rank groomed the most, closely related females in general were in close proximity, regardless of dominance rank.

Modeling with relatedness estimators

Recent studies have cautioned against the use of relatedness estimators as predictors in correlational analyses (Csilléry et al. 2006; Van Horn et al. 2008). Nevertheless, most primate studies – including our own – are limited in their knowledge of population pedigrees, due to the long life spans and slow reproductive histories of primates. Where deep pedigrees are unavailable, non-invasive genetic data are the only way to address specific biological questions, such as how kinship contributes to social partner preference. To help address this concern, we carried out 10,000 simulations testing the robustness of our models to variation in our relatedness estimators, thus, estimating the probability of a false positive. In each simulation, we added a random number from a uniform distribution to the relatedness estimator of each of the 416 dyads and then re-modeled the simulated data for all three outcome variables (CSI, grooming, and proximity). This approach simulates the possibility that our relatedness estimator could over- or under-estimate the true dyadic relatedness by a given amount. We used a range of random error from -0.32 to 0.32 as a conservative estimate of the error in our relatedness measure because all of the r_w values of the 224 known parent-offspring dyads were within 0.32 of their true relatedness (r=0.5). In fact, this error estimate is most likely hyper-conservative, as 95% of the r_w values of known parent-offspring dyads were within 0.19 of their true relatedness. The simulations revealed that our models were extremely robust to these perturbations. For our CSI and proximity models, the effect of relatedness on the dependent variable was a significant predictor in all 10,000 simulations. The effect of relatedness on grooming failed to reach significance ($t>1.66$; $df=111$) in only 13 of 10,000 simulations. In other words, the maximum probability of a false positive in our current analysis is less than 0.13% if we make the extremely conservative assumption that our relatedness estimators are accurate to within 0.32. This suggests that, while researchers should exercise caution when using relatedness estimators in correlational analyses, they may still be meaningful and informative when the effect of relatedness is large.

DISCUSSION

Despite working with a relatively shallow pedigree, incorporating genetic data on overall relatedness corroborates earlier findings that the factors mediating social relationships for female geladas resemble those of other cercopithecines, where both kinship and rank disparity are important (e.g., Dunbar and Dunbar 1977; Dunbar 1979; Dunbar 1984). Female geladas formed the strongest social bonds with females that were close kin and, among close kin, with females that were close in rank. Furthermore, partner preference varied according to both dominance rank and kinship: primary partners were close kin ($r_w \sim 0.40$, i.e., approaching the relatedness between a mother and daughter) and had lower rank disparity than both secondary partners and non-bonded dyads. While secondary partners were not closer in rank than non-bonded social partners, they were more closely related than non-bonded dyads (r_w ~ 0.25; i.e., comparable to half-sisters). Non-bonded partners were the least related dyads in each unit (r_w ~ 0.19).

Rank disparity had no predictive value for more distant kin. However, for close kin, females of similar rank were more closely bonded than females more distant in rank. Nevertheless, these closely-related but distantly-ranked females exhibited higher levels of bonding than all distant kin. Since geladas have maternal rank inheritance, we wanted to explore these closely related but distantly ranked females a bit further. Of all female dyads in this category (N=83), we were able to assign paternity for both females in 8 dyads. Intriguingly, in all 8 of these dyads, the females were paternal (and not maternal) kin. Certainly, a larger sample will be necessary to confirm any effect of paternal relatedness on partner preference (many of our current adult females were sired before the study began so we do not know their paternity). However, these data add to the growing support that paternal kinship cannot altogether be ignored (Widdig et al. 2002; Smith et al. 2003; Silk et al. 2006a; Schülke et al. 2013).

Two primary goals for research on social bonds are to (1) standardize objective criteria by which researchers can quantify social relationships (and to find suitable operational indexes), and (2) identify functional outcomes. Importantly, the instrumental outcomes of the relationship (i.e., the phenomena we wish to explain using bonds) should not be confused with the proxies used to identify the relationship (i.e., the criteria by which we quantify bonds; reviewed in Dunbar and Shultz 2010). Some of the results presented here have relevance for quantifying bonds. Although our results largely support the use of both social grooming and proximity as useful proxies for identifying female relationships in geladas (as in previous gelada research, e.g., Dunbar and Dunbar 1977; Dunbar 1979; Dunbar 1984), our analyses suggest that the measures of proximity generally used to measure social bonding (e.g., Silk et al. 2006, 2009) may need to be modified for use in geladas due to their high level of spatial overlap. For example, although the strongest grooming relationships (e.g., closely-related and closely-ranked dyads) were generally found in close proximity, it was also the case that dyads that exhibited weak grooming relationships were frequently found in close proximity (closely-related but distantly-ranked dyads). Therefore, in this case, proximity may not help us identify those dyads that form the strongest, and most preferred, social bonds. These results may reflect the unique demands of gelada social life, where direct competition over food is rare and large foraging herds often consist of many intermingling reproductive units. Regardless of why geladas exhibit such a high degree of social tolerance, proximity measures may reflect an individual's social circle (e.g., their closest kin network), but not their closest social partners. Alternatively, it may be that geladas simply have a smaller threshold for discriminating neighbors, and if we were to define proximity differently (e.g., two females within 1 m), we might find that proximity is a much better predictor of social bonds. Regardless, the proxies for identifying social bonds need to be carefully considered for each species, particularly if predation or foraging conditions select for larger or tighter aggregations of individuals (reviewed in Dunbar and Shultz 2010, Silk 2002).

With respect to the second goal, at present, we are unable to say whether a preference for closely-related or closely-ranked individuals might have functional consequences for gelada females. Studies that document direct and indirect fitness benefits associated with social bonds suggest that the formation and maintenance of relationships with specific individuals may confer fitness benefits. For example, Silk et al. (2009) demonstrated that female baboons not only preferentially associated with close maternal kin, but that the strength of these kin bonds enhanced offspring survival. Rank-based associations, on the other hand, may reflect a different strategy, where females of adjacent rank are important allies in coalitions (Silk et al. 1999). Indeed, subtle differences exist in the quality and longevity of relationships between close kin and closely ranked females, with social bonds between kin emerging as more stable, less aggressive, and more equitable over the long-term (than bonds between non-kin; Silk et al. 2010). Further analyses on female geladas that incorporate measures of bond equality, diversity, and duration in combination with short-term and long-term fitness outcomes will help complete the picture as to (1) whether, like baboons, social bonds confer a fitness advantage to gelada females, and (2) whether social bonds with some partners may be more beneficial than those with others.

This, then, opens the door to intriguing possibilities for additional proxies for social bonds that may not require physical contact. One possibility that may be particularly relevant for geladas is the exchange of vocalizations. Gelada females exchange vocalizations while foraging throughout the day, which Dunbar (1996) suggested might be akin to “vocal grooming,” allowing females to maintain bonds with primary partners even while engaged in other activities. Indeed, unlike proximity, vocal contact is confined to members of the same unit (Dunbar 1996), suggesting that vocal exchanges may identify important aspects of gelada social relationships that may not emerge from grooming or proximity indexes. It will be important, however, to carefully consider whether such vocalizations are proxies for, or outcomes of, the social relationship itself before we can incorporate them properly into our understanding of female gelada social bonds.

In sum, this study demonstrates that genetic analyses of relatedness can reveal fundamental aspects of primate sociality. Even without knowledge of a deep pedigree, we were able to determine the effect of kinship on social bonds because relatedness had such a profound and strong effect on social bond strength. Indeed, a simple simulation demonstrated that the model was robust to the inherent variation that comes with using relatedness estimators. Thus, while researchers should exhibit caution when using relatedness estimators in correlational studies of biological phenomena (see Csillery 2006; van Horn 2008), we should not “throw the baby out with the bath water”. There is great value in using relatedness estimators when a pedigree is absent - as is the case with new study populations. The novel method that we outline in this paper is one way in which researchers can determine whether or not relatedness plays a significant role in answering biological questions. Furthermore, we have begun to distinguish between two variables that are often highly correlated in female-bonded primate groups: kinship and rank. This study shows that, for gelada females, both relatedness and dominance rank influence the strength of close social bonds. We are now in the position to ask why kinship and rank structure gelada female social relationships.

TABLES

Table 2.1. Effects (β +/- SE) of rank disparity and relatedness on each of the three social metrics in the best-supported models, i.e., the lowest AIC.

Social index	Rank disparity	Relatedness	Rank Disparity × Relatedness
CSI	-0.00005	2.93*	-0.0026*
Grooming	-0.0003	3.84*	-0.0046*
Proximity	N/A[a]	1.08*	N/A

Significant predictors at *P* < 0.05 are denoted with asterisks.

[a] Note that we do not report the effects of rank disparity and the interaction between rank disparity and relatedness for the proximity model because these two variable were not predictors in the model with the best support. Instead, the model with the best support for proximity was the univariate model with relatedness as the sole predictor.

FIGURES

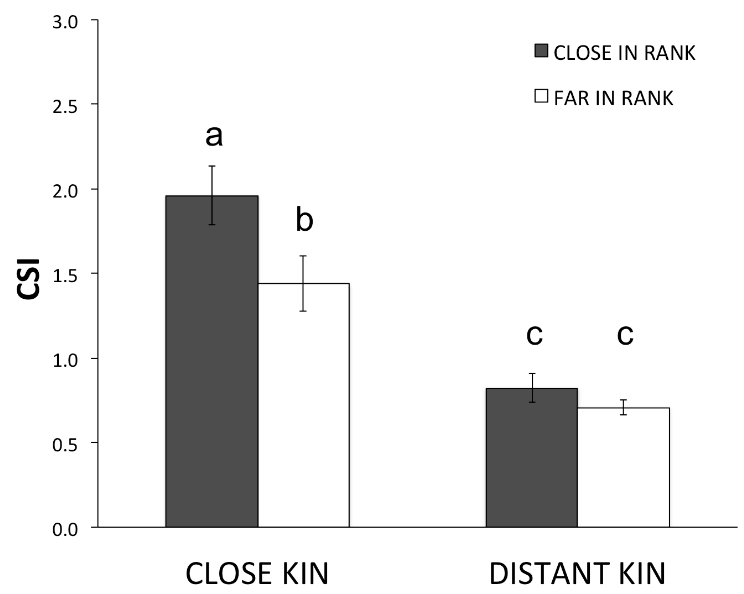


Figure 2.1. The interaction between relatedness and rank disparity on the average composite sociality index (CSI) score. For visualization purposes only, we performed a median-split of rank disparity values, with values below the median labeled as close in rank and values above the median labeled as far in rank. Relatedness was also divided into two categories: where rw was greater than 0.25, females were labeled close kin and where rw was less than 0.25, females were labeled as distant kin. Using these cutoffs, 98% (251/256) of known full sibling and parent-offspring dyads in the entire study population were classified as close kin. Mean dyadic CSI scores for the following females are plotted: (1) close in rank and close kin (mean=1.96 +/- 0.17 SEM, n=121); (2) far in rank and close kin (mean=1.44 +/- 0.16 SEM, n=83); (3) close in rank and distant kin (mean=0.82 +/- 0.09 SEM, n=87); (4) far in rank and distant kin (mean=0.71 +/- 0.05 SEM, n=125). Means with different letters are significantly different.

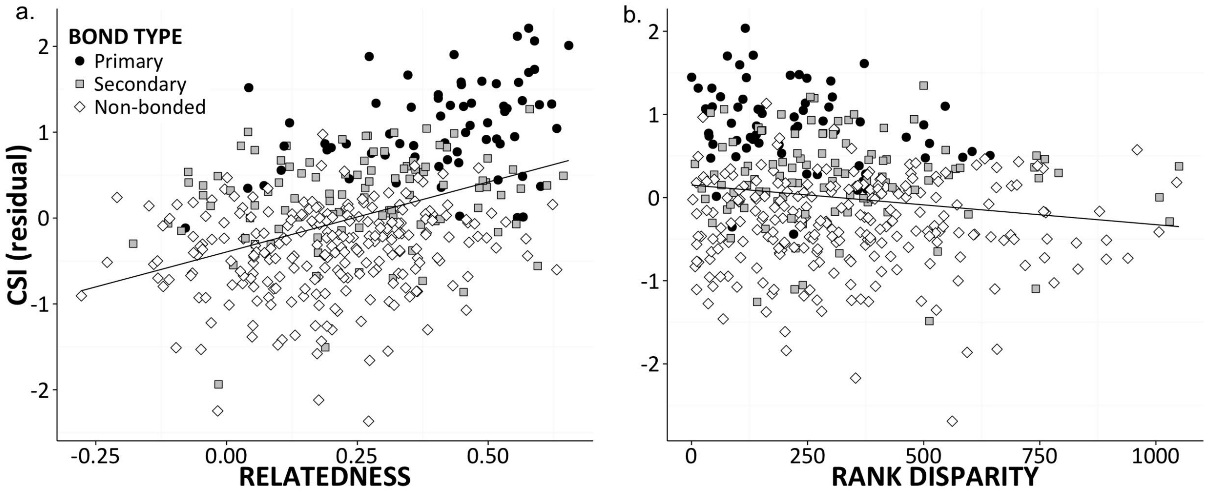


Figure 2.2. Partial residual plots of the effects of **(a)** dyadic relatedness, and **(b)** rank disparity on composite sociality index (CSI). Dyads with high CSI scores have higher relatedness values and lower rank disparity. Furthermore, primary partners (black circles) are **(a)** more related and **(b)** closer in rank than secondary partners (grey squares) and non-bonded partners (white diamonds).

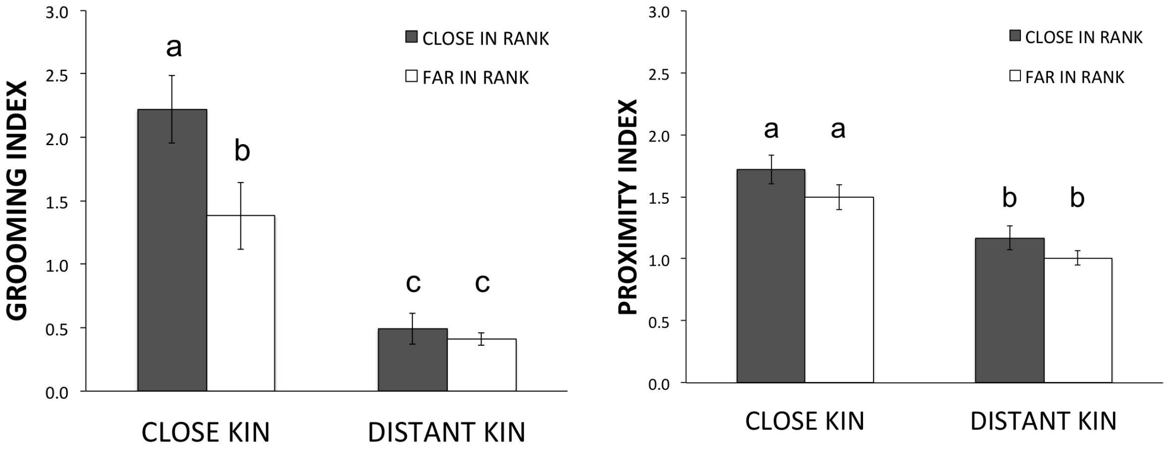


Figure 2.3. The interaction between relatedness and rank disparity on **(a)** the average grooming index, and **(b)** proximity index score. Categories were defined as in Fig. 3.1. Means with different letters are significantly different. **(a)** The mean dyadic grooming index is plotted for: (1) close in rank and close kin (mean=2.22 +/- 0.26 SEM, n=121); (2) far in rank and close kin (mean=1.38 +/- 0.26 SEM, n=83); (3) close in rank and distant kin (mean=0.49 +/- 0.12 SEM, n=87); (4) far in rank and distant kin (mean=0.41 +/- 0.05 SEM, n=125). **(b)** The mean dyadic proximity index is plotted for: (1) close in rank and close kin (mean=1.72 +/- 0.11 SEM, n=121); (2) far in rank and close kin (mean=1.49 +/- 0.10 SEM, n=83); (3) close in rank and distant kin (mean=1.17 +/- 0.10 SEM, n=88); (4) far in rank and distant kin (mean=1.00 +/- 0.06 SEM, n=127).

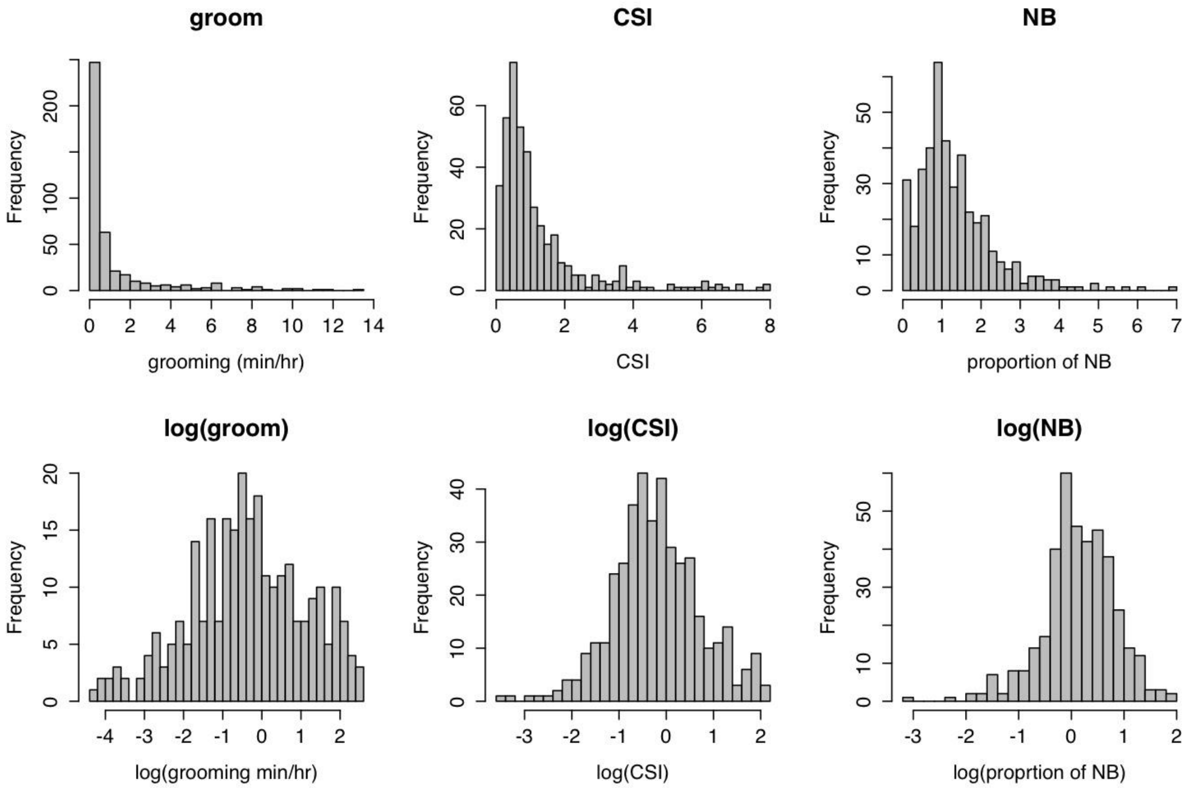


Figure 2.4. Distributions of behavioral indices and the log-transformed values used in modeling. From left to right: the grooming index, the composite sociality index, and the proximity index.

CHAPTER 3

SOCIAL AND ECOLOGICAL DRIVERS OF REPRODUCTIVE SEASONALITY IN GELADAS

INTRODUCTION

The ways in which ecology interacts with reproductive timing can be characterized as a continuum, reflecting various species-specific energy-use strategies and patterns (Negus and Berger, 1972; Drent and Daan, 1980; Brockman and van Schaik, 2005; Janson and Verdolin, 2005). In the strictest sense, income breeders, at one end of the continuum, rely on external cues (e.g., photoperiod) to time conceptions so that vulnerable stages of the reproductive cycle, such as births or weaning periods, coincide with optimal ecological conditions. As a result, income breeders are typically strict seasonal breeders, with a discrete breeding season and birth season each year (though there may be some flexibility in birth timing in certain cases, e.g., Tecot, 2010; Carnegie et al., 2011). Capital breeders, at the other end of the continuum, rely on internal cues of condition (e.g., energy balance, or the ratio between energy intake and energy expenditure: Valeggia and Ellison, 2004), which allows for reproduction at any point in the year, as long as energetic requirements are met. Therefore, the timing of births for capital breeders depends on the seasonality and predictability of the environment: in a highly seasonal and predictable environment, capital breeders may demonstrate a strict birth season, much like income breeders do. On the other hand, in a less seasonal or less predictable environment, capital breeders may exhibit no seasonal patterns in births, or they may exhibit some degree of birth seasonality (where births cluster around the same time each year) or birth synchrony (where births cluster around certain times within a year: Heideman and Utzurrum, 2003) following periods of energetic abundance.

At a proximate level, birth seasonality is shaped by ecological factors that impact a female's ability to "finance" a reproductive event across critical stages, from ovulation to conception and through parturition. Energy balance can impact a female's ability to initiate (e.g., ovulation and conception: Bronson, 1989; Wade and Schneider, 1992; McCabe and Emery Thompson, 2013) or sustain (e.g., gestation and lactation: Roberts et al., 1985; Clutton-Brock et al., 1989; Wade and Schneider, 1992; Beehner et al., 2006; Maestripieri and Georgiev, 2016) a reproductive event. Birth seasonality (i.e., either a birth peak, when a high proportion of births are concentrated at a particular time of year, or a birth valley, when the proportion of births drops significantly at a particular time of year: Lancaster and Lee, 1965; Janson and Verdolin, 2005; Tecot, 2010; Carnegie et al., 2011; Erb et al., 2012) can arise when maternal condition, specifically maternal energy balance, varies consistently across seasons.

Energy balance is a function of energy intake and energy expenditure, and both are known to shape birth seasonality across many mammalian species (reviewed in: Di Bitetti and Janson, 2000; Brockman and van Schaik, 2005; Janson and Verdolin, 2005). Because directly assessing energy intake can be methodologically challenging, many studies have successfully used food availability and/or rainfall as proxies for energetic condition in a number of studies (reviewed in Martinez-Mota et al., 2016). Both high food availability (e.g., in insectivorous mouse-eared bats, *Myotis blythii*: Arlettaz et al., 2001) and low food availability (e.g., in a survey of neotropical mammals: Dubost and Henry, 2017) have been associated with either birth peaks or birth valleys, respectively.

Energy expenditure can vary according to a number of different factors, from day range length to thermoregulation. In mammals, thermoregulatory demands due to both extreme heat and cold are known to hinder female reproduction (e.g., in owl monkeys, *Aotus azarai*: Fernandez-Duque et al., 2002; in black-and-white snub-nosed monkeys, *Rhinopithecus bieti*: Xiang and Sayers, 2009; reviewed in Bronson, 1985; 1989; Loudon and Racey, 1987; Manning and Bronson, 1990). For example, in captive conditions, the energetic demands of thermoregulation during extremely cold months were shown to impact reproduction even when energy intake was not restricted (e.g., in captive hamadryas baboons, *Papio hamadryas*: Polo and Colmenares, 2016). Moreover, cold stress is known to be compounded by the hypoxic (i.e., low oxygen) conditions of high altitude where thermogenic capacity is even more constrained (e.g., Hayes, 1989; Ward et al., 1995; Chappell and Hammond, 2004; Cheviron et al., 2013).

One way to identify the harsh conditions that hamper female reproduction is to measure energy constraints (or their proxies), as outlined above. Another informative approach is to measure the internal physiological state of the organisms living through these adverse conditions. In particular, glucocorticoids (glucocorticoid metabolites, or GCMs) are steroid hormones that lend themselves to this endeavor: first, GCMs rise in response to the energetic demands that accompany ecological and/or social challenges, such as food scarcity (e.g., Pride, 2005; Gesquiere et al., 2008; Foerster et al., 2012), extreme temperatures (e.g., Weingrill et al., 2004, Beehner and McCann, 2008; reviewed in Jessop et al., 2016), or the threat of infanticide from an incoming male (e.g., Beehner et al., 2005). Second, GCM concentrations in fecal, urine, and hair samples have been shown to increase with an individual's recent exposure to ecological and/or social challenges (e.g., Fardi et al., 2017; reviewed in Dantzer et al., 2014; Beehner and Bergman, 2017). Activation of the hypothalamic-pituitary adrenal axis (HPA-axis), which results in an increase in GCM secretion, has also been repeatedly associated with reproductive suppression (via the inhibition of pulsatile leutenizing hormone: Wasser, 1996; Landys et al., 2006; Breen et al., 2007). Therefore, GCM profiles used in conjunction with measurements of challenging conditions (ecological or social) can help identify circumstances where reproductive constraints might be greatest.

Group-living animals must contend with challenging social environments in addition to any harsh climatological conditions; correspondingly, the social environment can also alter the timing of female reproduction. For example, reproductive synchrony among females (where births cluster together within a year) can arise in response to social as well as ecological forces (reviewed in Ims, 1990). One salient social threat to female reproduction known to promote reproductive synchrony is infanticide by males (reviewed in Agrell et al., 1998). Infanticide occurs when non-sire males kill the dependent offspring of females to expedite reproductive cycling and mating receptivity in the mother (Sugiyama, 1965; Hrdy, 1974; reviewed in: Hrdy, 1979; Fedigan, 2003; Palombit, 2015). Perhaps in response to the threat of infanticide, lactating females often prematurely wean their dependent offspring (i.e., accelerated weaning: e.g., vervet monkeys, *Chlorocebus pygerythrus*: Fairbanks and McGuire, 1987; siamangs, *Symphalangus syndactylus*: Morino and Borries, 2017; reviewed in Smuts and Smuts, 1993). Similarly, non-sire males can cause the death of a fetus *in utero* directly (i.e., sexually-selected feticide, Zipple et al., 2017) or indirectly (i.e., the Bruce effect: Bruce, 1959; e.g., prairie voles, *Microtus ochrogaster*: Fraser-Smith, 1975; wild horses, *Equus caballus*: Berger, 1983; geladas, *T. gelada*: Roberts et al., 2012). Therefore, the arrival of non-sire males represents a challenging social environment that is known to “reset” the reproductive cycles of females. In social species, such as primates, the arrival of a non-sire male poses an infanticidal threat primarily when he takes over the dominant male position of a group (i.e., a takeover: Teichroeb and Jack, 2017). Takeovers impact all females in a group simultaneously – effectively synchronizing their estrous cycles in the months that follow (e.g., Packer and Pusey, 1983; Colmenares and Gomendio, 1988; Ims, 1990) and altering the timing of subsequent births.

As a result, male takeovers have the potential to alter reproductive timing to such an extent that ecological patterns of reproductive seasonality are disrupted, which may result in fitness costs for affected females. In some species, females may need to delay conceiving until ecological conditions improve, while in others, females may conceive immediately following the death of their infant, resulting in births that fall outside any seasonal birth peak. If such “mis-timed” births occur during periods of negative energy balance, then it stands to reason that females will suffer downstream costs (e.g., neonatal loss, slow infant development and/or a prolonged interbirth interval) over and above the costs of infanticide alone. For example, in recent decades many species are experiencing rapid changes in their ecology due to climate change; these changes are causing slight shifts in birth timing that can result in mis-timed and, as a result, less successful births (e.g., in cattle, *Bos taurus* L.: Burthe et al., 2011; reviewed in Bronson, 2009; Campos et al., 2017). Moreover, if male takeovers are seasonal (e.g., in white-faced capuchins, *Cebus capucinus*: Schoof and Jack, 2013; reviewed in Teichroeb and Jack, 2017), then takeovers themselves may produce a distinct “social birth peak” in addition to (or instead of) the usual “ecological birth peak.”

Here, we examined the impact of male takeovers on reproductive seasonality in a population of wild primates, the gelada (*T. gelada*), living in the Simien Mountains National Park, Ethiopia. Geladas are an ideal species for this inquiry for a number of reasons. First, the social structure of geladas allows us to study dozens of groups, or “reproductive units,” at once. Reproductive units (hereafter, “units”) comprise the core groups of gelada multi-level society, and are composed of a dominant leader male, 1-12 adult females and their offspring, and possibly one or more subordinate follower males (Dunbar, 1980; Snyder-Mackler et al., 2012b). Bachelor males form peripheral “all-male groups,” and challenge dominant leader males for reproductive control of the females within a unit (Dunbar and Dunbar, 1974; Dunbar, 1984).

Second, male takeovers (i.e., when a bachelor male defeats a dominant leader male) are a frequent occurrence in this population (0.32 takeovers/unit/year, Beehner and Bergman, 2008) and have severe consequences on female reproduction. Following takeovers, incoming males are known to commit infanticide (killing up to half of unit infants: Beehner and Bergman, 2008), they trigger pregnancy termination (via the Bruce effect in 80% of females: Roberts et al., 2012), and they may cause lactating females to begin cycling sooner than they would otherwise (Dunbar, 1980). Moreover, because male takeovers in this population follow a seasonal pattern themselves (with a peak between Feb-Apr each year, Pappano and Beehner, 2014), takeovers have the potential to not only disrupt reproductive patterns for females that experience a takeover but to also produce their own seasonal peak in reproduction for these same females.

Third, geladas represent an opportunity to examine the separate ecological effects of rainfall and temperature (as proxies for green grass availability and thermoregulatory constraints, respectively) on reproductive timing. Availability of green montane grass, the staple food for geladas, fluctuates throughout the year and peaks following the rainy season (Jarvey et al., In press). However, this optimal period of green grass availability also coincides with the *least optimal* temperatures for this region, when temperatures routinely fall below freezing (Iwamoto and Dunbar, 1983; Ohsawa and Dunbar, 1984). Previous research has demonstrated that male geladas in this same population exhibited the highest fecal GCMs during these cold-wet months (Beehner and McCann, 2008), however, seasonal patterns of GCMs in females have never been examined. Females geladas (like males) should also be sensitive to thermoregulatory constraints, but females (unlike males) are expected to be sensitive to fluctuations in green grass availability due to the energetic demands of reproduction (Crook and Gartlan, 1966; reviewed in Schülke and Ostner, 2012). Indeed, for this same population of geladas, Dunbar (1980) identified a seasonal pattern to births that included not one, but two distinct birth peaks – one during the dry season and another during the wet season. He suggested that the two peaks reflected a compromise between the constraints of food and temperature: females were more likely to conceive when food availability was high, but also avoided giving birth to vulnerable infants during the cold-wet season.

Our first aim in this study is to confirm the nature of reproductive seasonality in geladas with a larger dataset across nearly a decade (9 years) in conjunction with seasonality in rainfall and temperature. Our second aim is to use fecal hormone profiles (GCMs) to test two separate predictions about seasonal causes of metabolic stress. If green grass availability represents a significant metabolic constraint for females, then we expect to see higher female GCMs during the dry season, when green grass is scarce. Alternatively, or additionally, if thermoregulatory pressures represent a significant metabolic constraint for females, then we expect to see higher GCMs during the late rainy season, when temperatures are lowest. We predicted that, as capital breeders, the onset of female gelada reproduction would coincide with periods of low metabolic demands as indicated by low GCM profiles overall. Our third aim is to assess the extent to which male takeovers, with their known effects on female reproduction, explain seasonal variation in birth patterns. We predicted that male takeovers would be associated with higher GCM profiles and within-unit reproductive synchrony for affected females. Moreover, due to the seasonality of takeovers, we predicted that takeovers would produce some degree of across-unit reproductive seasonality. Finally, to consider the costs of giving birth outside of the ecological birth peak, we compared infant survival for births within versus outside of the ecological birth peak.

METHODS

Study site and subjects

The data for this study were collected between 2006 and 2014 from a population of wild geladas living in the Simien Mountains National Park, in northern Ethiopia (13°13.5’ N latitude). The Simien Mountains Gelada Research Project (SMGRP – formerly called the University of Michigan Gelada Research Project) has collected behavioral, demographic, genetic, and hormonal data from individuals since Jan 2006. All gelada subjects are habituated to human observers on foot and are individually recognizable. Here, we used longitudinal data from 167 adult females comprising 25 reproductive units. All adult females had known or estimated birth dates from which we calculated age (mean age = 11.4 years; range = 4.3-27.0 years). Most estimated birth dates (N=51) were calculated by subtracting the mean female age at major life history milestones from known dates for each milestone (e.g., maturation, first birth: Roberts et al., 2017). For a subset of older females (N=60), date of birth was estimated based on age of oldest offspring, or number of known offspring.

Reproductive events

We recorded all known births (N=341; “births dataset”) and then assigned an estimated conception date for each birth based on the mean gestation length for this population (183 days; Roberts et al., 2017; “conceptions dataset”). For many of these births, the day of birth was known within 7 days (n = 291), but in cases where it was not, the birth date was estimated for the missed observation days as the mid-point of the period from which we last saw the mother until the time we saw the mother again with the new infant (n = 50 births; mean range = 37 ± 5.3 SE days; see Beehner and Bergman, 2008 for more detail on assigning birth dates). The return to cycling for postpartum females was assigned as the first day we observed sexual swellings (i.e., swollen, bead-like vesicles surrounding a patch of exposed skin on the chest and neck, Roberts et al., 2017; “return to cycling” dataset) following the period of postpartum amenorrhea. The return to cycling dataset was independently observed from the conceptions and births datasets; and not all conceptions and births are included in the return to cycling dataset (e.g., females conceiving for the first time, females that were never observed to resume postpartum sexual swellings). By contrast, the conceptions dataset is not independent from the births dataset (i.e., the conception dates are derived from the birthdates). Nevertheless, we analyzed these two datasets separately to understand how the climatological data that correspond to each event contribute (or not) to the timing of female reproduction. In this way, we were able to separately examine the weather surrounding conceptions from the weather surrounding births. We have no cases where we included a conception that did not result in a live birth (since, for this dataset, live birth was how we estimated the date of conception). With respect to examining the costs of birth seasonality, we selected infant survival to 2 years as our fitness measure because the mean age at weaning in this population is approximately 1.5 years (Roberts et al., 2017) and thus the 2-year mark is sure to include the majority of weaned infants in our analyses. We opted against using additional measures that overly restricted our dataset (e.g., interbirth-intervals) or did not adequately account for infant losses prior to weaning (e.g., infant survival prior to 2 years).

Weather data

As part of our long-term climatological monitoring, we recorded daily cumulative rainfall and maximum and minimum temperature. Seasonal patterns of green grass availability in this area are known to be positively correlated with rainfall from the previous 90 days (Jarvey et al., In press). Therefore, because we did not directly collect food abundance data (or intake rates) across the entire study period, we used the total rainfall over the 90 days prior to each reproductive event (or hormone sample) as our proxy for green grass availability (e.g., Hill et al., 2000; McFarland et al., 2014). The physiological effects of temperature on reproduction are more direct than rainfall (via changes in core body temperatures). Therefore, as our proxy for thermoregulatory constraints, we calculated the mean maximum and minimum daily temperatures for the 30 days preceding each reproductive event or hormone sample (e.g., Dunbar et al., 2002).

Takeovers

We recorded the dates of all observed male takeovers (n = 72) of known reproductive units. Most takeovers were recorded within days of occurrence (n = 62; range = 0-7 days). For takeovers that were not directly observed (n = 18), we were able to assign the day of takeover to within a mean of 30.7 ± 5.3 SE days of occurrence. These takeovers were assigned the mid-point of the missing observation period. Because we were primarily concerned with how takeovers might alter the timing of reproductive events (e.g., due to infanticide, the Bruce effect, or accelerated weaning: Beehner and Bergman, 2008; Roberts et al., 2017), we labeled any return to cycling and conception dates that occurred during the 3 months following a takeover as *takeover return to cycling/conception dates*, and those that did not follow a takeover we labeled *non-takeover return to cycling/conception dates*. The 3-month window was chosen based on the observation that most known or suspected infanticides occur during this 3-month window (in rare cases, infanticide may occur up to 9 months after a takeover, but we wanted to reflect the immediate impact of takeovers on female reproduction in the seasonality analysis: Beehner and Bergman, 2008). Similarly, we labeled all births that occurred between 6-9 months following a takeover as *takeover births* (this time period reflects all births that resulted from conceptions by the new dominant male during his first 3 months as leader male, plus the period of gestation, 183 days, or just over 6 months; Roberts et al., 2017). Births that did not occur between 6-9 months after a takeover were labeled *non-takeover births*.

Hormone collection and analysis

We collected fecal samples from 148 known adult females between 2006-2014 (N=3,841 hormone samples; mean=26 samples per female; range: 1-150 samples per female). Fecal samples were collected using non-invasive methods developed by the

SMGRP for hormone extraction and preservation under field conditions (Beehner and Whitten, 2004; Beehner and McCann, 2008). In brief, we mixed the full fecal samples prior to placing a small aliquot in 3 ml of a methanol:acetone solution (4:1). Samples were vortexed and later filtered and extracted using a solid-phase cartridge. All samples were washed with 2.0 ml of 0.1% sodium azide (NaN_3) solution, placed in a sterile Whirl-pak bag with a silica desiccant, and stored frozen until shipment to J. Beehner's endocrine laboratory at the University of Michigan for radioimmunoassay (RIA). Dry fecal weights from all samples were obtained to the nearest +/- 0.0001 g, and hormones values were calculated as ng/g dry feces.

At the University of Michigan, all samples were assayed for glucocorticoid metabolites (GCMs) using reagents from the ImmuChem^{TM} double antibody corticosterone ^{125}I RIA kit (MP Biomedicals, LLC, Orangeburg, NY). This antibody has been validated both analytically and biologically for use in geladas (Beehner and McCann, 2008). The primary antibody in this kit cross-reacts 100% with corticosterone, 0.34% with desoxycorticosterone, 0.1% with testosterone, 0.05% with cortisol, 0.03% with aldosterone, and 0.02% with progesterone. We ran all standards, controls, and samples in duplicate. We used a low (~20% binding) a mid- (~50% binding) and a high (~80% binding) fecal pool control in all assays. The respective inter-assay coefficients of variation (CVs) were: low fecal pool: 20.69%; mid fecal pool: 21.43%; high fecal pool: 20.93%; high kit control: 24.03%; and low kit control: 18.85% (N=177 assays). Our intra-assay CV for a high and low fecal pool was 6.3% (N=10 assays) and 8.7% (N=10 assays), respectively, with a high kit control CV of 6.3% (N=12 assays) and a low kit control of 4.1% (N=12 assays).

Data analyses

We conducted five sets of models (described in detail below) that correspond to each of the five outcome variables (GCMs, return to cycling, conceptions, births, infant deaths).

Model averaging

For each of the first four sets of models (GCMs, return to cycling, conceptions, and births), we took an information theoretic approach based on Akaike's Information Criterion (using AIC for the GCMs model; AICc, corrected for small sample sizes, for the return to cycling, conceptions, and births models; Anderson and Burnham, 2002) to average all candidate models for each outcome variable (Table 3.1; Johnson and Omland, 2004). Candidate models represent all combinations of the predictor variables of interest and their interactions (mean maximum temperature, mean minimum temperature, cumulative rain, and takeover, Table 3.1. Model averaging was done using the Mu-MIn package (version 1.15.6: Barton, 2016) in R (version 3.3.2: R Development Core Team, 2012) to produce estimates of predictors within an averaged model. We considered predictors to have a meaningful effect on the outcome variable if the 95% confidence intervals of the averaged effect size did not overlap zero (i.e., "reliable" predictors: Table 3.2, though see Table 3.4 for full averaging results).

Glucocorticoid seasonality

To assess the effects of ecological and social seasonality on GCMs, we first log-transformed GCM values to approximate a normal distribution, and then modeled logGCMs as a function of the following candidate predictors (including interaction terms; see Table 3.1 for descriptions): (1) mean maximum temperature, (2) mean minimum temperature, (3) cumulative rainfall, and (4) takeover (yes/no). We controlled for the repeated measures of individual identity, unit, and year as random effects, as well as the known effects of age and reproductive state on GCMs (Beehner and Bergman, 2017) by including an interaction term between reproductive state (pregnant, cycling, or lactating) and age (both as a linear and as a quadratic term; see Fig. 3.5 for full averaged model results). We constructed 41 candidate linear mixed-effects models (including an intercept model and a model controlling for age and reproductive state alone) with the *lme4* package in R (version 1.1-12: Bates et al., 2015). The candidate models represent all combinations of predictor variables and their interactions (mean maximum temperature, mean minimum temperature, cumulative rain, and takeover), and the model fits were compared using AIC and Akaike model weights (Anderson and Burnham, 2002).

Initiating reproduction

To assess how ecological (i.e., rainfall, temperature) and social (i.e., male takeover) factors were associated with the initiation of reproduction, we considered two different events that could indicate the start of a reproductive event for gelada females: (1) the resumption of cycling from postpartum amenorrhea (based on observational data on each female), and (2) the date of conception for each birth (estimated backwards from each observed birth). We conducted two separate analyses using binomial generalized linear mixed models (GLMMs). We coded the reproductive events as binary variables by month, where females either returned to cycling or not, or conceived or not. Because we were interested in population-level patterns of reproductive seasonality (since populations, and not individuals, exhibit birth peaks), we analyzed reproductive seasonality across the entire population, not at the level of the unit. Therefore, the dependent binomial variable for the first model was *Return to Cycling* (or the number of postpartum females in the population that had resumed cycling in a given month out of the total females in the study population that month). The dependent binomial variable for the second model was *Conceptions* (or the number of females in the population that had conceived in a given month out of the total females in the study population that month).

We also coded these reproductive events according to whether or not the event occurred within the context of a takeover. Using conceptions as an example, in a given month we calculated how many of all of our known females conceived in that month out of the total number of known females. This variable was calculated separately for females that did not experience a takeover in the previous 3 months (*non-takeover conceptions*) and those that did (*takeover conceptions*). Therefore, each month of the study is featured twice in the dependent variable column, once for reproductive events following takeovers and once for reproductive events not following takeovers.

For each outcome variable (the number of *Return to Cycling* and the number of *Conception* events), we created 40 models (including an intercept model) predicting the number of reproductive events for each month based on a set of candidate predictor variables and their interactions (Table 3.1). Specifically, we considered the following predictors (as well as all two-way interactions between them): (1) mean maximum daily temperature (across the previous 30 days), (2) mean minimum daily temperatures (across the previous 30 days), (3) cumulative rainfall (across the previous 90 days), and (4) the categorical predictor of whether or not a takeover had occurred prior (yes or no). Because each month was represented twice in our dataset, all models also included month and year as random effects to control for any potential monthly differences that were unrelated to the predictor variables.

Birth seasonality

To identify fluctuations in birth rates across the year due to either ecological or social factors (e.g., birth peaks and/or birth valleys), we first characterized the degree of seasonality in births qualitatively. We used cut-offs to distinguish between moderate seasonality (where 33-67% of births occur in a 3-month period), strict seasonality (where more than 67% of births cluster in a 3-month period), or no seasonality (where births occur all year with no clear peak; see van Schaik et al., 1999). We also characterized the degree to which these patterns changed (i.e., became more or less seasonal, or shifted in timing) when we considered takeover versus non-takeover births separately. Second, we constructed a third set of binomial GLMMs (with the lme4 package version 1.1-12: Bates et al., 2015) to assess when females were most likely to give birth (Table 3.1). For the births model, the dependent binomial variable was the number of females in the population that gave birth in a given month out of the total females in the study population that month. As with the cycling and conceptions models, we calculated this outcome variable as a function of whether or not each female had experienced a takeover, but rather than a 3-month window, this time we considered the 6-9 months prior to the birth (to identify births resulting from conceptions in the 3 months following a takeover plus the ~6 months of gestation).

Again, we created 40 models (including an intercept model) predicting the number of births each month based on the same set of candidate predictor variables and their interactions used in the *Return to Cycling* and *Conception* models, reflecting hypotheses about which ecological and social variables influenced birth timing (Table 3.1). Specifically, we considered the following predictors (as well as all two-way interactions between them): (1) mean maximum daily temperature (across the previous 30 days), (2) mean minimum daily temperatures (across the previous 30 days), (3) cumulative rainfall (across the previous 90 days), and (4) the categorical predictor of whether or not a takeover had occurred prior (yes or no). Again, because each month was represented twice in our dataset (once for births following takeovers, and once for births that did not follow takeovers), all models also included month and year as random effects to control for any potential monthly differences that were unrelated to the predictor variables.

Costs to birth timing

To assess whether there was a cost to giving birth at a certain time of the year, we considered the effect of birth timing on survival to 2 years of age (extending beyond the mean age of weaning in this population, 1.5 years of age, to be sure to include all weaned infants; Roberts et al., 2017). Specifically, because we identified a birth peak (see *Birth seasonality* in Results), we were interested in the potential costs of giving birth outside of this peak (which we defined as a 3-month period where 33-67% of births occurred: van Schaik et al., 1999). We constructed a series of binomial GLMMs to assess whether being born during the birth peak predicted infant survival to 2 years of age (yes/no). For each model, our predictor was whether the infant had been born "in-peak" or "off-peak" according to the seasonality analysis described above. First, we considered births and deaths for all infants until they reached 2 years of age (births=306; deaths=69; note that this dataset is slightly reduced from the one used in the seasonality analysis. To assess survival to 2 years of age we could only include births prior to 2014). Second, to focus solely on infant deaths due to "ecological reasons" we removed all suspected infanticide deaths (n=33) and constructed another binomial GLMM with births (n=273) and non-infanticide deaths (n=36). Third, because takeovers force females to shift their reproductive cycles (see *Birth seasonality* in Results), we conducted a third binomial GLMM removing all births following takeovers to determine whether there was a cost to non-peak births outside of the potential influence of takeovers (non-takeover births: n=195; non-infanticide deaths: n=26). For each model, we controlled for the repeated effects of birth year and the identity of the mother.

RESULTS

Ecological and social seasonality

The climate in the Simien Mountains National Park can be broadly divided into three distinct seasons: a cold-dry season, a hot-dry season, and a cold-wet season (Fig. 3.1). The cold-dry season typically occurred between Oct-Jan and featured the lowest minimum temperatures and very little rainfall (mean daily minimum temperature = 7.02°C ± 1.39 SD; mean daily maximum temperature = 16.46°C ± 1.64 SD; mean daily precipitation = 1.25 mm ± 4.61 SD). The hot-dry season typically occurred between Feb-May, and featured the warmest temperatures seen throughout the year with low (but variable) levels of rainfall (daily minimum temperature = 9.03°C ± 1.39 SD; mean daily maximum temperature = 20.59°C ± 2.19 SD; mean daily precipitation = 2.21 mm ± 6.64 SD). Finally, the cold-wet season typically occurred between Jun-Sep and featured the lowest maximum temperatures with the highest levels of daily precipitation (mean daily minimum temperature = 8.34°C ± 1.38 SD; mean daily maximum temperature = 15.58°C ± 2.42 SD; mean daily precipitation = 13.03 mm ± 17.35 SD). Typically, peak rainfall occurred between Jun-Aug, which corresponds with a peak in green grass availability between Oct-Nov (Fig. 3.2a).

In total, we observed 72 takeovers during the study period, which demonstrated a moderately seasonal pattern (a subset of these data were analyzed and reported in Pappano and Beehner, 2014): 45.8% of all takeovers occurred during a 3-month period

(Feb-Mar, n=33, Fig. 3.1), and the highest number of takeovers out of all months occurred in March (n=16).

Seasonality of glucocorticoid metabolites

Log glucocorticoid metabolites (logGCMs) were highly seasonal: high temperatures predicted low logGCMs (Fig. 3.2b; Fig. 3.2d). LogGCMs decreased during the hot-dry season, reaching a nadir from Apr-Jul, and increased in the colder months, peaking twice: Sep-Oct and Dec-Jan (Fig. 3.2b). Mean maximum and minimum temperatures were included as predictors in the top four models, which together contributed 90% of model weight and performed substantially better than the intercept only null model (Table 3.2). In the averaged model, mean maximum temperature (estimate = -0.0378, SE = 0.119, z-value = 3.179; Table 3.3) and mean minimum temperature (estimate = -0.0368, SE = 0.008, z-value = 4.563; Table 3.3) were strong and reliable negative predictors of logGCMs (i.e., 95% confidence intervals of mean estimates did not overlap zero, Fig. 3.3a). This effect size corresponds to a 1.4% or a 2.9% decrease in GCMs for every 1˚C increase in mean maximum or mean minimum temperature, respectively (see Fig. 3.2d for a comparison between mean residual GCMs in hot versus cold months, categories which were used for visualization purposes only). Rainfall, on the other hand, was not a strong or reliable predictor of logGCMs in the averaged model (estimate = -0.0075, SE = 0.011, z-value = 0.660; Table 3.3), although it was included as a predictor in one of the top four models (Table 3.2). Together, these results suggest that females are cold-stressed, and that thermoregulation rather than green grass availability may limit female energy balance.

Seasonality of postpartum return to cycling

We identified a seasonal peak in when females returned to cycling following postpartum amenorrhea, which mirrored the seasonality of logGCMs: 51.7% of all non-takeover cycling events occurred within a 3-month period during the hot-dry season (76 out of 147 total, Mar-May; Fig. 3.4a: Return to cycling). Mean maximum temperature was included as a predictor in the top model (which comprised 19.1% of the model weight, Table 3.2), and was highly reliable based on 95% confidence intervals in the overall averaged model (Fig. 3.3b). Mean maximum temperature significantly predicted the number of postpartum returns to cycling observed (estimate = 0.641, SE = 0.202, z-value = 3.175; Table 3.3), corresponding to a 35.6% increase in the number of females that returned to cycling for every 1°C increase in maximum temperature.

Seasonality of conceptions

The number of conceptions also exhibited a moderate peak at the beginning of the hot-dry season, with 35.9% of non-takeover conceptions occurring between Feb-Apr (89 out of 248, Fig. 3.4a: Conceptions). Rainfall was included in the top three models based on AICc comparison, which all performed better than the intercept only null model and together contributed over 90% of the model weight (ΔAICc = 37.03, Table 3.2). In our averaged model, rainfall (estimate = -0.3761, SE = 0.1223, z-value = 3.074; Fig. 3.3c; Table 3.3) reliably predicted fewer conceptions, and every additional 1mm of rain corresponded to a 0.07% decrease in the number of conceptions.

Effect of takeovers on reproductive seasonality

Females that experienced a takeover demonstrated 6.2% higher GCMs than females that did not experience a takeover (estimate = 0.0598, SE = 0.0238, z-value = 2.509, Fig. 3.2c; Table 3.3). Takeovers also resulted in significantly different seasonal patterns for both post-partum return to cycling and conceptions (Fig 3.4b). After takeovers, the seasonal pattern of returns to cycling was more distinct than that observed outside of takeovers, with 57.6% of all takeover cycling events occurring within the same 3-month period (34 out of 59 total, Mar-May, Fig. 3.4b: Return to cycling). However, females that experienced a takeover were also significantly more likely to return to cycling than females that did not experience a takeover, regardless of the time of year (estimate = 1.145, SE = 0.2019, z-value = 5.669; Table 3.3). This translated to a more than 200% increase in the number of females that returned to cycling post-takeover compared to the number of non-takeover females that returned to cycling.

Females that experienced a takeover conceived later in the year than females that did not experience a takeover, and takeover conceptions demonstrated a clear peak at the start of the wet season, from Jun-Aug (52.8% of all takeover conceptions, 38 out of 72 total, Fig. 3.4b: Conceptions). Takeovers also had a reliably positive effect on the number of conceptions that occurred in the following 3 months, regardless of the season (estimate = 0.7821, SE = 0.1472, z-value = 5.312, Fig. 3.3c). Females that experienced a takeover were 118.6% more likely to conceive than females that did not experience a takeover. Furthermore, the interaction between rainfall and takeovers was highly reliable (estimate = 0.407, SE = 0.1973, z-value = 2.063, Fig. 3.3c), reflecting a shift in conceptions by 4 months (from Mar-Jul, Fig. 3.4a: Conceptions) if a takeover had occurred. In other words, if a female experienced a takeover, she was 50.2% more likely to conceive during the cold-wet season, when temperatures were at their lowest, than during the hot-dry season.

Birth seasonality

We found two distinct birth patterns depending on whether or not births followed a takeover. First, while female geladas gave birth throughout the year (mean monthly birth rate = 0.03 births per female ± 0.03 SD), 37.4% of all non-takeover births occurred between Aug-Oct (102 out of 273 total, mean birth rate = 0.05 births per female ± 0.03 SD, Fig. 3.4a: Births). This non-takeover peak was tightly coupled with seasonal patterns in both rainfall and mean minimum temperature, and both were included as predictors in the top two birth models (which together represent over 90% of the model weight, Table 3.2). Rainfall was the strongest predictor of the number of births (estimate = 0.4739, SE = 0.1336, z-value = 3.556, Table 3.3; Fig. 3.3d): an increase of 1mm of rainfall corresponded to a 0.1% increase in births. In contrast, mean minimum temperature was negatively associated with births (estimate = -0.3128, SE = 0.132, z-value = 2.369, Table 3.3; Fig. 3.3d); an increase of 1°C corresponded to a 35.7% decrease in births. Non-takeover births peaked at the end of the cold-wet season, which also corresponded with peak food availability (Fig. 3.4a: Births).

On the other hand, takeover births peaked later in the year: 54.4% of all takeover births occurred between Dec-Feb, during the cold-dry season (37 out of 68 total, mean birth rate = 0.14 births per female ± 0.09 SD, Fig 3.4b: Births). In our averaged model, takeovers positively predicted births (estimate = 1.016, SE = 0.1525, z-value = 6.663, Table 3.3), and experiencing a takeover resulted in 176.2% more births 6-9 months later than observed for those females that did not experience a takeover. Because takeovers themselves followed a seasonal pattern, we observed a "birth valley" between Apr-Jul, immediately following the takeover season, when only 7.4% of takeover births occurred (5 out of 68, Fig 3.4b: Births). However, birth rates recovered sharply, and during the takeover birth peak, birth rates were double those observed during the non-takeover birth peak (e.g., the mean takeover birth rate in Jan = 0.13 births per female ± 0.07 SD, while the mean non-takeover birth rate in Sep = 0.06 births per female ± 0.03 SD). This increase likely reflects the synchronizing effect that takeovers had on the reproductive timing of females within the same unit. Finally, the interaction between takeovers and rain was a reliable negative predictor of the number of births (estimate = -0.6493, SE = 0.1781, z-value = 3.646, Table 3.3; Fig. 3.3d), reflecting the shift in the takeover birth peak to the cold-dry season, which is when we see minimal rainfall. In other words, the takeover birth peak is characterized by a 47.8% increase in births during the driest months of the year.

Costs to birth timing

We found no evidence that there were costs associated with giving birth outside the birth peak. Of the 306 births observed (from our reduced dataset of infants born prior to 2014), 69 of the infants subsequently died before reaching 2 years of age (rate = 0.225 infant deaths per birth). Approximately half of these deaths were attributed to infanticide and half were attributed to other factors (n=33 possible infanticide deaths; n=36 non-infanticide deaths; Fig. 3.6). Being born during the birth peak (Aug-Oct) versus outside of the birth peak (Nov-Jul) did not significantly predict whether an infant died before reaching 2 years of age (in-peak: estimate = -0.021, SE = 0.309, z-value = -0.069). When we removed infanticide deaths from the analysis, we still found no effect of being born in-peak on infant survival (in-peak: estimate = -0.405, SE = 0.470, z-value = -0.862). Finally, when we completely removed the potential influence of takeover (i.e., births that followed a takeover and deaths due to infanticide), we still found no effect of being born in-peak (in-peak: estimate = 0.021, SE = 0.966, z-value = 0.022).

DISCUSSION

Our results highlight the effect that male takeovers can have on the timing of female reproduction: in addition to the direct effects from infanticide (reviewed in Hrdy, 1979; Fedigan, 2003; Palombit, 2015) and from the Bruce effect and/or accelerated weaning (reviewed in Smuts and Smuts, 1993), we demonstrated that takeovers can disrupt reproductive seasonality within a population across years. Specifically, we identified two distinct seasonal birth patterns: one that we believe is shaped by energetic constraints related to thermoregulation (“ecological birth peak”) and one shaped by the timing of male takeovers (“social birth peak”). These results demonstrate the separate effects that ecological and social variables can have on seasonal patterns of female reproduction.

Although female geladas are not seasonal breeders, births follow a moderately seasonal pattern (as defined by van Schaik et al., 1999), with 37.4% of all non-takeover births occurring at the end of the cold-rainy season (Aug-Oct). This ecological birth peak corresponds with a peak in conceptions that occurs in the middle of the hot-dry season (Feb-Apr). The hot-dry season is also when we observed the lowest concentrations of glucocorticoid metabolites and a peak in the number of females that returned to cycling. The seasonal variation in female glucocorticoid metabolites mirrors the pattern identified in cold-stressed males (Beehner and McCann, 2008). These data indicate that, for some females in this population, thermoregulatory requirements due to cold temperatures may be a significant barrier to the onset of reproduction.

Although food scarcity has been associated with poor energetic condition and reproductive performance in a number of species (reviewed in Di Bitetti and Janson, 2000 and Brockman and van Schaik, 2005; though see: Weingrill et al., 2004), we were unable to detect a relationship between the initiation of reproduction and the availability of green grass – the staple food source of geladas (Jarvey et al., In press). We acknowledge, however, that green grass availability may be a poor proxy for energy intake in this population. Although the hot-dry season is when the availability of green grass is at its lowest, we also know that geladas readily switch to fallback foods during this time (e.g., underground storage organs and tubers: Jarvey et al., In press), which may provide sufficient energy to offset any additional costs associated with foraging for them (Hunter, 2001). Furthermore, although females are able to give birth at other points in the year, the ecological birth peak aligns with the peak in green grass availability (ecological birth peak = Aug-Oct; peak green grass = Jul-Nov), suggesting that females that give birth at this time may be able to maintain better body condition throughout the energetically-costly period of lactation. Therefore, although our data suggest that the constraints of temperature are more significant than the constraints of green grass availability, it remains likely that food availability may still shape gelada reproductive patterns. Addressing this important question will require a cross-year assessment that includes periods of intense scarcity (e.g., in yellow baboons, *Papio cynocephalus*: Lea et al., 2015).

In contrast, the birth pattern following takeovers was characterized by a decrease in the number of births during the months immediately following a takeover (e.g., a *birth valley*: Lancaster and Lee, 1965), followed by a birth peak 6-9 months after the “takeover season.” This social birth peak differed from the ecological birth peak in two ways. First, it occurred later in the year than the ecological birth peak (in the cold-dry season instead of the cold-rainy season). Second, it resulted in a significantly higher birth rate than that recorded for the ecological birth peak, indicating that births following a takeover were more synchronized than births solely tracking fluctuations in temperature and/or rainfall.

From an evolutionary perspective, reproductive synchrony among females is hypothesized to be a counterstrategy to male reproductive tactics such as coercion, monopolization, or infanticide. Some of the benefits of synchronous mating may include, for example, a higher degree of female mate choice (Ostner et al., 2008; Roberts et al., 2014), higher rates of extra-pair fertilizations (Stutchbury and Morton, 1995), and a reduced risk of harassment and/or infanticide (Boness et al., 1995; Gilchrist, 2006; Hodge et al., 2011; Riehl, 2016). Although the exact mechanism causing reproductive synchrony may vary among species, the end result is thought to be increased female fitness.

These potential fitness benefits do not explain the results we report here for the gelada system: geladas live in polygynous groups where female mate choice is limited (Snyder-Mackler et al., 2012a) and synchrony appears to result from, rather than prevent, the fitness costs associated with male takeovers (i.e., due to infanticide and/or the Bruce effect). At the proximate level, females show higher rates of post-partum resumptions of cycling only after experiencing a takeover, regardless of their reproductive state at the time of takeover (cycling, lactating, or pregnant) or the time of year. For most of these females, we were unable to distinguish “deceptive” signals of fertility (i.e., non-ovulatory and/or non-conceptive swellings), a known female counterstrategy to infanticide (e.g., Zinner and Deschner, 2000), from “true fertility.” Nevertheless, although we expect that some postpartum returns to cycling were indeed deceptive, male takeovers were also associated with high conception rates in the following months, suggesting that the majority of females truly returned to cycling after a takeover.

Two additional lines of evidence suggest that male takeovers drive reproductive synchrony in geladas and not the reverse. First, experiencing a takeover (even during the ecological peak in conceptions) actually delayed the conception peak by 4-6 months for the majority of females in these units as compared to females unaffected by takeovers. Second, most of the females that return to cycling following a takeover were pregnant or lactating at the time of takeover. We have hormonal evidence that 80% of females terminate pregnancies after a takeover (Roberts et al., 2012); and we have statistical evidence that incoming males kill nearly half of the infants of lactating females (Beehner and Bergman, 2008). Although we have not examined reproductive changes across individual females, the overall pattern indicates that female receptivity increases after, and not before, male takeovers.

In addition, because takeovers themselves are seasonal in this population (this manuscript; see also Pappano and Beehner, 2014), the post-takeover reproductive synchrony described here also produced a distinct pattern of birth seasonality. Why are male takeovers seasonal? In some systems, seasonal periods of female cycling and receptivity appear to attract male takeovers and/or influxes of males (e.g., Sugiyama and Ohsawa, 1974; Borries, 2000; Cords, 2000; Morelli et al., 2009; Zhao et al., 2011; Hongo et al., 2016). However, most of these examples come from strict seasonal breeders, where females only conceive during a narrow window of time due to ecological constraints, and males target that seasonal peak in reproductive activity. Although we do not yet have a complete answer as to why takeovers cluster during one time of the year, we do not believe male geladas target a conception season in quite the same way, in part because geladas are not strict seasonal breeders. In addition, our finding that takeovers alter subsequent patterns of female fertility (i.e., the takeover precedes the increase in females that return to cycling and delays the birth peak) suggests that the timing of male takeovers does not simply “mirror” female reproductive seasonality. Finally, previous research in this population has suggested that relative male body condition is one important factor determining the outcome of male takeovers (Pappano and Beehner, 2014). Therefore, we suggest that the timing of male takeovers is more or less independent from the timing of female reproductive seasonality, and we are currently conducting a more fine-grained analysis in order to determine the causal factors involved.

Together, the evidence we report here for reproductive synchrony and seasonality following male takeovers is in line with the neuroendocrine literature on chemosensory mechanisms that stimulate or inhibit female reproduction. Specifically, in rodents we see male-mediated resumption of cycling in females (the Whitten effect: Whitten et al., 1968), male-mediated female maturation (the Vandenbergh effect: Vandenbergh et al., 1972) and male-mediated pregnancy termination (the Bruce effect: Bruce, 1959), in addition to sexually selected infanticide (Hrdy, 1979). While we have yet to identify the mechanism(s) at work in geladas, our results suggest that such male-mediated proximate mechanisms shape gelada birth patterns. Further research will help untangle the evolutionary significance of such a response, which requires an analysis of individual females to see whether those that “reset” have a reproductive advantage over those that do not. We suspect that this kind of male-mediated birth seasonality could help explain seasonal reproductive patterns in species that experience infanticide, feticide, and/or the Bruce effect, or where alpha male replacements themselves (or their equivalent) are seasonal. For example, in white-faced capuchins male takeovers are seasonal, and often result in infanticide (Fedigan, 2003; Schoof and Jack, 2013). Births show a seasonal peak in March, but also increase roughly 5 months after the peak takeover season (Carnegie et al., 2011).

Here, we found no evidence that infants born outside of the ecological birth peak were more likely to die before 2 years of age. As likely capital breeders, this result is perhaps unsurprising: reproduction in capital breeders can only occur once females reach a certain condition threshold, which is thought to represent the appropriate energetic stores required to successfully carry a pregnancy to term. As such, any costs associated with reproduction should be paid upfront via infertility and/or miscarriage. We were unable to identify pregnancy loss in our dataset (we did not have hormonal data for most of these pregnancies) to address this directly. However, we expect that infertility is the primary “bottleneck” for reproduction in this population because females routinely give birth during off-peak periods.

Still, there may be more subtle costs associated with birth timing. That is, births that occur out-of-peak (and not during the period of maximum food availability) may carry costs relating to maternal condition or to infant growth and development. Because our analysis was at the population-level, we did not examine individual-level characteristics that may influence infant survival. Therefore, the next questions are: (1) whether there is variability in infant survival if we factor in individual characteristics of the mother such as age, dominance rank, or unit size; and (2) whether there are any life history or developmental costs to giving birth outside of the ecological birth peak beyond the one we use here (infant survival to 2 years of age). For example, a female that gives birth outside of the peak may have a longer subsequent interbirth interval or suffer decreased longevity herself. Birth timing may also impact the availability of weaning foods at critical developmental periods for the infant (e.g., Koenig et al., 1997), or show overall effects on infant growth and development.

The two birth peaks described here are reminiscent of those first described by Dunbar (1980). However, we give them very different interpretations. First, Dunbar (1980) described a dry season birth peak (Nov-Jan) that he attributed to a prospective strategy for females to avoid giving birth to vulnerable infants during the cold-wet season. By contrast, our dry season birth peak is driven by post-takeover females that give birth about 4 months after the population-wide seasonal birth peak. Second, Dunbar (1980) attributed his early wet-season birth peak (Jun-Aug) to a capital breeding strategy for females to exploit the plentiful food following the short rains (rain that we did not detect in our dataset). By contrast, while our late cold-wet season birth peak (Aug-Oct) falls within the window of peak green grass availability, it is also tightly associated with warm weather and low glucocorticoid metabolites at the time of conception. Therefore, our current working hypothesis is that reproduction in female geladas is limited by the energetics of thermoregulation in a cold, hypoxic environment. Testing this hypothesis further will require physiological data on energy balance.

Finally, although the takeover birth peak helps explain some of the variation in birth timing observed, we still do not know why some females give birth outside of either birth peak. It may be that females that are shifted from the general ecological pattern (e.g., as the result of a takeover) have difficulties shifting themselves back to the ecological birth peak again. If costs to giving birth outside of the ecological peak are low (as our results suggest), then perhaps the time it takes to delay a reproductive event is a higher cost than just giving birth at a less opportune time. Future exploration of developmental costs associated with off-peak births will help elucidate whether our data are consistent with this hypothesis.

TABLES

Table 3.1 Description of outcome variables and predictors used in model selection

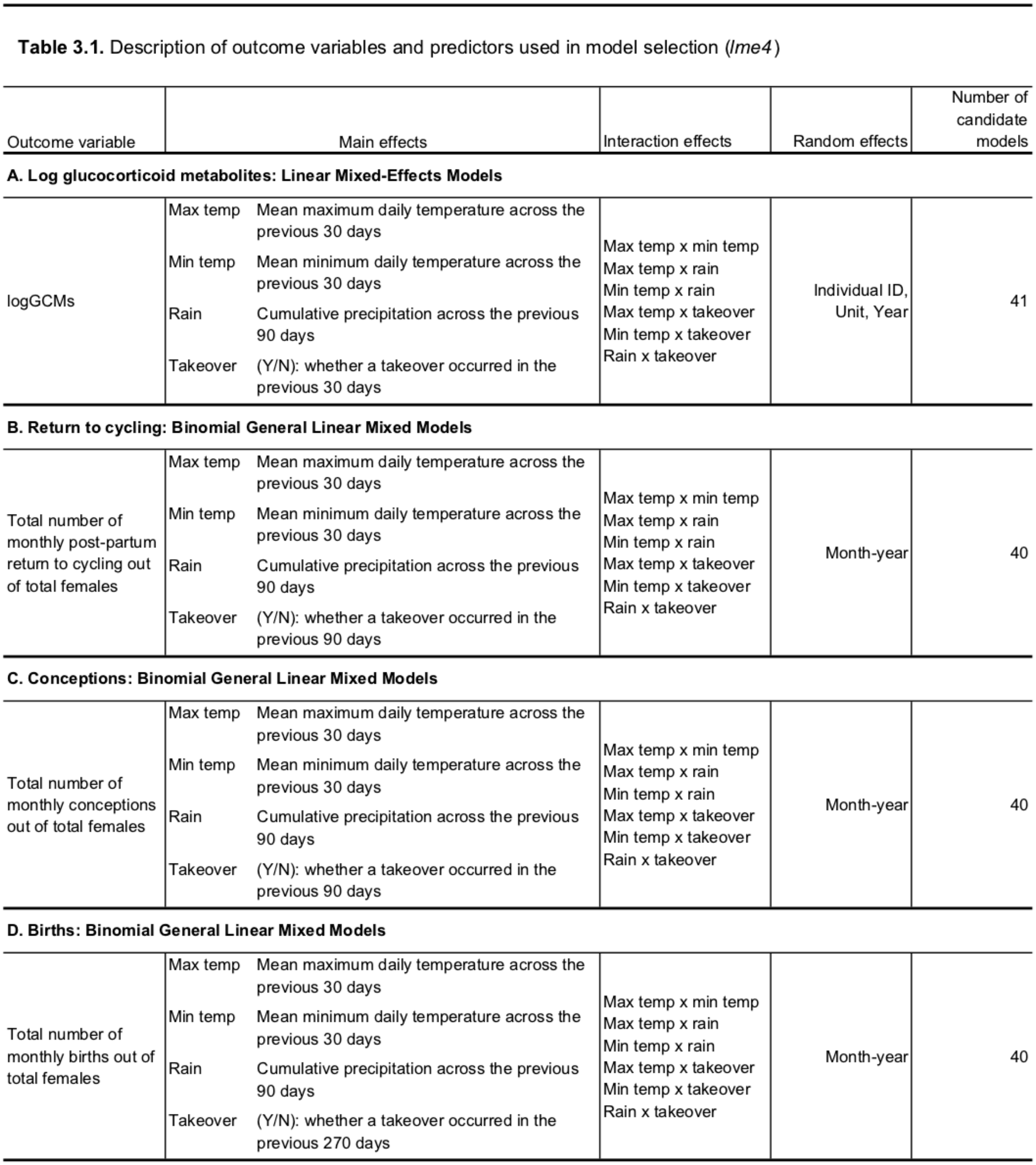


Table 3.1. Description of outcome variables and predictors used in model selection (*lme4*)

Outcome variable	Main effects		Interaction effects	Random effects	Number of candidate models
A. Log glucocorticoid metabolites: Linear Mixed-Effects Models					
logGCMs	Max temp Min temp Rain Takeover	Mean maximum daily temperature across the previous 30 days Mean minimum daily temperature across the previous 30 days Cumulative precipitation across the previous 90 days (Y/N): whether a takeover occurred in the previous 30 days	Max temp x min temp Max temp x rain Min temp x rain Max temp x takeover Min temp x takeover Rain x takeover	Individual ID, Unit, Year	41
B. Return to cycling: Binomial General Linear Mixed Models					
Total number of monthly post-partum return to cycling out of total females	Max temp Min temp Rain Takeover	Mean maximum daily temperature across the previous 30 days Mean minimum daily temperature across the previous 30 days Cumulative precipitation across the previous 90 days (Y/N): whether a takeover occurred in the previous 90 days	Max temp x min temp Max temp x rain Min temp x rain Max temp x takeover Min temp x takeover Rain x takeover	Month-year	40
C. Conceptions: Binomial General Linear Mixed Models					
Total number of monthly conceptions out of total females	Max temp Min temp Rain Takeover	Mean maximum daily temperature across the previous 30 days Mean minimum daily temperature across the previous 30 days Cumulative precipitation across the previous 90 days (Y/N): whether a takeover occurred in the previous 90 days	Max temp x min temp Max temp x rain Min temp x rain Max temp x takeover Min temp x takeover Rain x takeover	Month-year	40
D. Births: Binomial General Linear Mixed Models					
Total number of monthly births out of total females	Max temp Min temp Rain Takeover	Mean maximum daily temperature across the previous 30 days Mean minimum daily temperature across the previous 30 days Cumulative precipitation across the previous 90 days (Y/N): whether a takeover occurred in the previous 270 days	Max temp x min temp Max temp x rain Min temp x rain Max temp x takeover Min temp x takeover Rain x takeover	Month-year	40

Table 3.2 Akaike's information criterion (AIC/AICc) model results

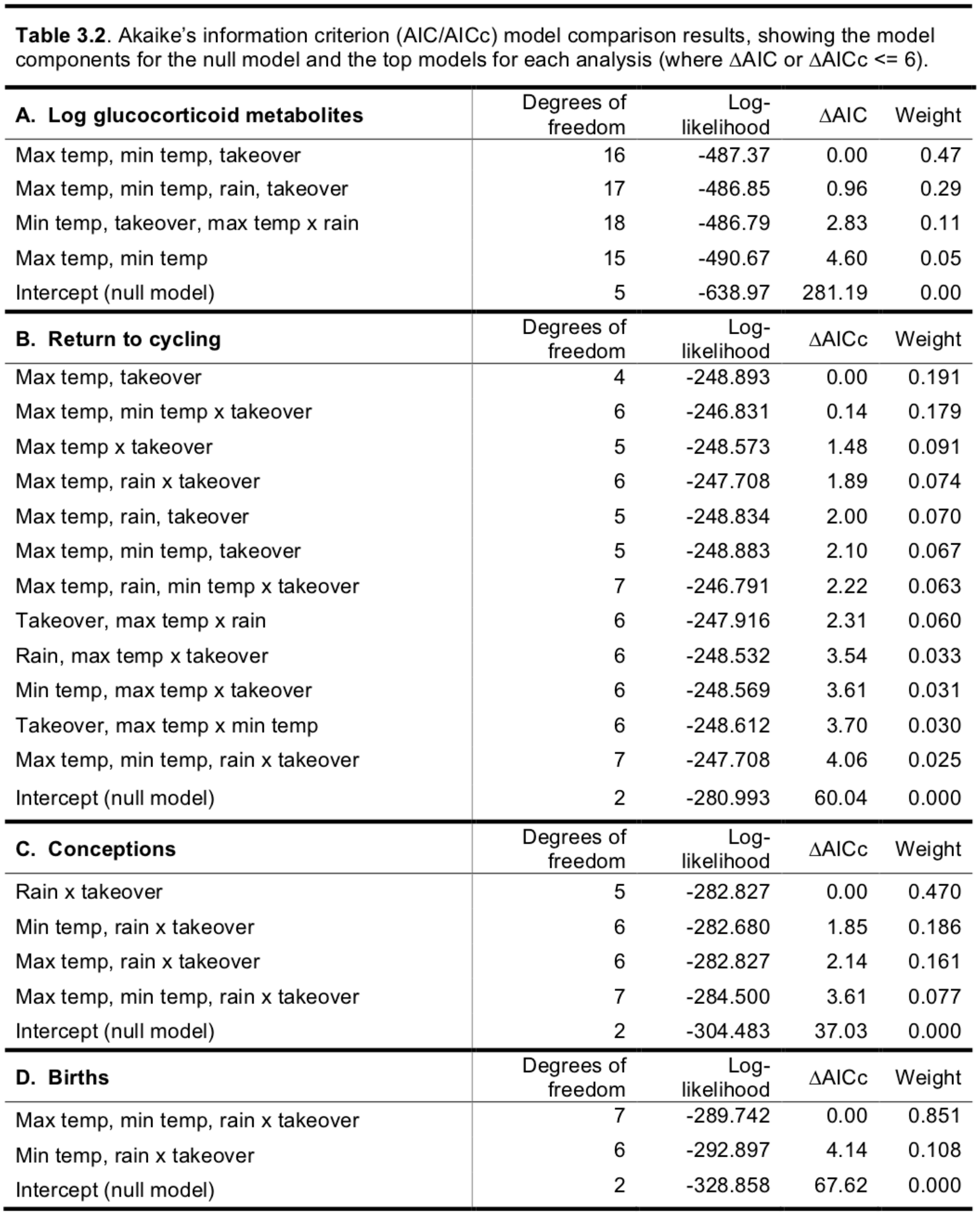


Table 3.2. Akaike’s information criterion (AIC/AICc) model comparison results, showing the model components for the null model and the top models for each analysis (where ∆AIC or ∆AICc <= 6).

A. Log glucocorticoid metabolites	Degrees of freedom	Log-likelihood	∆AIC	Weight
Max temp, min temp, takeover	16	-487.37	0.00	0.47
Max temp, min temp, rain, takeover	17	-486.85	0.96	0.29
Min temp, takeover, max temp x rain	18	-486.79	2.83	0.11
Max temp, min temp	15	-490.67	4.60	0.05
Intercept (null model)	5	-638.97	281.19	0.00

B. Return to cycling	Degrees of freedom	Log-likelihood	∆AICc	Weight
Max temp, takeover	4	-248.893	0.00	0.191
Max temp, min temp x takeover	6	-246.831	0.14	0.179
Max temp x takeover	5	-248.573	1.48	0.091
Max temp, rain x takeover	6	-247.708	1.89	0.074
Max temp, rain, takeover	5	-248.834	2.00	0.070
Max temp, min temp, takeover	5	-248.883	2.10	0.067
Max temp, rain, min temp x takeover	7	-246.791	2.22	0.063
Takeover, max temp x rain	6	-247.916	2.31	0.060
Rain, max temp x takeover	6	-248.532	3.54	0.033
Min temp, max temp x takeover	6	-248.569	3.61	0.031
Takeover, max temp x min temp	6	-248.612	3.70	0.030
Max temp, min temp, rain x takeover	7	-247.708	4.06	0.025
Intercept (null model)	2	-280.993	60.04	0.000

C. Conceptions	Degrees of freedom	Log-likelihood	∆AICc	Weight
Rain x takeover	5	-282.827	0.00	0.470
Min temp, rain x takeover	6	-282.680	1.85	0.186
Max temp, rain x takeover	6	-282.827	2.14	0.161
Max temp, min temp, rain x takeover	7	-284.500	3.61	0.077
Intercept (null model)	2	-304.483	37.03	0.000

D. Births	Degrees of freedom	Log-likelihood	∆AICc	Weight
Max temp, min temp, rain x takeover	7	-289.742	0.00	0.851
Min temp, rain x takeover	6	-292.897	4.14	0.108
Intercept (null model)	2	-328.858	67.62	0.000

Table 3.3 Model-averaging results for significant predictors of interest

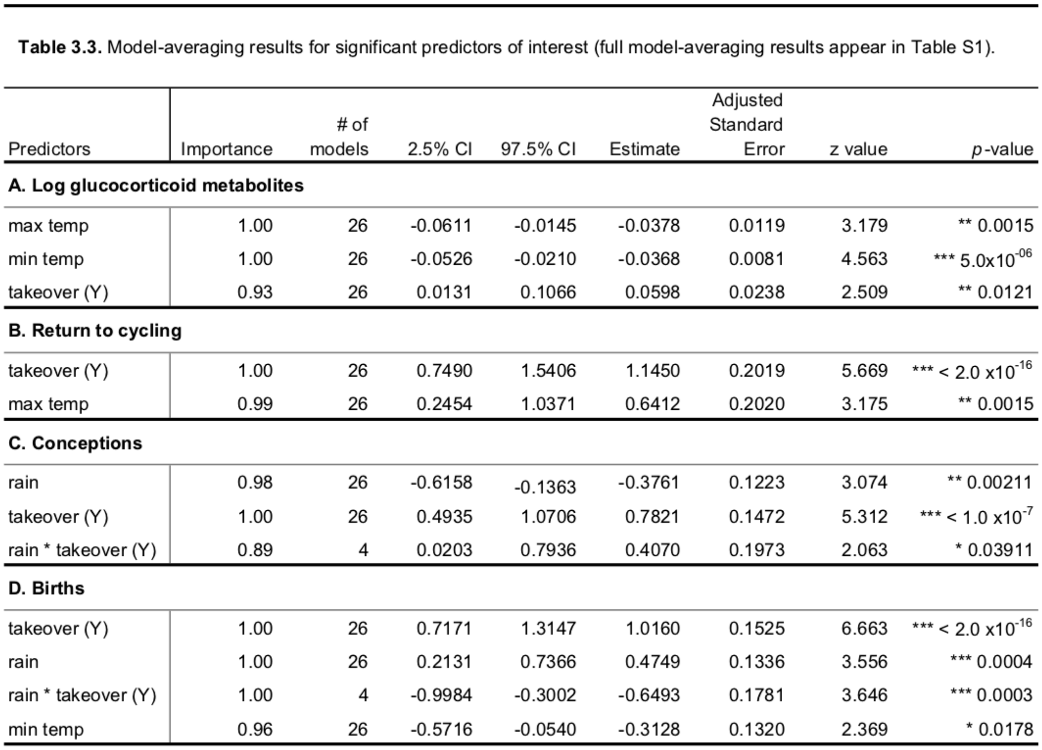
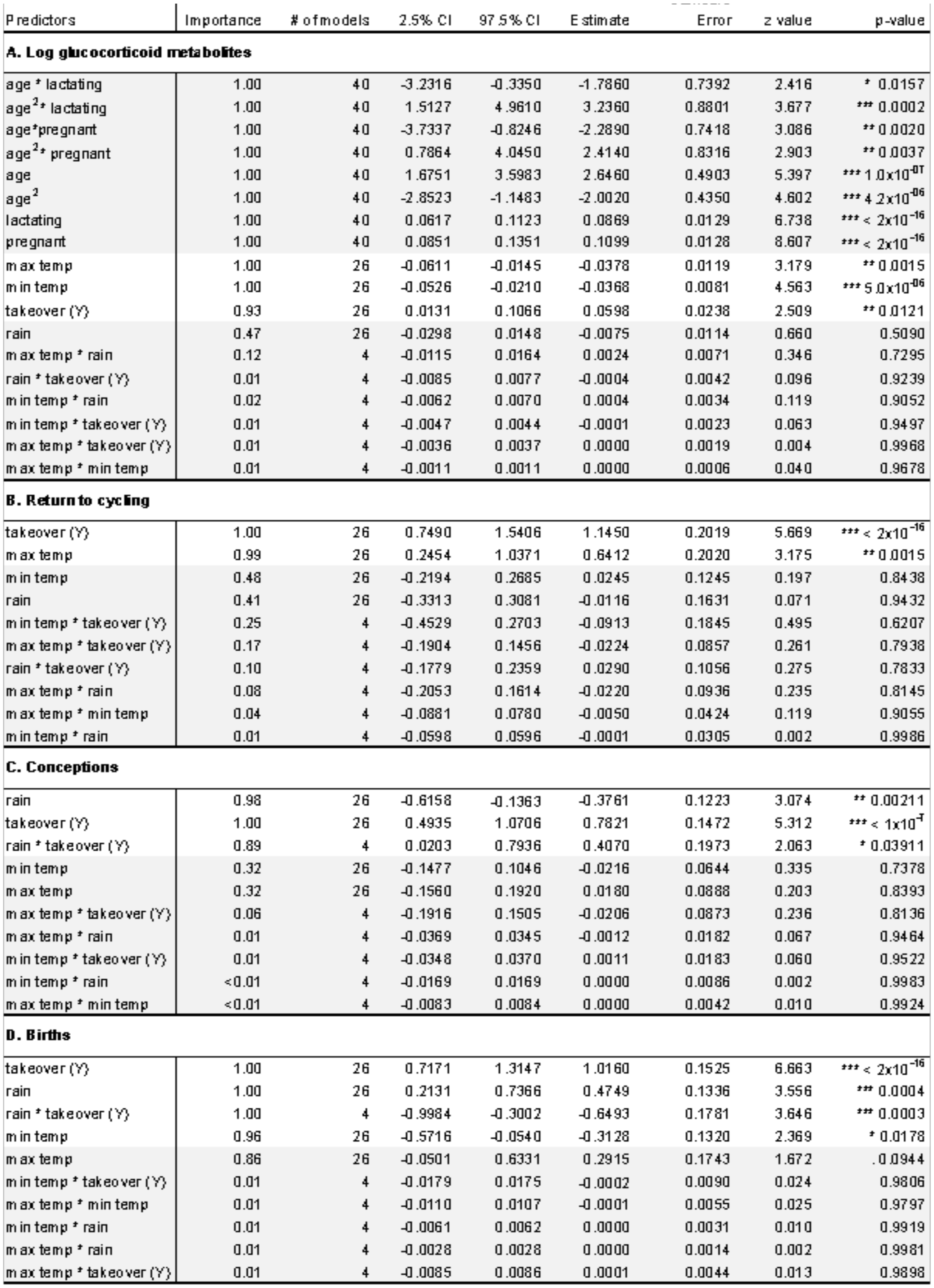


Table 3.3. Model-averaging results for significant predictors of interest (full model-averaging results appear in Table S1).

Predictors	Importance	# of models	2.5% CI	97.5% CI	Estimate	Adjusted Standard Error	z value	*p*-value
A. Log glucocorticoid metabolites								
max temp	1.00	26	-0.0611	-0.0145	-0.0378	0.0119	3.179	** 0.0015
min temp	1.00	26	-0.0526	-0.0210	-0.0368	0.0081	4.563	*** $5.0\text{x}10^{-06}$
takeover (Y)	0.93	26	0.0131	0.1066	0.0598	0.0238	2.509	** 0.0121
B. Return to cycling								
takeover (Y)	1.00	26	0.7490	1.5406	1.1450	0.2019	5.669	*** $< 2.0\ \text{x}10^{-16}$
max temp	0.99	26	0.2454	1.0371	0.6412	0.2020	3.175	** 0.0015
C. Conceptions								
rain	0.98	26	-0.6158	-0.1363	-0.3761	0.1223	3.074	** 0.00211
takeover (Y)	1.00	26	0.4935	1.0706	0.7821	0.1472	5.312	*** $< 1.0\ \text{x}10^{-7}$
rain * takeover (Y)	0.89	4	0.0203	0.7936	0.4070	0.1973	2.063	* 0.03911
D. Births								
takeover (Y)	1.00	26	0.7171	1.3147	1.0160	0.1525	6.663	*** $< 2.0\ \text{x}10^{-16}$
rain	1.00	26	0.2131	0.7366	0.4749	0.1336	3.556	*** 0.0004
rain * takeover (Y)	1.00	4	-0.9984	-0.3002	-0.6493	0.1781	3.646	*** 0.0003
min temp	0.96	26	-0.5716	-0.0540	-0.3128	0.1320	2.369	* 0.0178

Table 3.4 Full model-averaging results



Predictors	Importance	# of models	2.5% CI	97.5% CI	Estimate	Error	z value	p-value
A. Log glucocorticoid metabolites								
age * lactating	1.00	40	-3.2316	-0.3350	-1.7860	0.7392	2.416	* 0.0157
age^2* lactating	1.00	40	1.5127	4.9610	3.2360	0.8801	3.677	*** 0.0002
age*pregnant	1.00	40	-3.7337	-0.8246	-2.2890	0.7418	3.086	** 0.0020
age^2* pregnant	1.00	40	0.7864	4.0450	2.4140	0.8316	2.903	** 0.0037
age	1.00	40	1.6751	3.5983	2.6460	0.4903	5.397	*** 1.0x10^{-07}
age^2	1.00	40	-2.8523	-1.1483	-2.0020	0.4350	4.602	*** 4.2x10^{-06}
lactating	1.00	40	0.0617	0.1123	0.0869	0.0129	6.738	*** < 2x10^{-16}
pregnant	1.00	40	0.0851	0.1351	0.1099	0.0128	8.607	*** < 2x10^{-16}
max temp	1.00	26	-0.0611	-0.0145	-0.0378	0.0119	3.179	** 0.0015
min temp	1.00	26	-0.0526	-0.0210	-0.0368	0.0081	4.563	*** 5.0x10^{-06}
takeover (Y)	0.93	26	0.0131	0.1066	0.0598	0.0238	2.509	** 0.0121
rain	0.47	26	-0.0298	0.0148	-0.0075	0.0114	0.660	0.5090
max temp * rain	0.12	4	-0.0115	0.0164	0.0024	0.0071	0.346	0.7295
rain * takeover (Y)	0.01	4	-0.0085	0.0077	-0.0004	0.0042	0.096	0.9239
min temp * rain	0.02	4	-0.0062	0.0070	0.0004	0.0034	0.119	0.9052
min temp * takeover (Y)	0.01	4	-0.0047	0.0044	-0.0001	0.0023	0.063	0.9497
max temp * takeover (Y)	0.01	4	-0.0036	0.0037	0.0000	0.0019	0.004	0.9968
max temp * min temp	0.01	4	-0.0011	0.0011	0.0000	0.0006	0.040	0.9678
B. Return to cycling								
takeover (Y)	1.00	26	0.7490	1.5406	1.1450	0.2019	5.669	*** < 2x10^{-16}
max temp	0.99	26	0.2454	1.0371	0.6412	0.2020	3.175	** 0.0015
min temp	0.48	26	-0.2194	0.2685	0.0245	0.1245	0.197	0.8438
rain	0.41	26	-0.3313	0.3081	-0.0116	0.1631	0.071	0.9432
min temp * takeover (Y)	0.25	4	-0.4529	0.2703	-0.0913	0.1845	0.495	0.6207
max temp * takeover (Y)	0.17	4	-0.1904	0.1456	-0.0224	0.0857	0.261	0.7938
rain * takeover (Y)	0.10	4	-0.1779	0.2359	0.0290	0.1056	0.275	0.7833
max temp * rain	0.08	4	-0.2053	0.1614	-0.0220	0.0936	0.235	0.8145
max temp * min temp	0.04	4	-0.0881	0.0780	-0.0050	0.0424	0.119	0.9055
min temp * rain	0.01	4	-0.0598	0.0596	-0.0001	0.0305	0.002	0.9986
C. Conceptions								
rain	0.98	26	-0.6158	-0.1363	-0.3761	0.1223	3.074	** 0.00211
takeover (Y)	1.00	26	0.4935	1.0706	0.7821	0.1472	5.312	*** < 1x10^{-7}
rain * takeover (Y)	0.89	4	0.0203	0.7936	0.4070	0.1973	2.063	* 0.03911
min temp	0.32	26	-0.1477	0.1046	-0.0216	0.0644	0.335	0.7378
max temp	0.32	26	-0.1560	0.1920	0.0180	0.0888	0.203	0.8393
max temp * takeover (Y)	0.06	4	-0.1916	0.1505	-0.0206	0.0873	0.236	0.8136
max temp * rain	0.01	4	-0.0369	0.0345	-0.0012	0.0182	0.067	0.9464
min temp * takeover (Y)	0.01	4	-0.0348	0.0370	0.0011	0.0183	0.060	0.9522
min temp * rain	<0.01	4	-0.0169	0.0169	0.0000	0.0086	0.002	0.9983
max temp * min temp	<0.01	4	-0.0083	0.0084	0.0000	0.0042	0.010	0.9924
D. Births								
takeover (Y)	1.00	26	0.7171	1.3147	1.0160	0.1525	6.663	*** < 2x10^{-16}
rain	1.00	26	0.2131	0.7366	0.4749	0.1336	3.556	*** 0.0004
rain * takeover (Y)	1.00	4	-0.9984	-0.3002	-0.6493	0.1781	3.646	*** 0.0003
min temp	0.96	26	-0.5716	-0.0540	-0.3128	0.1320	2.369	* 0.0178
max temp	0.86	26	-0.0501	0.6331	0.2915	0.1743	1.672	. 0.0944
min temp * takeover (Y)	0.01	4	-0.0179	0.0175	-0.0002	0.0090	0.024	0.9806
max temp * min temp	0.01	4	-0.0110	0.0107	-0.0001	0.0055	0.025	0.9797
min temp * rain	0.01	4	-0.0061	0.0062	0.0000	0.0031	0.010	0.9919
max temp * rain	0.01	4	-0.0028	0.0028	0.0000	0.0014	0.002	0.9981
max temp * takeover (Y)	0.01	4	-0.0085	0.0086	0.0001	0.0044	0.013	0.9898

FIGURES

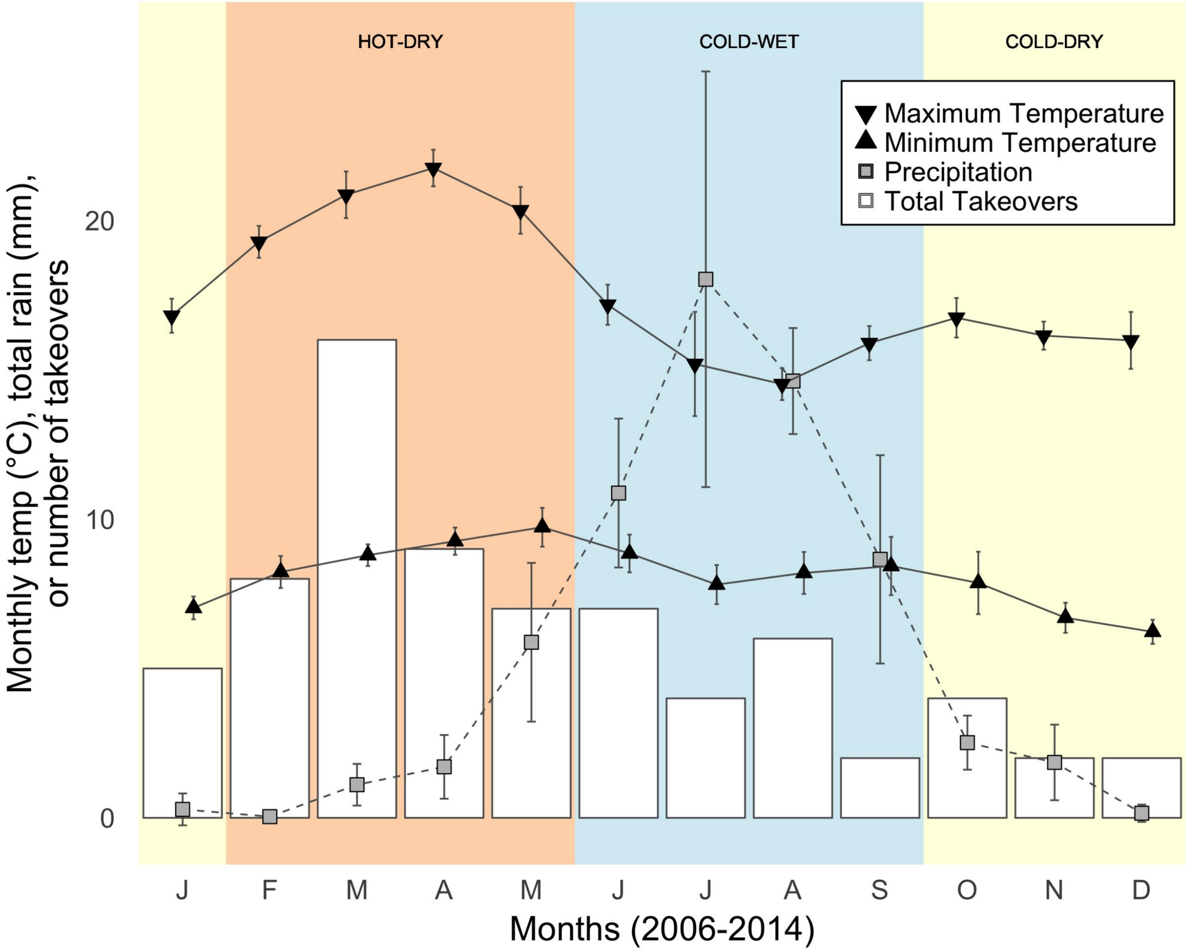


Figure 3.1. Seasonality of ecological (temperature and rainfall) and social (takeovers) predictors. Mean maximum and minimum daily temperatures by month ± 95% confidence intervals (maximum = downward triangles; minimum = upward triangles; solid line); mean total rainfall by month (grey squares; dashed line) ± 95% confidence intervals; total number of takeovers observed by month (white bars). Background colors indicate season: orange = hot-dry season; light blue = cold-wet season; pale yellow = cold-dry season.

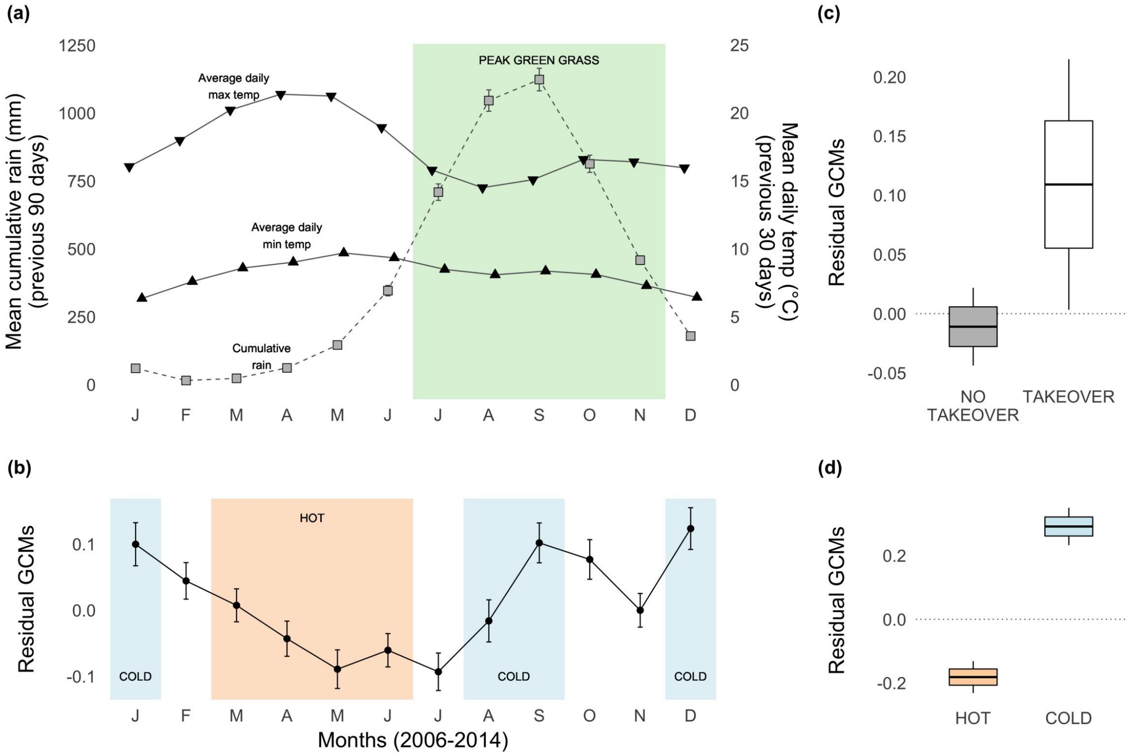
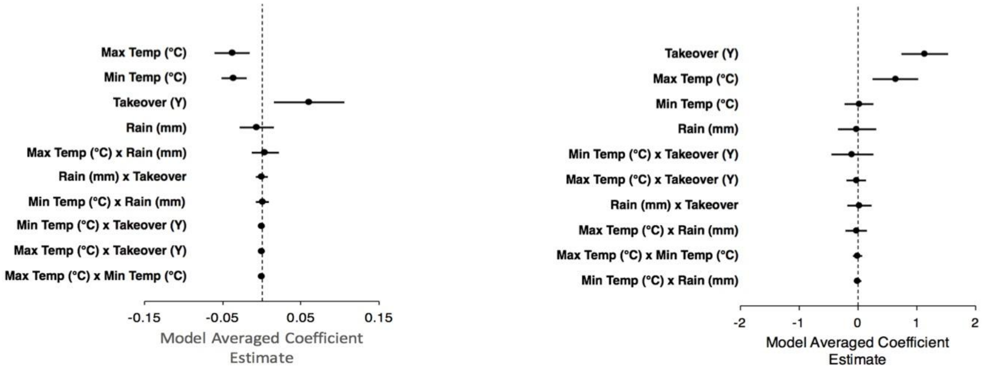


Figure 3.2. (a) Cumulative seasonality predictors in relation to peak green grass availability, indicated by the shaded region (July to November). All models included the following variables as predictors: mean maximum (downward triangles; solid line) and minimum (upward triangles; solid line) daily temperature across the previous 30 days as a proxy for thermoregulatory requirements and cumulative rainfall (grey squares; dashed line) across the previous 90 days (as a proxy for green grass availability). **(b)** Seasonal patterns of mean residual log-transformed glucocorticoid metabolites (logGCMs) ± 95% confidence intervals (after controlling for the effects of reproductive state, age, and experiencing a takeover 30 days prior to sample collection). Warm and cold months were determined by taking the average of the mean maximum and mean minimum daily temperatures over the previous 30 days for each month (see **Figure 3.2a**; note that these categories were used for visualization purposes only). Background shades indicate the 4 warmest months (Mar-Jun) and the 4 coldest months (Aug-Sep; Dec-Jan). **(c)** Mean residual logGCMs ± standard error (after controlling for the effects of reproductive state, age, and temperature) for females that did not experience a takeover in the previous 30 days (grey box) vs. females that did (white box). **(d)** Mean residual logGCMs ± standard error (after controlling for the effects of reproductive state, age, and takeover) for females during the 4 warmest months (Mar-Jun; shaded box labeled "HOT" in Fig. 3.2b) and during the 4 coldest months (Aug-Sep and Dec-Jan; shaded boxes labeled "COLD" in **Figure 3.2b**). For both **(c)** and **(d)** mean = solid line; standard error = box outline; 95% confidence intervals = whiskers.

a. Log glucocorticoid metabolites model

b. Return to cycling model



c. Conceptions model

d. Births model

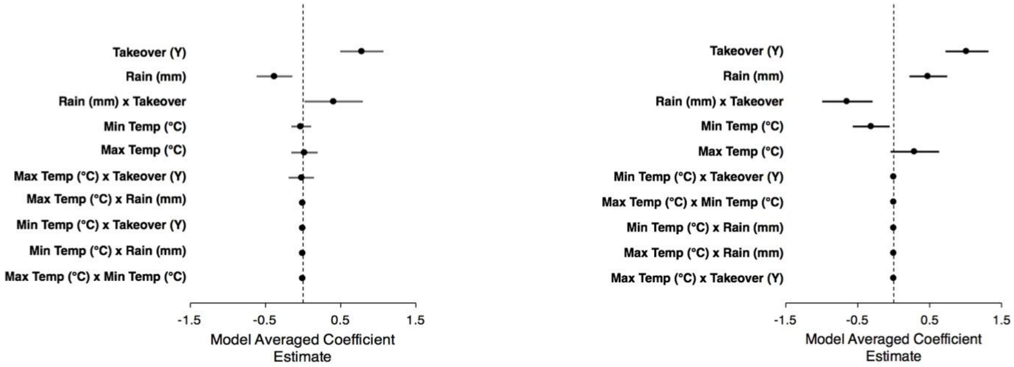


Figure 3.3. Model-averaged coefficient estimates ± 95% confidence intervals for averaged models for each outcome variable: **(a)** log glucocorticoid metabolites (here showing only predictors of interest; each model also controlled for reproductive status and age-squared: see Figure 3.5), **(b)** return to cycling, **(c)** conceptions, and **(d)** births. Coefficient estimates less than zero result in a lower than expected outcome while those greater than zero result in a higher than expected outcome. Note that these plots depict the direction and reliability of each estimate (i.e., predictors are considered reliable when the 95% confidence intervals do not cross zero), not the relative effect size. Predictors are displayed in descending order of relative importance assigned by the MuMIn comparison.

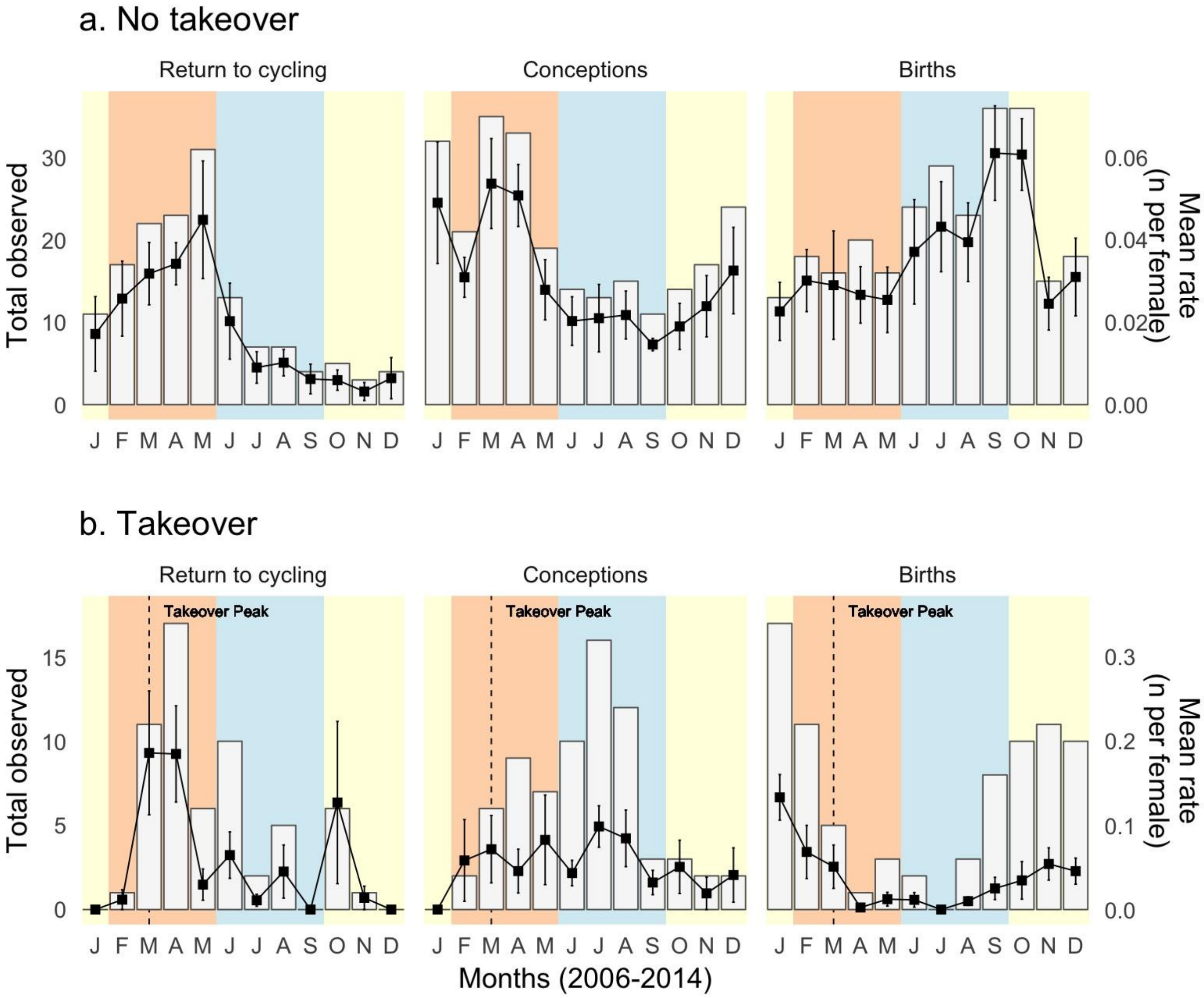


Figure 3.4. Seasonal patterns of reproductive events. **(a)** No takeover events: post-partum return to cycling where a takeover did not occur within the previous 3 months; conceptions where a takeover did not occur within the previous 3 months; and births where a takeover did not occur within the previous 6-9 months. **(b)** Reproductive events following takeovers: post-partum return to cycling observed within 3 months of a takeover; conceptions where a takeover did occur within the previous 3 months; and births where a takeover did occur within the previous 6-9 months. In all panels: left axis = total observed (bars); right axis = mean rates ± standard error (i.e., the number of reproductive events per female per month; black squares). Background shades indicate season: hot-dry (February to May); cold-wet (June to September); cold-dry (October to January).

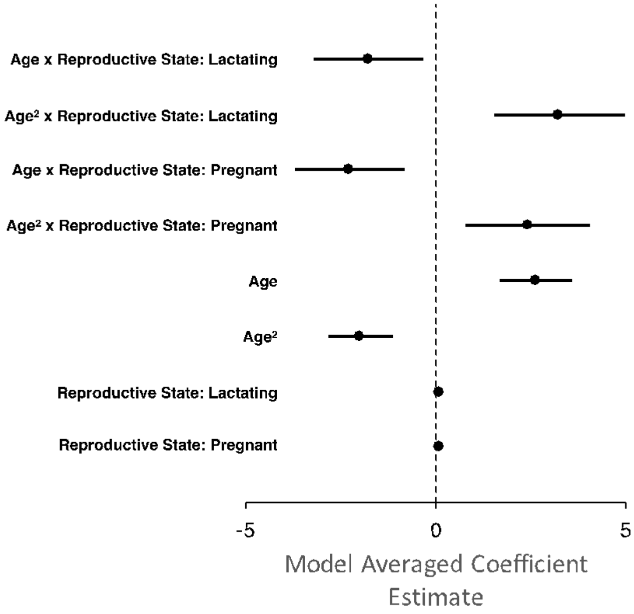


Figure 3.5. Model-averaged coefficient estimates and 95% confidence intervals for averaged glucocorticoid models, showing estimates for reproductive state, age, and age-squared. All continuous predictors (temperature, precipitation) were scaled. Predictors are displayed in decreasing order of importance assigned by AICc comparison.

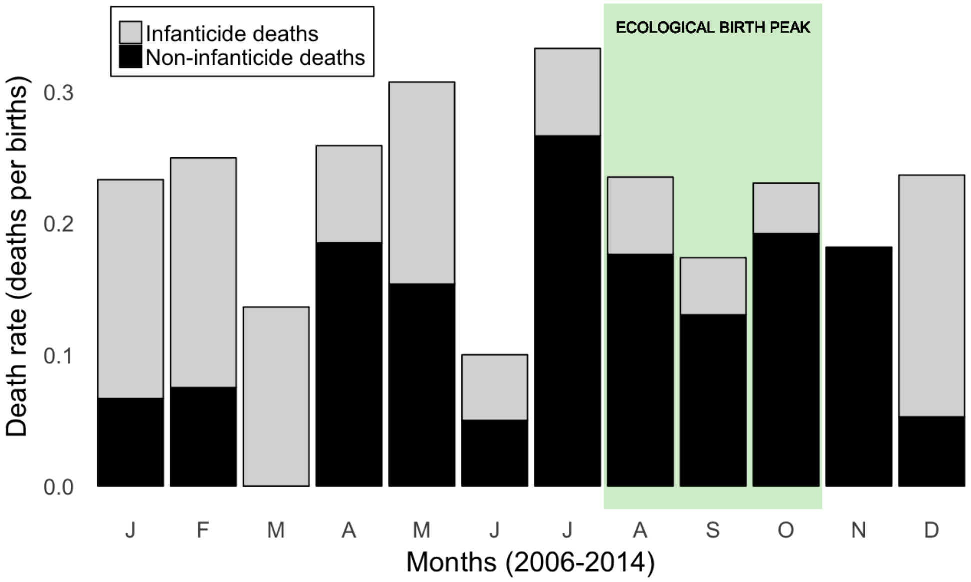


Figure 3.6. Death rate (deaths per total births) by month of birth and cause of death (infanticide vs. non-infanticide deaths). Infants born during the ecological birth peak (green) were not more or less likely to survive than infants born outside of the birth peak.

CHAPTER 4

EVIDENCE FOR OPTIMAL GROUP SIZE IN WILD GELADAS

INTRODUCTION

Social species live in groups of variable size. For a given species, the maximum group size observed within this range is thought to represent a “breaking point,” where the costs of group-living far outweigh the benefits (Higashi and Yamamura 1993). These costs and benefits are typically attributed to ecological pressures: for example, the costs of increased foraging competition (Janson and Goldsmith 1995; Chapman and Chapman 2000; Majolo et al. 2008; Grove 2012; Markham et al. 2015; Markham and Gesquiere 2017) versus the benefits of decreased predation risk (Pulliam 1973; Van Schaik 1983; Sterck et al. 1997a; Caro 2005; Beauchamp 2008). Individuals in groups with minimal costs and maximal benefits will have the highest fitness (i.e., better survival and overall reproductive performance: (Clutton-Brock 1988). In contrast, individuals in groups that fall outside of this optimal range should face some degree of compromise that results in diminished fitness (Giraldeau 1988).

Understanding how and why group size affects individual fitness is complicated by the fact that group living also exposes individuals to social pressures, such as infanticide from either male (Hrdy 1979; Crockett and Janson 2000; Zipple et al. 2017) or female

(Kruuk 1972; Agrell et al. 1998; Digby and Saltzman 2009; Clutton-Brock et al. 2010) conspecifics. While infanticide by females is thought to result from increased resource competition in large groups, infanticide by males typically occurs in the context of alpha male replacements, or “takeovers” (Teichroeb and Jack 2017). Takeovers, which are also associated with male-mediated pregnancy termination (e.g., the Bruce effect: Roberts et al. 2012; embryocide/feticide: (Zipple et al. 2017) in addition to infanticide, are a strong selective force that may override ecological pressures. For example, because folivores feed on widely-dispersed food resources, they should face low feeding competition, and should correspondingly live in large groups for predator protection. However, a striking number of folivores nevertheless remain in small groups (i.e., the “Folivore Paradox”: Isbell 1991; Janson and Goldsmith 1995; Treves and Chapman 1996; Crockett and Janson 2000; Steenbeek and van Schaik 2001; Koenig and Borries 2002; Snaith and Chapman 2007). The leading hypothesis for these small groups is that they are less attractive targets for takeovers (Treves and Chapman 1996; Steenbeek and van Schaik 2001; Teichroeb et al. 2012), although within-group feeding competition may also play a role (Steenbeek and van Schaik 2001; Snaith and Chapman 2007; Zhao et al. 2011). Therefore, optimal group size is the outcome of this balance between the costs and benefits associated with both ecological factors and social factors (e.g., Smith et al. 2008).

Identifying an optimum for natural groups in long-lived species has been methodologically challenging for at least two reasons. First, lifetime fitness in long-lived species is notoriously difficult to measure. Instead, short-term measures of reproductive performance (e.g., birth rate, interbirth interval, infant survival) are often used as proxies for fitness, and measuring longevity requires longitudinal data that span multiple generations to generate a sufficient sample size. Second, there is an inverse relationship between the accuracy of measures of fitness (which are more accurate over a longer period of time) and the precision of measures of group size (which are more precise over a shorter period of time). To circumvent this problem, we developed a novel measure of reproductive performance that can account for changes in an individual's environment. Specifically, we considered how changes in group size (an aspect of the social environment) predicted variation in reproductive performance.

Here, we used female geladas (*Theropithecus gelada*) as a test species to identify optimal group size and the selective forces that shape it. Geladas are long-lived, folivorous primates that live in social groups (hereafter, "units") that vary in size from 2 to 15 adults – variation that is present even within the same population (Snyder-Mackler et al. 2012a). In geladas, multiple units sleep and forage together in bands, yet each unit remains socially and reproductively closed (Snyder-Mackler et al. 2012b). Social factors such as takeovers are frequent and are highly disruptive for female reproduction (Beehner and Bergman 2008; Roberts et al. 2012; Tinsley Johnson et al. 2018). Infanticide by new males during takeovers is the leading cause of infant mortality in this population (incoming males kill over half of the infants of lactating females: Beehner and Bergman 2008), and larger units experience more takeovers than smaller units (Bergman et al. 2009). It is therefore reasonable to expect that females in larger units might incur disproportionately higher costs than females in smaller units. Finally, gelada units can undergo drastic changes in size during fissions (i.e., the permanent split of one unit into two daughter units) and fusions (i.e., the permanent joining of two units into one). Presumably these changes are in response to living in a suboptimal unit.

We tested three predictions relating to gelada unit size: (1) females in mid-sized units should demonstrate higher measures of fitness (as measured by reproductive performance and death rates); (2) both social factors related to male takeovers and infanticides and ecological factors should explain why both smaller and larger units are suboptimal; (3) individuals in suboptimal units should alter their behavior to mediate changes in unit size, which may improve their situation.

We analyzed data from 33 units (20 original "founding" units plus 13 "daughter" units resulting from fissions) to determine whether there was an optimal unit size for females in this gelada population. Unit size changes over time (unit size was defined here as the number of adult females in a unit, although the number of adult females is highly correlated with the total number of individuals in a unit, see *Supplementary Methods*): in addition to demographic changes due to female maturations and deaths, we also observed dramatic changes due to unit fissions and fusions (Fig. 4.1). To address this issue, we used two independent measures of female fitness:

> (a) *Reproductive performance*: A monthly binary score, where "successful" females (those that produced an infant that survived to 18 months of age, the average age at weaning for this population, Roberts et al. 2017) received 1 point

for each month of pregnancy and lactation (6 months of gestation + 18 months of lactation = 24 successful months). If the infant died before reaching 1.5 years of age, no points were awarded to the months of gestation/lactation prior to the infant death. We binned these monthly scores into subsequently longer time periods (over 3 months and 6 months) to reduce problems associated with temporal autocorrelation, with qualitatively similar results (see *Supplementary Methods*). Importantly, this monthly reproductive performance variable can be associated with a precise measure of group size (i.e., the maximum number of adult females in a unit in a given month).

(b) *Adult female death rate*: For each study year, we calculated the total time (in female-years) each unit was observed at a particular size and summed the number of female deaths observed in that unit at that size. The death rate was calculated for each unit-size as the number of adult female deaths out of the number of individual females observed at that unit size for each year, and was modeled as a function of unit size, controlling for time observed (in female-years) at each size.

Although units in this population can range in size from 1-13 adult females, females in units in the middle of this range (i.e., between 5-7 adult females, hereafter “mid-sized” units) demonstrated the highest fitness. First, after controlling for female age, females in mid-sized units had the highest reproductive performance (maximum females^2 estimate = -11.22 +/- 3.34 SE, *p*-value = 7.86×10^{-4}, Fig. 4.2AB). Second, females in mid-sized units had the lowest mortality overall (maximum females^2 estimate = 13.52 +/- 3.01 SE, *p*-value = 7.03 x 10^{-6}, Fig. 4.2CD), with females in smaller units demonstrating the highest death rates (maximum females estimate = -23.10 +/- 3.12 SE, *p*-value = 1.25 x 10^{-13}, Fig. 4.2CD). Taken together, females in mid-sized units had the highest reproductive success and lowest mortality.

We next investigated why females in mid-sized units had the highest fitness, focusing on factors that relate to our reproductive performance variable. We first examined how infanticide risk, as measured by both takeover frequency and infanticide rates, varied across unit size. As previously reported (Dunbar and Dunbar 1974; Beehner and Bergman 2008), takeover frequency increased with unit size (maximum females estimate = 0.51 +/- 0.20 SE, *p*-value = 1.29 x 10^{-2}; Fig. 3A). However, infanticides, the leading cause of infant death (12.3% of all infants born during this study period died of infanticide, accounting for 50.8% of all infant deaths), did not follow this same pattern. Rather, infanticide rates decreased with unit size (maximum females estimate = -18.35 +/- 6.51 SE, *p*-value = 4.8 x 10^{-3}; Fig. 4.3B) and were highest in both small and large units (maximum females^2 estimate = 24.40 +/- 5.85 SE, *p*-value = 3.0 x 10^{-5}; Fig. 4.3B). Thus, while females in large units experienced more frequent takeovers and the highest number of infanticides (17 out of 33 observed infanticides occurred in large units), females in small units experienced the second highest number of infanticides (10 out of 33) and females in both small and large units experienced higher infanticide rates than females in mid-sized units (0.14 infanticides per birth for both small and large units; 0.08 infanticides per birth in mid-sized units). Although takeovers of small units were less frequent, when males did take over small units they killed disproportionately more infants than when they took over mid-sized units. In this population, male takeovers dramatically alter female reproductive patterns (Roberts et al. 2012; Tinsley Johnson et al. 2018); here we show that females in mid-sized units have a selective advantage over females in smaller or larger units when it comes to these male-mediated birth patterns.

We next analyzed the energetic costs of unit size. Socioecological theory predicts that females in larger groups will have higher levels of within-group feeding competition that ultimately will limit the size of a group, while females in smaller group will have higher levels of between-group feeding competition, making smaller groups sub-optimal (Sterck et al. 1997b). Increased competition will be reflected in the amount of time females spend foraging (Chapman 1990) and/or in one or more measures of their overall energetic condition (van Schaik et al. 1991; Emery Thompson 2017; Markham and Gesquiere 2017). Therefore, we considered whether either foraging effort (as measured by time spent feeding) or glucocorticoid levels (a class of hormones that rise in response to increased metabolic demands) varied across unit size.

Despite feeding primarily on dispersed grasses (Jarvey et al. 2018), we found evidence that geladas may experience feeding competition associated with unit size. Specifically, unit size predicted foraging effort: females in mid-sized units spent the less time foraging than females in smaller or larger units (maximum females^2 estimate = 2.30 +/- 0.73 SE, z-value=3.16, *p*-value = 3.2×10^{-3}; Fig. 4.3C).

In contrast, our results for glucocorticoid metabolites (GCMs) were mixed. The number of females in a unit did not significantly predict individual female GCMs (maximum females estimate = -0.87 +/- 0.60 SE, *p*-value = 0.15; maximum females^2 estimate = 0.60 +/- 0.45 SE, *p*-value = 0.18), even after controlling for other factors known to influence GCMs (i.e., reproductive state, age, experiencing a takeover: Tinsley Johnson et al. 2018). However, the categorical predictor of unit size did significantly predict GCMs: females in medium and large units had lower GCMs than females in small units (medium estimate = -0.08 +/- 0.02 SE, *p*-value = 5.21 x 10^{-5}; large estimate = -0.08 +/- 0.03 SE, *p*-value = 1.68 x 10^{-3}; Fig. 4.3D). However, females in large units did not have significantly higher GCMs than females in medium units (large estimate = -8.14 x 10^{-4} +/- 0.02 SE, *p*-value = 0.97; Fig. 4.3D).

Our results suggest that mid-sized units are optimal for female fitness due to social (i.e., reduced infant mortality) and ecological (i.e., reduced foraging effort) reasons, while females in smaller and larger units experienced higher infant mortality and spent more time feeding. These findings raise the question: what, if anything, can females in suboptimal units do? As the philopatric sex, female geladas may have limited options for switching units. Therefore, we next examined the means by which females sought to change their unit size (i.e., beyond the passive changes due to deaths and maturations).

Females in our population changed their unit size via unit transfers, fissions, and fusions. Permanent female transfers were rare (with only 2 documented cases, or a transfer rate = 0.003 transfers per female-year) and were only observed in larger units. Fusions were also relatively rare, and only observed in smaller units (3 documented cases; fusion rate = 0.004 fusions per female-year). In contrast, fissions were 3 times more common than fusions: specifically, females in larger units tended to fission into 2 (or 3) daughter units (9 total cases; fission rate = 0.01 fissions per female-year). Thus, females in suboptimal groups improved their circumstances by forming a smaller unit when they were in large units or by forming a larger unit when they were in small units. We then hypothesized that individual female behavior may mediate these changes.

From a proximate perspective, the probability of a fission increases when the number of social ties between group members decreases (Koyama 2003; Van Horn et al. 2007; Sueur et al. 2010; Sueur et al. 2011). However, maintaining multiple social relationships requires a significant investment of time and energy. Because females in smaller and larger units spend more time feeding, they may be particularly constrained in the amount of time they can devote to grooming (the primary means by which primates maintain social relationships), which in turn could limit the number of social ties in these units. To test this, we first examined whether grooming time and/or the number of grooming partners varied by unit size.

First, time spent grooming did not vary according to unit size (maximum females estimate = 1.35 +/- 4.43 SE; *p*-value = 0.76; maximum females^2 estimate = -3.47 +/- 3.74 SE; *p*-value = 0.36; Fig. 4.4A). This suggests that, even in the face of increasing time spent foraging (Fig. 4.3C), gelada females conserve their social time. In contrast, the number of grooming partners increased with unit size (range: 0-6 maximum females estimate = 9.19 +/- 1.93 SE; *p*-value = 1.27 x 10^{-5}; Fig. 4.4B), suggesting that females in larger units may spend less time socializing with each partner than females in smaller units. Still, the mean number of grooming partners reached an asymptote between 2-3 grooming partners in large units (maximum females^2 estimate = -4.83 +/- 1.51 SE; *p*-value = 1.59 x 10^{-3}; Fig. 4.4B). Therefore, females in small or mid-sized units groomed with more than half (and, in some cases, all) of the females in their unit, while females in the largest units groomed, at best, with less than half of the individuals available.

These changes in individual grooming behavior suggest that larger units could be more vulnerable to fission than smaller units. To test this, we used social network analysis to consider network connectivity in each unit. Specifically, we examined the network average clustering coefficient, which reflects how interconnected members of a group are to one another (e.g., are an individual's social partners also partners with each other?). The clustering coefficient is often used as a measure of group cohesion, with lower values reflecting a less cohesive group. We found that the clustering coefficient decreased as unit size increased – in small units, all individuals were likely to be connected with all other unit members, while in large groups individuals were more fractured (maximum females estimate = -0.93 +/- 0.41 SE; *p*-value = 3.39 x 10^{-2}; Fig. 4.4C).

Taken together, our results demonstrate female fitness in mid-sized units exceeds that of females in smaller or larger units. Takeovers appear to influence this relationship, providing support for the hypothesis that infanticide risk is a major driver of group size in folivores (Sterck et al. 1997a). Additional ecological factors (specifically, time spent feeding) also contribute to the of costs of either smaller or larger units (or both).

The nature of social interactions within units, and specifically the number of individuals a female socializes with, may represent a mechanism by which females can alter their group size. Specifically, females in large groups, where fitness costs begin to accrue, may respond by focusing their interactions on a subset of individuals (Engh et al. 2006). This alters the social network structure of the group, which increases the odds of fissions and eventually decreases group size. Gelada social structure may offer a unique opportunity for fissions to occur: gelada units form larger aggregations, such as bands, which may reduce the cost of fissions. However, gelada social structure may also explain why fusions, although possible, as less frequent: although it might benefit females in smaller units to join together to form a mid-sized unit, leader males of small units may limit inter-unit interactions. Indeed, the three fusions we have observed all followed the disappearance of a leader male of one of the units.

Although foraging effort has been linked to physiological measures like glucocorticoid metabolites in other species (Emery Thompson 2017), here we did not find strong evidence that female glucocorticoids metabolites were higher in small or large units compared to mid-sized units. Previous analysis in this population have indicated that temperature, and not the availability of green grass, most strongly predicts glucocorticoid levels (Beehner & McCann 2008; Tinsley Johnson et al. 2018).

Therefore, thermoregulatory demands (which presumably would affect all individuals equally across units of different size) may represent more of a constraint on metabolic needs than food. In addition, individual characteristics are likely important predictors of variation in glucocorticoid levels. For example, Barbary macaques that survive the harsh winter have more social partners, and form larger huddles (which carry thermoregulatory benefits), than individuals with fewer social partners (Campbell et al. 2018). Further investigation into how social behavior interacts with environmental metabolic demands in geladas is needed.

The impact of group size on individual fitness has a strong theoretical basis, yet it is often difficult to demonstrate how and why group size shapes fitness in long-lived species. Here, we demonstrate not only that group size shapes female fitness in a wild primate, but also consider the extent to which both social and ecological factors contribute to this effect. Moreover, we highlight how individual social behavior may vary in response to group size in such a way that individuals may alter their group size, thus improving their social situation.

SUPPLEMENTARY METHODS

Study site and subjects

The data for this study derive from 9 years of observation (2006-2014) on a population of wild geladas living in the Simien Mountains National Park, in northern Ethiopia (13°13.5’ N latitude). The Simien Mountains Gelada Research Project (SMGRP, formerly the University of Michigan Gelada Research Project) has collected behavioral, demographic, genetic, and hormonal data from individuals since Jan 2006. All gelada subjects are habituated to human observers on foot and individually recognizable. Daily precipitation was measured using a rain gauge. Daily maximum and minimum temperatures were measured using a digital thermometer placed in a permanently shaded area. We used longitudinal data from 189 adult females in 33 reproductive units (20 original “founding” units plus 13 “daughter” units resulting from fissions). All adult females had known or estimated birth dates from which we calculated age (mean age at the mid-point of the study, 2010 = 12.47 +/- 5.27 SD years; overall range = 4.75 - 27.83 years). Estimated birth dates were calculated based on known dates for other reproductive events (e.g., maturation, first birth, age of oldest offspring, or number of known offspring).

Demographic data

Unit size

The identities of all individuals present in a unit were recorded each day the unit was seen. Here we define unit size as the maximum number of adult females in a unit for each month: for each month of the study period, we recorded the total number of adult females in each unit; where changes in unit size occurred (i.e., due to adult female deaths or subadult female maturations), we used the maximum number of adult females in a unit in a given month. This is because we have longitudinal records of the number of adults in each unit, but started recording the total number of individuals (juveniles, infants) in 2012. However, when we compared the maximum number of adult females in a unit to the total number of individuals in a unit for the subset of data where we have both (2012-2014), we found that both values were highly and significantly correlated (Pearson correlation coefficient = 0.91, p-value < 2.2×10^{-16}). We also calculated the maximum number of adult males in each unit for each month, which was not highly correlated with the maximum number of females (Pearson correlation coefficient = 0.08, p-value = 4.5×10^{-2}).

Unless noted, all statistical models included the number of females as a continuous predictor variable. However, for visualization purposes, we also categorized unit size into small, medium, and large units based on the observed range in variation in sizes. Specifically, cut-offs were determined by calculating the tertiles of the observed monthly distribution of sizes: “small” indicates units of less than or equal to 4 adult females; “medium” indicates units between 5 and 7 adult females; “large” indicates units of 8 or more adult females.

Changes in the number of adult females in a unit were either due to female maturations or to deaths. Maturations were recorded as the first observation of a sex skin swelling (details are outlined in Roberts et al. 2017). Deaths were recorded as the first day an individual was no longer observed with a unit when that individual was consistently absent for three consecutive encounters with that unit (and not observed in a different unit, as in the case of transfers, which were rare, or fissions).

Takeovers, fissions, and fusions

We recorded the dates of all observed male takeovers (*n* = 72) of known reproductive units (following Tinsley Johnson et al. 2018) as well as the number of mature females in the unit at the time of takeover. Dates of fissions, fusions, and female dispersals were assigned to the first day unit females were no longer observed together and subsequently observed either in a separate daughter unit with a new leader male (in the case of fissions), together with non-unit females and a new leader male (in the case of fusions), or associating with a different unit and new leader male (in the case of female dispersals). In all cases, we immediately identified known females in daughter units or new units following their disappearance from their natal unit.

Reproductive performance

For all infants born during the study period (n = 272), a date of birth was either known (n = 243) or assigned (n = 29; assigned birth dates followed the criteria outlined in Tinsley Johnson et al. 2018). From these birth dates we were able to calculate conception dates based on mean gestation length (n = 183 days; Roberts et al. 2017).

We used a binary scoring system to assign female reproductive performance. Females were “successful” when their infant survived to 1.5 years of age, which is the average age of weaning in this population (regardless of actual weaning date). Successful females received 1 point for each month of pregnancy and lactation leading up to the designated end point of 1.5 years (6 months gestation + 18 months of lactation = 24 successful months). If the infant died before reaching 1.5 years of age, no points were awarded to the months of gestation/lactation prior to the infant death.

The disappearance of any infant prior to weaning was assumed to be a case of infant mortality. The cause of mortality was assigned based on the following characteristics: if the infant's mother died at the same time, the cause of death was recorded as "maternal death." If the mother did not die at the same time, and the infant death occurred within 9 months of a takeover, the cause of death was recorded as "infanticide" (Beehner and Bergman 2008; Tinsley Johnson et al. 2018). All other causes of infant deaths were recorded as "unknown."

Adult female death rates

For each study year, we calculated the total time (in female-years) each unit was observed at a particular size and summed the number of female deaths observed in that unit at each size. The death rate was calculated for each unit-size as the number of adult female deaths out of the number of individual females observed in that unit size for each year, and was modeled as a function of unit size, controlling for time observed (in female-years) at each size.

Behavioral data collection

We used 15-min focal animal samples (Altmann 1974) to record all social behaviors involving adult females, focusing on broad behavioral states (feeding, resting, moving, socializing) and on grooming behavior (including total time spent grooming and the identities of grooming partners). This dataset represents 1845.5 hours of focal observation (mean = 4.23 +/- 3.57 SD focal hours per female-year).

Feeding time was recorded by noting the broad behavioral state (feeding, moving, resting, or social) continuously throughout each 15-min focal. For each month, we calculated total time spent feeding (minutes per focal hour) and, to control for potential variation due to the time of day of a focal, we limited our analysis to females who had 3 or more separate focals for that month (>= 0.75 focal hours: *n* = 132 adult females over 58 months of observation).

All grooming interactions, including the duration and identities of the grooming partners, were also recorded. For each year, we first calculated *grooming time* (minutes of grooming, both given and received, per focal hour) for all co-resident females (i.e., for all potential grooming partners). We also summed the number of adult female grooming partners each focal was observed to groom with each year to calculate their *total number of grooming partners*. Finally, we used social network analysis to assess the global properties of the social network of each unit (Wasserman and Faust 1994). Specifically, we used the package *igraph* (version 1.0.0; Csardi and Nepusz 2006) in R to first calculate the individual clustering coefficient, or weighted transitivity, for each female in a unit based on dyadic grooming rates (using the function *transitivity*, Barrat et al. 2004); at the local, or individual level, the clustering coefficient reflects how embedded an individual is in a social network; i.e., how well-connected they are as well as how well-connected their associates are). We limited this analysis to units with 3 or more adult females, because the clustering coefficient is based on the number of "closed" triangles in a network (i.e., how many triplets each share ties). To assess the interconnectivity of the unit at the global level, or the *network average clustering coefficient*, we calculated the mean individual clustering coefficient for all adult females in the same unit each year (Watts and Strogatz 1998). The network average clustering coefficient indicates the degree to which all individuals in a unit cluster together.

Hormone collection and analysis

We collected fecal samples from 148 known adult females between 2006 and 2014 (*n* = 3835 hormone samples; mean = 26 samples per female; range: 1-150 samples per female). Fecal samples were collected using noninvasive methods developed by the SMGRP for hormone extraction and preservation under field conditions (Beehner and Whitten 2004). All samples were assayed for glucocorticoid metabolites (GCMs) using reagents from the ImmuChem^{TM} double antibody corticosterone ^{125}I RIA kit (MP Biomedicals, LLC, Orangeburg, NY). For more details on hormone extraction and assay methods see: (Tinsley Johnson et al. 2018).

Data analyses

Reproductive performance model

To assess the effects of unit size on female reproductive performance, we constructed a binomial generalized linear mixed-effects model (GLMM) using the *lme4* package (version 1.1-12: Bates et al. 2015) in R (version 3.3.2: R Core Team 2016). The dependent binary variable was the monthly success variable for each female-month.

We modeled this outcome variable as a function of the following predictors: female age (both the linear and quadratic term, to control for the known effects of female age on reproductive output), maximum number of males in the unit that month (as the number of adult males in a unit varies independently from the number of adult females), and maximum number of females in the unit that month (both the linear and the quadratic term). We controlled for the repeated measures of individual identity, month, and year as random effects.

To account for the potential effect of pseudoreplication in our approach we also binned our success variable across two different time periods (3 months and 6 months) and constructed two new binomial GLMMs. For each of these models, the outcome variable was the number of successful months for each female over the given period out of the number of unsuccessful months over the given period. We included individual identity and the time period (i.e., the specific 3- or 6-month window) as random effects.

Female death rate

To assess whether the rate at which adult females died varied by unit size we first calculated the number of deaths observed for each unit-year and the size of the unit at the time of each death. For each year in our analysis, we summed the total time (in female-years) we observed each unit at a specific size and matched the time observed at a given size with the total deaths observed that year at that size. We constructed a binomial generalized linear mixed-effects model (GLMM) using the *lme4* package. The dependent binomial variable was the number of females that died out of the number of females that survived during the time a unit was observed at a specific size. We modeled this outcome variable as a function of the following predictors: unit size (the maximum number of females in the unit, including both the linear and the quadratic term) and the mean age of all unit females observed (to control for the increasing risk of death with age). We controlled for the repeated measures of unit and year as random effects, and to control for observation time we offset our outcome variable by the number of female-years a unit was observed at that specific size in a given year.

Infanticide risk and infant deaths

To assess how infanticide risk varied with unit size we first considered takeover frequency, as infanticides almost exclusively occur within the context of takeovers. We calculated the total number of takeovers observed according to the size of the unit (i.e., number of adult females) at the time of takeover. We modeled this number as the dependent variable in a generalized linear mixed-effects model (GLMM, fit with a Poisson distribution), offset by the total observation time (unit-years) of all units at each unit size. We controlled for the repeated effects of unit by including unit as a random intercept. Finally, we included two fixed effect variables: the maximum number of adult females in the unit and the average number of males in each size of unit (to control for the separate effect of the number of males in a unit on takeover frequency).

Next, we considered whether infanticide rates varied by unit size. We first calculated the number of infant births for each unit-year and the size of the unit at the time of each birth (total N births = 269). Out of these births, we also calculated the number of infants that subsequently died due to infanticide before reaching 1.5 years of age, i.e., the average age at weaning in this population (Roberts et al. 2017; total *N* infanticides = 33). For each year in our analysis, we summed the total time (in female-years) we observed each unit at a specific size and matched the time observed at a given size with the number of births and the subsequent number of infanticides observed that year at that unit size. We constructed a binomial generalized linear mixed-effects model (GLMM) using the *lme4* package. The dependent binomial variable was the number of births that resulted in an infanticide out of the number of births that did not result in an infanticide. We modeled this outcome variable as a function of unit size (the maximum number of females in the unit, including both the linear and the quadratic term). We controlled for the repeated measures of unit and year as random effects, and to control for observation time we offset our outcome variable by the number of female-years a unit was observed at that specific size in a given year.

Feeding time

To investigate the relationship between feeding time and unit size we constructed a series of linear mixed-effects models (LMM) using the *lme4* package. Our dependent variable was the total minutes an individual spent feeding in a given month offset by the time observed that month (focal minutes). We considered six variables in total. First, we included factors related to the size of the unit: maximum number of males in the unit that month, and maximum number of females in the unit that month (including either the linear term or the quadratic term for number of females). Second, we included factors related to the seasonal variation in temperature and food availability: maximum temperature (mean maximum temperature across the previous 30 days) or rain (cumulative rain over the previous 90 days). For maximum temperature, we included either the linear or the quadratic term. Because temperature and rain were correlated (Pearson's correlation: $r = -0.696$, $p < 2.2 \times 10^{-16}$), we ran two sets of LMMs, one that included temperature (or temperature-squared) and one that included rain. Finally, each model included factors related to individual condition, which could impact energetic demand: age (maximum female age for the month) and reproductive state (cycling, lactating, or pregnant).

We compared all candidate models using AIC and present here the results of the top model, which included the following predictors: maximum number of females^2, maximum number of males, maximum temperature^2, maximum female age, and reproductive state (see Table 4.1).

Glucocorticoid metabolites

To assess the effect of unit size on GCMs, we log-transformed GCM values to approximate a normal distribution, and then modeled logGCMs (in a LMM using *lme4*) as a function of the following predictors. First, we included a variety of predictors previously shown to affect female GCMs (Tinsley Johnson et al. 2018) due to a) seasonal variation in temperature, b) individual characteristics, and c) social events. Specifically, we included mean maximum and minimum temperature over the 30 days prior to sample collection, female age (which we included as both a linear and quadratic term), and reproductive state (pregnant, cycling, or lactating), as well as the interactions between age and age-squared and reproductive state. We also included a categorical predictor reflecting whether the sample had been collected in the 30 days following a takeover, and the interaction between takeover and reproductive state.

Finally, we included three predictors reflecting unit size: maximum number of unit females (both the linear and quadratic term), maximum number of unit males, and a categorical variable of unit size (small, medium, large) based on the maximum number of unit females (where cut-offs were determined by calculating tertiles of the observed range of variation in unit size: small <= 4 adult females; medium = 5-7 adult females; large = 8+ adult females). We included the categorical variable of unit size in this analysis because our hormone sampling in units of 8+ females was sparse compared to that of smaller units. We ran two separate LMMs, the first with the continuous predictor of unit size (maximum females and maximum females-squared) and the second with the categorical variable, and present the results of both models. Both models controlled for the repeated effects of individual identity, month, unit, and year.

Grooming time, partners, and network average clustering coefficient

To assess the effect of unit size on female social behavior, we constructed three sets of LMMs using the *lme4* package. The outcome variables for each set of models were: (1) *grooming time*: total yearly minutes grooming per focal hour; (2) *grooming partners*: total yearly adult female grooming partners per focal female; and (3) *network average clustering coefficient*. We modeled each outcome variable as a function of the following predictors: the maximum number of adult females in the unit (including the linear and the quadratic terms), the maximum number of males in the unit, and (for the first two individual-level measures) the focal female’s age at the end of the year. We controlled for the repeated effects of individual identity (for *grooming time* and *grooming partners*), unit, and year, and limited our analysis to females that had at least 1 hour of focal observation during the year (four 15-min focals). Each model set included the intercept-only null model, univariate models that considered only a single fixed effect, and multivariate models that considered all combinations of fixed effects. Model fits were compared using AIC and the results of the top model are reported here.

Figures were constructed using *ggplot2* (Wickham 2011).

SUPPLEMENTARY RESULTS

Feeding time

The amount of time adult females spent feeding varied significantly according to a number of factors, in addition to unit size, which we would like to highlight here.

First, females in units with more adult males spent less time feeding (estimate = -2.12 +/- 0.54 SE, t-value = -3.92, *p*-value = 9.64×10^{-5}; Table 4.1). This may indicate that females primarily compete with each other for access to food resources, and do not compete with males (i.e., as is the case in chimpanzees, where female energetics was most affected by the number of males in a party, as males are dominant over all females in chimpanzee society: Emery Thompson and Georgiev 2014). On the other hand, it could indicate that there is a benefit to having more males in a unit, which could be relevant if between-unit competition over food resources occurs (although there is limited evidence that it does in geladas). One final possibility is that the number of males in a unit can reflect the degree of social upheaval being experienced at a given time: specifically, there is usually only one male in a unit (the dominant leader male), and occasionally there are 1-2 follower males (Snyder-Mackler et al. 2012b). When we see more that 3 adult males in a unit is typically during periods surrounding takeovers, especially so-called “messy” takeovers, where multiple bachelor males enter a unit and once, and continue to compete over the top leader male position, a chaotic period that can last up to a month at a time. Therefore, it’s possible that females spend less time feeding when there are many males in the unit because they are being herded, or are investing time bonding with new potential leader males instead of feeding. If so, takeover periods could be particularly energetically stressful (and not just socially stressful) for females. In a previous analysis, we found that female glucocorticoid metabolites increase following male takeovers, but only in females that are pregnant at the time (Tinsley Johnson et al. 2018). Pregnant females are also known to abort their pregnancies following a takeover (i.e., the Bruce effect: Roberts et al. 2012), however, the mechanism behind the Bruce effect in geladas is not yet known. Further analysis around female energetics at the time of takeovers, and especially around “messy” takeovers, may help explain this phenomenon.

Second, the time females spent feeding was significantly related to the mean maximum temperature over the previous 30 days. Interestingly, females spent the most time feeding during periods of extreme temperatures (i.e., when temperature were highest and when they were lowest: estimate^2 = 3.06 +/- 1.40 SE, z-value = 2.18, *p*-value = 0.03; Table 4.1). While previous characterizations of gelada feeding behavior (Dunbar et al. 2009) suggested that females spend more time feeding during the hot-dry season (due to the extra work required to obtain their primary fall-back foods, underground tubers: (Jarvey et al. 2018), here we find evidence that the cold-rainy season, when geladas also experience the highest glucocorticoid metabolites in response to cold temperatures (Tinsley Johnson et al. 2018), is also a period of higher investment in feeding. Notably, the cold-rainy season is also a period of peak green grass availability; perhaps females take advantage of the relatively brief period (roughly 5 months every year: Jarvey et al. 2018) when food is abundant, dedicating more time to foraging. Alternatively, or in addition, geladas may need to spend more time foraging at this time of year in order to make up for increased energetic expenditure due to thermoregulatory demands.

Finally, we found a significant effect of female age on time spent feeding, which will be discussed in detail below.

Female age

Female age was a significant predictor for both reproductive performance and female mortality, even after controlling for the effects of unit size. As is typical for female primates (Atsalis and Videan 2009; Roberts et al. 2017), younger and older females had the lowest reproductive performance (age^2 estimate= -41.23 +/- 4.42 SE, *p*-value $< 2.0 \times 10^{-16}$), while units with the oldest females exhibited higher mortality rates (maximum age of unit females estimate = 0.08 +/- 0.04 SE, *p*-value = 4.97 x 10^{-2}). Older females also spent less time feeding than younger females (age estimate = -1.01 +/- 0.45 SE, *p*-value = 2.69 x 10^{-2}; Table 4.1), which could either reflect reduced energetic demands due to decreased reproductive performance, or could reflect decreasing physical ability. We did not consider time spent moving or resting in this analysis, which might also change with age. Finally, age also significantly predicted both time spent grooming and the number of grooming partners. As they aged, females spent significantly less time grooming with other adults (age estimate: -4.60 +/- 1.83 SE; *p*-value = 1.28 x 10^{-2}) and interacted with fewer adult grooming partners (age estimate: -0.17 +/- 0.08 SE; *p*-value = 3.31 x 10^{-2}). However, our grooming analysis only considered grooming with other adult females, therefore they do not necessarily reflect decreased investment in socializing. Future analyses could help determine whether older females really do spend overall less time socializing, or whether they use their social time differently (i.e., grooming with younger offspring instead of with adults). It also raises the question of whether older females have other means of maintaining social ties with other unit members as they age (i.e., via vocalizations), which will be addressed in Chapter 5.

TABLES

Table 4.1. Results from top model for monthly feeding time

Predictor	Estimate	Standard Error	t-value	*p*-value
Maximum females^2	2.30	0.73	3.16	** 3.2×10^{-3}
Maximum males	-2.12	0.54	-3.92	*** 9.6×10^{-5}
Maximum temperature^2	3.06	1.40	2.18	* 3.1×10^{-2}
Female age	-1.01	0.45	-2.23	* 2.7×10^{-2}
Reproductive state: lactating	1.14	1.05	1.08	0.28
Reproductive state: pregnant	0.27	1.30	0.21	0.83

FIGURES

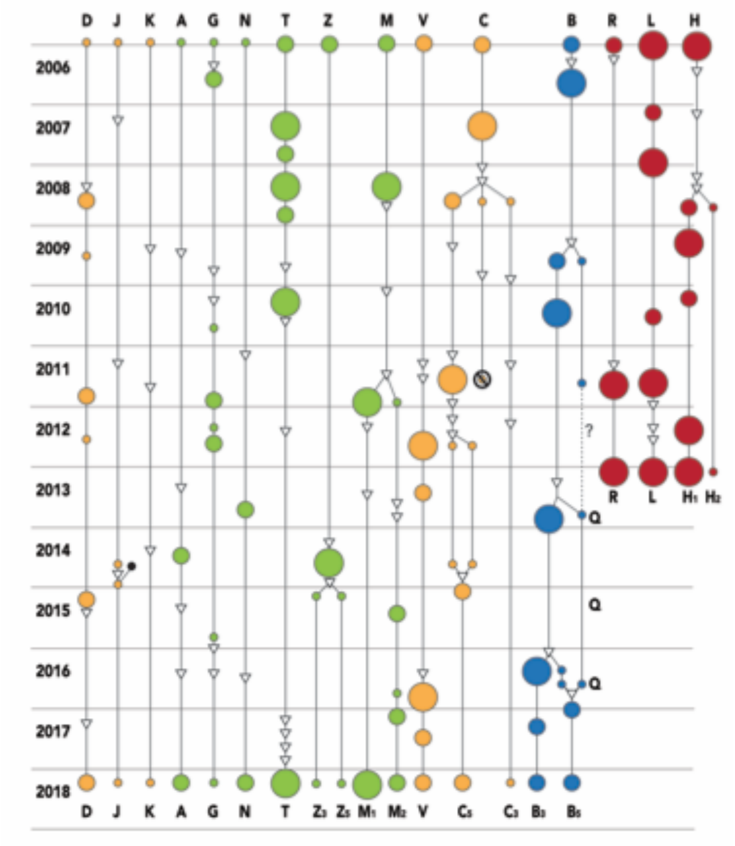


Figure 4.1. Changes in unit size over time. Founding units (where observation started in 2006) are coded by letters and arranged along the top axis according to initial size (which is also indicated by the size of the node). Color of node indicates band affiliation. Triangles indicate takeover events (where more than one takeover occurred in a month, only one triangle is used). Fissions and fusions are indicated by diagonal lines.

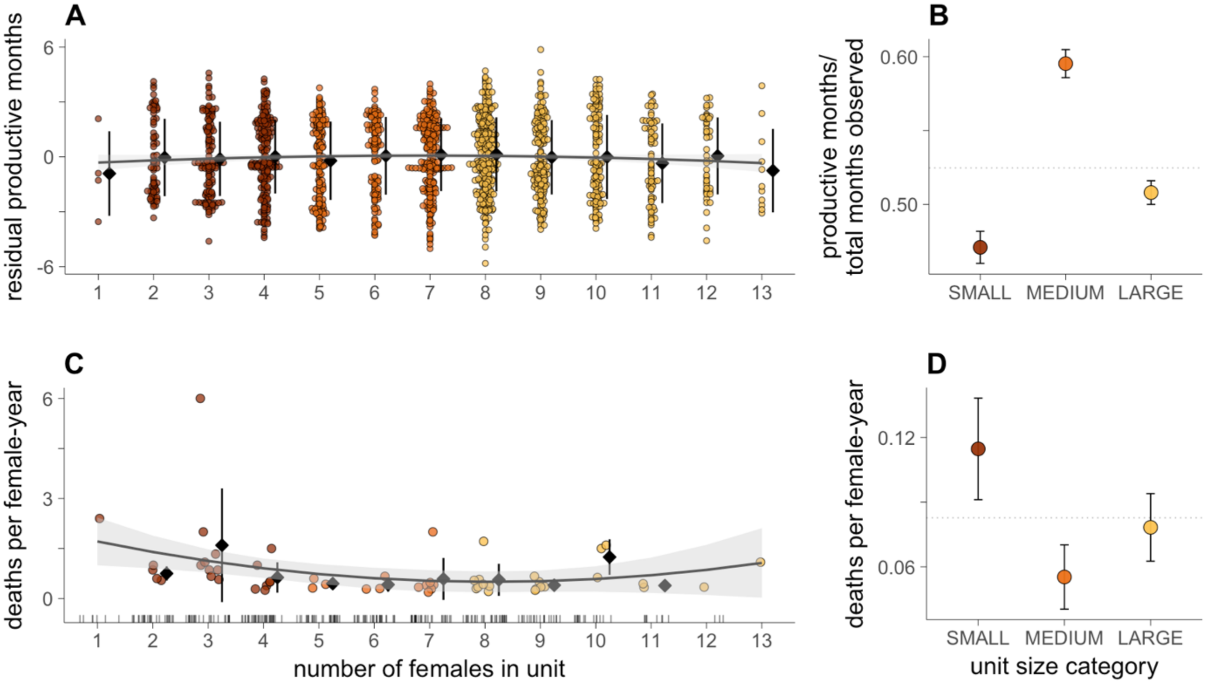


Figure 4.2. Females in mid-sized units had the highest fitness. (A) Residual productive months (controlling for age) by unit size (number of adult females). Each circle indicates the summed reproductive performance for a female over a 6-month period (n = 1677 observations from n = 185 females). Black diamonds indicate the mean for each unit size, and error bars indicate the standard deviation around the mean; **(B)** Total productive months divided by total months observed for all females by unit size category. The dotted horizontal line = 0.52 (the population mean); **(C)** Female death rates (deaths per female-year observed) by unit size (*n* = 32 distinct units; each circle represents a unit-size-year where at least one death occurred, i.e., for each year, we summed the number of deaths for each unit at a specific unit size and controlled for the total female-years observed at that size, *n* = 55 unit-size-years). Unit-size-years where no deaths occurred (n = 250 unit-size-years) are represented as tick marks along the x-axis. Black diamonds indicate the mean death rates for each unit size, and error bars indicate the standard deviation around the mean; **(D)** Female death rates by unit size category. The dotted horizontal line = 0.08 (the population mean). Unit size categories were used for visualization purposes only (see *Supplementary Methods*).

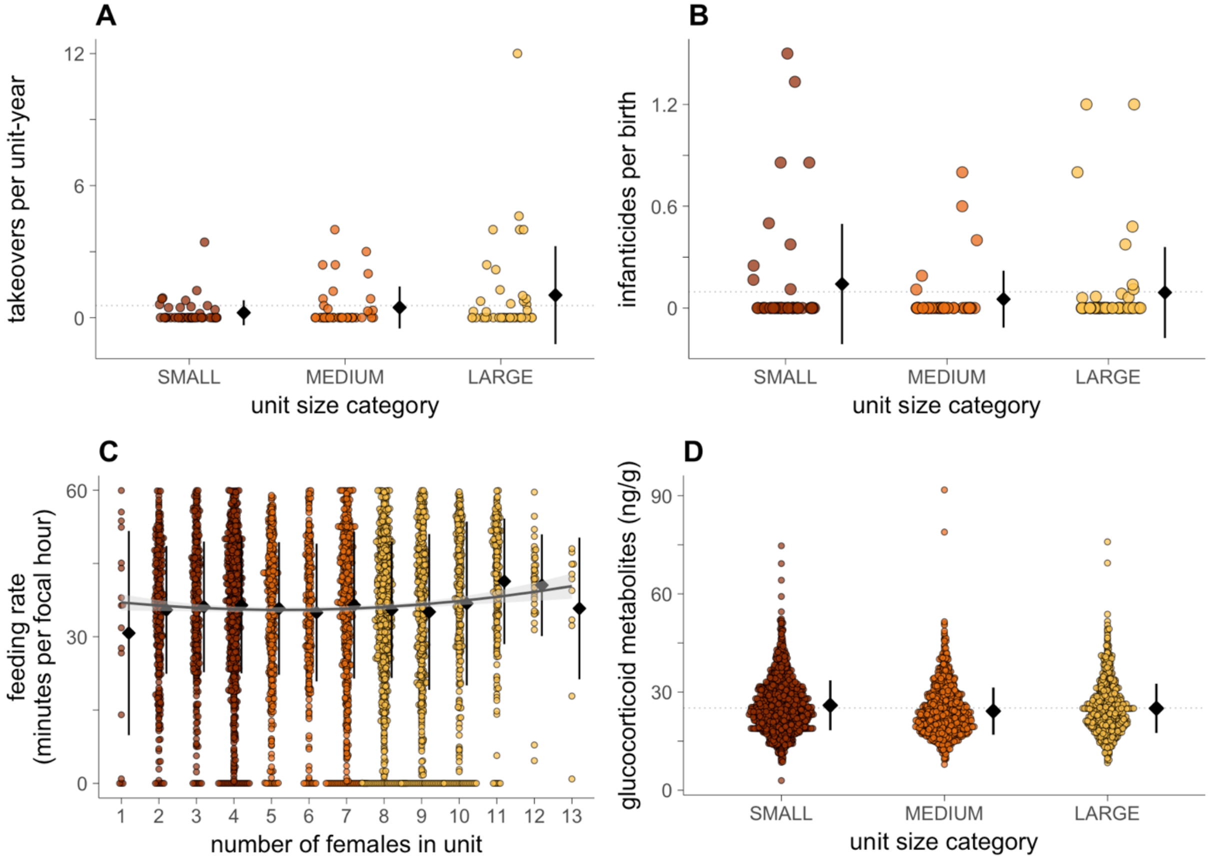


Figure 4.3. Both social and ecological factors explain why mid-sized units were optimal. (A) Number of takeovers per unit-year observed. Each circle represents the takeover rate for each unit at a specific size. The dotted grey horizontal line indicates the overall mean takeover rate (0.55 takeovers per unit-year); **(B)** The infanticide rates (number of infanticides per infants born for each unit-size-year) for each unit size in a given year. Years where no infants were born were excluded from the figure (n = 32 unit-size-years out of 97 total). The dotted grey horizontal line indicates the overall mean infanticide rate (0.01 infanticides per birth); **(C)** Feeding rates for each focal female for each month observed (n = 4,350 female-months). Rates were calculated by dividing the total minutes observed feeding by the focal hours observed; **(D)** Glucocorticoid metabolites (ng/g) for all adult females by unit size category (n = 3835 samples). The dotted grey horizontal line indicates the overall mean (25.11 ng/g). For all figures, black diamonds reflect the mean for each unit-size category, with bars representing the standard deviation.

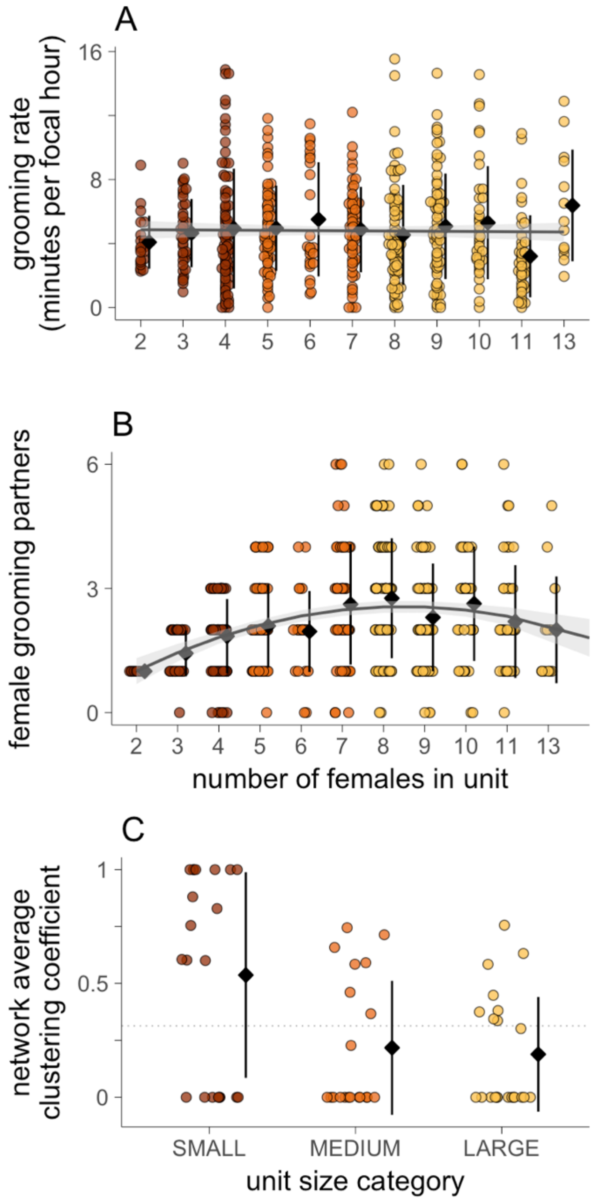


Figure 4.4. Larger units are less socially cohesive than smaller units. (A) Total minutes spent grooming by focal hour for each female-year (n = 557 female-years). X-axis reflects the maximum number of females in at unit across the year. **(B)** Number of female grooming partners a focal female was observed to groom with for each year. **(C)** Network average clustering coefficient by unit size category. Each circle indicates the mean clustering coefficient for a unit at a specific size category for each year. For all figures, black diamonds reflect the mean each unit-size category, with bars representing the standard deviation.

CHAPTER 5

A TEST OF THE VOCAL GROOMING HYPOTHESIS IN WILD GELADAS

INTRODUCTION

Language is a versatile tool that has many functions, from the exchange of information to the creation and maintenance of social relationships. But unlike other tools, there is little archaeological evidence that can help us understand the origin and evolution of language. Still, thinking of language as a tool begs the question – what is it a tool for? More specifically, what problem did language initially evolve to solve? Among the numerous hypotheses surrounding these questions, two main camps have emerged: one that contends that language evolved to convey information between individuals (Deacon 1996; Cheney and Seyfarth 2005; Fedurek and Slocombe 2011), and another other that suggests that language is a social tool, used to mediate relationships and convey emotional attachment, where the information content is of secondary importance (Aiello and Dunbar 1993; Dunbar 1996). For example, the vocal grooming hypothesis (Aiello and Dunbar 1993; Dunbar 1996) suggests that language evolved as an efficient social tool that allowed us to maintain large, complex groups.

One way to test these hypotheses involves a comparative approach (Nunn 2011) to the study of human language, and specifically focusing on nonhuman primate vocal communication (Seyfarth and Cheney 2010; Fedurek and Slocombe 2011). Nonhuman primates are a useful comparison in the study of the evolution of language, and share neural and genetic homologies with humans that relate to vocal learning and production (Berwick et al. 2013). They are also, like humans, intensely social animals, forming long-term social relationships with other individuals and navigating complex dominance hierarchies (Cheney and Seyfarth 2008). Therefore, one way to investigate the social origins of language proposed by the vocal grooming hypothesis would be to test its predictions in our primate relatives. Here we adopt such an approach to assess whether primate vocalizations help mediate social relationships in contexts where social complexity and time constraints are high.

In both humans and non-human primates (and in a variety of other social species: Silk 2007a; Cameron et al. 2009; Frère et al. 2010), social bonds are important because they provide fitness benefits to individuals that invest in them (House et al. 1988; Christenfeld et al. 1997; Glynn et al. 1999; Silk 2007a; Silk et al. 2009; Silk et al. 2010). For example, in at least two species of baboons, females with strong social bonds have more offspring and live longer than those with weak social ties (Silk et al. 2003; Silk et al. 2009; Silk et al. 2010). Further, bonds provide important social capital: preferred social partners are more likely to intervene in an ongoing dispute to aid their ally (Silk et al. 2004). Moreover, ‘stress hormones’ (i.e., glucocorticoids) are significantly lower in female baboons that maintain stable grooming networks with preferred partners (Crockford et al. 2008) and skyrocket following the loss of one of these partners (Engh et al. 2006). One of the main implications of the vocal grooming hypothesis for primates is that vocal contact could help individuals maintain these important social relationships, even, perhaps, substituting for grooming when time is tight.

Moreover, maintaining relationships with specific individuals is important: most social animals do not form social bonds indiscriminately. Rather, they form preferences based on individual characteristics, such as sex, kinship, reciprocity, and/or dominance rank (e.g., Silk et al. 1999; Mitani 2009; Thompson and Norconk 2011). In many female-bonded primates, primary social partners (individuals that form the closest social bonds) are closely related and share a similar position in the dominance hierarchy. Females can also form strong bonds with other females close to their own age, which may be especially prevalent in mating systems where males dominate reproduction, creating age-cohorts consisting of paternal siblings (Altmann 1979; Alberts 1999; Smith et al. 2003; J.B.B. Silk et al. 2006; J.B. Silk et al. 2006; Van Horn et al. 2007).

Typically, social bonds are identified by measuring pro-social behaviors, such as time spent in proximity (i.e., Hinde and Atkinson 1970; Sbeglia et al. 2010; King et al. 2011; Zhang et al. 2012), time engaged in social grooming (i.e., Sade 1965; Seyfarth 1977; Seyfarth 1980; Henzi and Barrett 1999; Wittig et al. 2008), or some combination of the two (i.e., Silk 2007b; Schülke et al. 2010). Because these kinds of pro-social behaviors require a significant investment of time and energy, the number of relationships an individual can maintain is limited by the amount of social time available (Dunbar 1992). In contrast, the vocal grooming hypothesis (Aiello and Dunbar 1993; Dunbar 1996) predicts that social bonds could also be maintained by calls, or specifically, by *call* *exchanges* (i.e., a call-and-response pattern of vocalizations between two or more individuals). Call exchanges provide two distinct benefits over proximity and grooming: first, they allow an individual to 'multi-task', as vocal contact can be maintained even while at a distance or engaged in another activity, such as foraging. Second, they allow individuals to maintain contact with more social partners simultaneously, resulting in extended social networks that contribute to the social cohesion of a group (Sueur et al. 2010; Sueur et al. 2011; Sueur and Maire 2014).

In addition to primary social partners, an individual's extended social network also impacts its fitness. While primary social partners are dyads that interact most frequently, the extended social network can refer to pairs that socialize less frequently than primary social partners, i.e., "weak ties" (Granovetter 1977; Maryanski 1987; Dunbar 2012; Sueur and Maire 2014) or "secondary partners" (Tinsley Johnson et al. 2014). For example, the number of weak ties an individual maintains is critical for group stability and cohesion (Sueur and Maire 2014): when the number of weak ties between group mates decreases, the odds of fissions increase (Sueur et al. 2010; Sueur et al. 2011; Sueur and Maire 2014; Larson et al. 2017). The extended social network can also refer to indirect connections between individuals in a group, or "friends of friends" (reviewed in Brent 2015). For example, in several species the interconnectedness between an individual and its social partners are (i.e., how many indirect connections an individual has via their direct connections) is better at predicting infant survival than dyadic measures alone (in chacma baboons, *Papio hamadryas ursinus*: (Cheney et al. 2016)). Although researchers have only recently begun to probe the predictive value of an individual's extended social network for any fitness benefits, these early results suggest that social bonds provide fitness benefits because they contribute to group stability and cohesion. Therefore, a second implication of the vocal grooming hypothesis is that vocal contact may allow individuals to maintain a more complex social network than is possible by grooming alone. That is, while they reserve grooming time for their primary partners, they may still preferentially interact with secondary partners via call exchanges – and these interactions may be equally important for individual fitness as primary social bonds.

Social complexity – i.e., group size and the number of varied relationships they entail – corresponds with greater vocal complexity across primates (McComb and Semple 2005). This relationship is particularly salient in species where the formation of long-term social bonds is critical for reproductive success (Gustison et al. 2012). Primate vocal communication can mediate social relationships in a number of ways. For example, call exchanges help coordinate movements and behaviors between pair-bonded Milne Edwards' sportive lemurs (*Lepilemur edwardsi*; Méndez-Cárdenas and Zimmermann 2009). In ring-tailed lemurs (*Lemur catta*), call exchanges are even more selective than grooming: individuals only responded to the calls of their top primary grooming partners (Kulahci et al. 2015). In some species, social bond strength predicts the frequency of certain vocalizations, suggesting such vocalizations could be interpreted as "grooming-at-a-distance" (e.g., in chimpanzees, *Pan troglodytes*: Mitani and Gros-Louis 1998; in Japanese macaques, *Macaca fuscata*: Arlet et al. 2015; Katsu et al. 2016). In contrast, chimpanzee (*Pan troglodytes*) vocal and gestural communication networks both supplement and extend grooming networks: individuals used synchronized pant-hoot calls with more partners than they groomed with, but also preferentially vocalized and gestured with individuals they were often in close proximity to (Roberts and Roberts 2016). Together, this evidence suggests that certain vocalizations may be used to either maintain primary social bonds or secondary social bonds, or both, and that call exchanges are just as socially selective (if not more so) as other prosocial behaviors associated with social bonds (i.e., grooming, proximity).

In this chapter, we present a test of the vocal grooming hypothesis in an exceptionally "chatty" wild primate, the gelada (*Theropithecus gelada*). Indeed, geladas were the original inspiration for the vocal grooming hypothesis, and they represent an ideal test species for a number of reasons. First, like humans, geladas call frequently, and the complexity of their vocal repertoire mirrors the complexity of their social system (Gustison et al. 2012). Of their remarkably varied and distinctive vocalizations, the most prominent is a *contact call*, which is often produced in a series (i.e., a *call exchange*). In baboons (*Papio* spp., a sister taxa of geladas), similar calls are used to maintain group cohesion and to reconcile after fights (Cheney and Seyfarth 1997; Silk et al. 2016). However, the function of call exchanges in female geladas is not yet known.

Second, like many cercopithecines, gelada females remain in their natal group throughout their lives, forming long-term primary social bonds with other females. These bonds are highly selective: individuals preferentially form bonds with only 1-2 close relatives that also share a similar position in the dominance hierarchy (Tinsley Johnson et al. 2014). Because rank is maternally-inherited, relatives that share a similar rank are likely mother-daughter pairs or maternal siblings (le Roux et al. 2011). In addition to primary social partners, females can also interact with 1-3 secondary social partners, who are closely related but not of similar rank (Tinsley Johnson et al. 2014). Because male geladas dominate reproduction during their tenure as leader males (which averages 3 years; (Snyder-Mackler et al. 2012), one hypothesis is that secondary social partners could represent paternal half-siblings, or members of the same age cohort, but we have only recently obtained sufficient long-term data (including known birth dates) to test this. Finally, primary and secondary social partners are also characterized by varying frequencies of prosocial behaviors. Specifically, females are often in proximity with both primary and secondary social partners and frequently groom with primary social partners, but only occasionally groom with secondary social partners.

Third, geladas live in a complex multi-level society. Reproductive units (hereafter, “units”) comprise the core groups of gelada society, and are composed of a dominant leader male, 1-12 adult females and their offspring, and possibly one or more subordinate follower males (Dunbar 1980; Snyder-Mackler et al. 2012). The size of these units has important implications for individual fitness, including shaping female reproductive success, survival, and the time females spend foraging (Tinsley Johnson et al., in prep). Specifically, we know that large units are sub-optimal, and often fission once they grow beyond 8 adult females. Females in larger units spend the most time foraging, and geladas already devote the maximum time possible to socializing (averaging 20% of their daily time budgets, the highest seen in any primate: (Iwamoto and Dunbar 1983). Perhaps as a result, females in large units do not maintain a sufficient number of relationships and instead fission into smaller units (e.g., Henzi et al. 1997; Sueur et al. 2011; Larson et al. 2017). However, optimal units (mid-sized units that range between 5-7 adult females) are still much larger than the number of primary social partners per female that we observe (1-2: Tinsley Johnson et al. 2014). Yet, these units have never been observed to fission, suggesting other prosocial behaviors beyond grooming may contribute to social stability.

Finally, available social time may also be constrained for female geladas due to seasonal variation in temperature and food availability, individual reproductive state, and age, regardless of unit size. First, geladas are cold-stressed (Beehner and McCann 2008; Tinsley Johnson et al. 2018), indicated by their relatively high glucocorticoid levels during the cold-rainy season (Jun-Sep). This period also overlaps with the highest availability of green grass (their staple food source; Jarvey et al. 2018). In contrast, the warmest months (Feb-May) are also the driest, meaning geladas switch to underground tubers as a fallback food, which are time-consuming to obtain (Dunbar 1984; Dunbar 1992; Jarvey et al. 2018). Our seasonal analysis of time spent foraging showed that both periods result in more time spent feeding (females spent the most time feeding when temperatures were lowest and when temperatures were highest; Tinsley Johnson et al., in prep). Therefore, females may rely on more time-efficient social behaviors than grooming during both the cold-rainy and the hot-dry season. Second, mammalian reproduction is energetically costly for females. Although our previous analysis did not find differences in time spent foraging by reproductive state (cycling, pregnant, or lactating), females may instead need to spend more time resting and less time socializing during late pregnancy and/or early to mid-lactation, which would again favor the use of call exchanges to maintain social relationships. Finally, as females age they spend less time feeding, less time socializing with other adults, and interact with fewer adult female grooming partners (Tinsley Johnson et al., in prep). Increased social isolation with age has been shown in a number of primates, including humans (Wenger et al. 1996; Nakamichi 2003; Farid et al. 2014). For female geladas, this change could reflect limited social time: older females have more offspring, and may spend most of their time grooming their infants and juveniles. If so, they may be able to compensate for this by relying more heavily on call exchanges as they age.

If call exchanges serve to maintain a female's primary social bonds, then call exchange frequency should be correlated with already-established features of social bond strength (as in Tinsley Johnson et al. 2014). More importantly, however, the vocal grooming hypothesis requires that call exchanges should also substitute for grooming when social time is constrained. Additionally, or alternatively, call exchanges may serve to maintain a much larger social network than females could through grooming alone, which, in turn facilitates cohesion among larger units (Aiello and Dunbar 1993; Dunbar 1996). If call exchanges allow females to maintain social cohesion beyond what is possible through grooming, females may reserve grooming for primary partners, but socialize with their extended social network using vocalizations. This could be a constant pattern across all contexts, or may only be evident in situations where females are time-constrained (i.e., in larger units, during the cold-rainy and/or hot-dry season, while pregnant or lactating, or as they age). Therefore, while season and reproductive state both represent instances where increased energetic demands potentially detract from social time, living in larger units (and potentially aging) results in more social relationships that must be maintained, and potentially less time to groom with each partner.

Here, we propose to investigate the function of call exchanges for female geladas. We first assess whether call exchange relationships overlap with grooming relationships, and then address the extent to which call exchanges substitute for grooming. Specifically, we will address two broad questions, using both call exchange rates and the number of call exchange partners to answer them:

Question 1: Do call exchange relationships overlap with grooming relationships?

1a. Who participates in call exchanges? First, we examine which females have the highest rates of call exchanges: Close kin? Females of similar rank? Age-mates? If call exchanges serve a similar role to grooming, then we expect to see the same relationship between call exchanges as we do for grooming; females should vocalize most with close kin and with females of similar dominance rank (Tinsley Johnson et al. 2014). We also build on our previous analysis of social bonds by considering whether age-mates are more likely to form primary or secondary bonds, and the extent to which they use call exchanges.

1b. Do call exchanges allow females to have more social ties than they do through grooming alone? Second, we compare the number of grooming relationships a female has with the number of call exchange partners. If call exchanges serve to maintain only primary social bonds, then the number of call exchange partners should mirror the number of close grooming partners. In contrast, if call exchanges allow females to extend their social network beyond just close grooming partners, then they should have more vocal ties than grooming ties.

Question 2: Do call exchanges substitute for grooming?

2a. When are calls used most frequently? Third, we examine whether calls are used more within or outside of the context of socializing (Dunbar 1984). If calls are used as a supplement for grooming, then a first requirement is that they occur more frequently outside of the context of socializing (i.e., while moving, feeding, and resting).

2b. How does the use of call exchanges vary according to restrictions in time budgets? Finally, we examine the extent to which variation in unit size, season, reproductive state, and age predicts the frequency of call exchanges and the number of individuals that interact via call exchanges. If call exchanges are used as a substitute for grooming when time is constrained, then they should occur more often (and between greater numbers of individuals) in larger units, during the cold-wet and hot-dry season and be used more frequently by pregnant and/or lactating females and older females.

METHODS

Study site and subjects

The data from this study derive from 6 years of fieldwork (2009-2014) from a population of wild geladas living in the Simien Mountains National Park, in northern Ethiopia (13°13.5' N latitude). The Simien Mountains Gelada Research Project (SMGRP, formerly the University of Michigan Gelada Research Project) has collected behavioral, demographic, genetic, and hormonal data from individuals since Jan 2006. All gelada subjects are habituated to human observers on foot and individually recognizable. Here, we used longitudinal data from 105 adult females from 24 reproductive units. All adult females had known or estimated birth dates from which we calculated age (mean age = 11.4 years; range = 4.3-27.0 years). Estimated birth dates were calculated based on known dates for other reproductive events (e.g., maturation, first birth, age of oldest offspring, or number of known offspring).

Behavioral data collection

We used 15-min focal animal samples (Altmann 1974) to record all social behaviors involving adult females, focusing on grunts (including the behavioral state – moving, feeding, resting, socializing – of the focal and identities of nearest neighbors and/or individuals that called within 15 seconds of the initial grunt), dominance interactions (i.e., visual threats, vocal threats, physical aggression, submission, and vocal submission), and grooming, for a total of 43052 h of focal observation (mean = 9.92 +/- 7.70 SD focal-hours per female per month). In addition, at 5-min intervals within each focal sample, we recorded the identity of the nearest intra-unit adult female and their distance (in meters) from the focal subject. Finally, because dominance interactions are relatively rare events (Dunbar and Bose 1991; Fashing et al. 2010), we supplemented focal data with additional *ad libitum* observations of dominance interactions, i.e., all approach-retreat interactions, both with and without aggression.

Weather data

Climatological data were collected at a central location in the geladas' home range and recorded on a near-daily basis. Daily cumulative precipitation (mm) was measured using a rain gauge. In our analyses, we summed rainfall over the 3-month period prior to each month. In a separate analysis on this study population, the best predictor of food availability (i.e., green grass blades) on any given day was the total precipitation over the previous 3-months (Jarvey et al. 2018). Daily maximum and minimum temperatures (°C) were measured using a digital thermometer placed in a permanently shaded area. Because temperature has more immediate physiological effects on thermoregulation than rainfall, we calculated the mean daily temperatures (for each day, the mean of the maximum and minimum temperature) for the one-month period preceding each month. For periods where we were missing more than 15 consecutive days of temperature data (missing data could be due to mechanical issues with the digital thermometer or when researchers were absent from camp), we calculated the mean maximum and/or minimum temperature for each day across the study period, and used these values to calculate the one-month mean.

Dominance ranks

We assigned dominance ranks to adult females within units using the Elo-rating system (Albers and de Vries 2001; Neumann et al. 2011); for detailed description, see (Tinsley Johnson et al. 2014). Elo-ratings were based on all dyadic dominance interactions between co-resident females during the study period. We set the initial Elo-rating for each female, i.e., the ranking each female gets when she “enters” the unit, at 1000. The number of points an individual gained or lost during an encounter (*k*) was set at 100 and weighted for each interaction by the expected probability of that individual winning or losing. Each female’s rank was calculated as her mean Elo-rating, i.e., rank, over the entire study period. Because the unit of analysis for this study is a female dyad, we subsequently calculated the absolute value of the difference in the Elo-ratings for the two females in the dyad (hereafter, *rank disparity*), which we then used in subsequent analyses.

Genetics and relatedness estimators

We collected fecal samples from all females (1-4 samples/female) and stored them in RNAlater for subsequent DNA extraction and genotyping (for methods of storage and extraction see (Snyder-Mackler et al. 2012). We genotyped samples using polymerase chain reactions (PCR) at 23 human derived MapPairs microsatellite loci (20 described in (Snyder-Mackler et al. 2012), three additional loci described in (Tinsley Johnson et al. 2014), which were found to be variable in this gelada population (average number of alleles/loci = 5.91). We successfully genotyped all individuals at the majority of all 23 loci (average percentage of loci typed per individual = 95%). Even with these genetic data, we could assign both maternity and paternity to both females in the dyad for only 10% (42/216) of the dyads because many of our subjects were born before the study began, and their parents were never sampled. Moreover, only 9% (39/416) of the dyads were known mother-daughter dyads. We therefore rely on pairwise estimates of relatedness for our analyses. Specifically, we used Wang's pairwise relatedness estimator (r_w: Wang 2002) because it provides the most accurate estimate of relatedness between individuals of known pedigree in our population (mean parent-offspring and full sibling r_w: 0.48 +/- 0.095 SD).

Dyadic sociality measures

For each focal female, we calculated yearly rates of grooming (minutes of grooming per focal hour) for all co-resident females (i.e., for all potential partners). For this calculation, we combined minutes of grooming given and received (and mutual grooming). We also counted the number of individual adult grooming partners a female interacted with for the year. Proximity rates were calculated by adding the number of point samples where the focal female was within 5 m of another co-resident female, controlling for total focal hours observed.

Call exchanges

We calculated five measures of call exchange frequency:

(1) *Dyadic call exchange frequency*: First, to test whether features of the dyadic relationship impacted call exchange frequency, we limited our analyses to instances where a non-focal individual called and the focal replied. We

considered a call to be a “reply” if it followed within 15 seconds of the initial vocalization. If more than two individuals called in a sequence, we only included the first two callers in our analyses (because it is less obvious who the third caller is responding to).

(2) *Yearly number of call exchange partners*: Second, to assess whether call exchanges allowed females to maintain more social ties than they did through grooming alone, we summed the total number of call exchange partners per female-year (here we considered both instances where a focal female called and a non-focal female replied and where a non-focal female called and a focal female replied).

(3) *Call frequency*: Third, to calculate the overall *call frequency* for each female-year, we summed the number of grunts produced by the focal according to their broad behavioral state at the time (i.e., feeding, resting, moving, socializing). Because our focus was primarily on whether grunts occurred outside of the context of grooming, we combined feeding, resting, and moving under the category “non-social”.

(4) *Individual call exchange frequency*: Fourth, to consider the effect of ecological, social, and individual factors on call exchange frequency, we summed the total number of call exchanges for each focal female for each month of observation.

(5) *Monthly number of call exchange partners*: Finally, to consider the effect of ecological, social, and individual factors on the number of call exchange partners a focal interacted with, we summed the total number of call exchange partners per female-month (considering together instances where a focal female called

and a non-focal female replied and where a non-focal female called and a focal female replied).

Data analysis

All analyses were conducted in R (version 3.3.2: R Core Team 2016) using the statistical package *lme4* (version 1.1-112: Bates et al. 2015). In models where the outcome variable was a rate (i.e., call exchange frequencies), we controlled for observation time by offsetting the outcome variable by either the focal-hours observed (for linear mixed-effects models, LMMs) or by the log of focal-hours observed (for negative binomial generalized linear mixed-effects models, GLMMs). In models where the outcome variable was not a rate, but was still likely dependent on the amount of time observed (i.e., number of call exchange partners), we controlled for observation time by including focal-hours as a fixed effect. Figures were constructed using *ggplot2* (Wickham 2011) and *sjPlot* (Lüdecke 2016).

Question 1: Do call exchange relationships overlap with grooming relationships?

1a. Who participates in call exchanges?

To test whether call exchange relationships overlap with grooming relationships, we first modeled the total call exchanges for each dyad-year (i.e., *dyadic call exchange frequency*; *N* = 2899 dyad-years) as the dependent variable in a negative binomial GLMM. We included the following predictors in the model: dyadic grooming rates, dyadic proximity rates, relatedness, dominance rank disparity, and age disparity. Both grooming and proximity are behaviors associated with close social bonds. Previous analyses (Tinsley Johnson et al. 2014) also indicated that individuals that form the closest social bonds share a similar dominance rank and are closely related. While this previous analysis did not consider age disparity, it did identify a category of “secondary” bonded partners that did not share a similar dominance rank, but were still closely related – dyads that could potentially represent paternal siblings, or members of the same age cohort. Therefore, we included age disparity in this analysis and also considered how grooming and proximity behaviors predicted age disparity in two separate models (details below). In the dyadic call exchange model, we controlled for the repeated measures of individual identity (of both the caller and the responder), unit, and year.

Previously, we established how both relatedness and rank disparity predicted dyadic grooming and proximity (Tinsley Johnson et al. 2014). Here, we wanted to add age disparity to this analysis to see if it helped explain any additional variation. We constructed two LMMs, based on the original models, which considered as outcome variables the frequency of (1) grooming and (2) proximity between dyads where each sociality measure was greater than zero. As such, the total number of dyads per model varied: grooming model (*N* = 1086 dyad-years), proximity model (*N* = 2487 dyad-years). In each model, we controlled for the repeated measures of individual identity (of both the caller and the responder), unit, and year. We started by re-constructing the top models for grooming (which included relatedness, rank disparity, and an interaction between the two) and proximity (which included only relatedness) based on our original analysis. To each model, we added age disparity as an additional predictor (including either the linear term or both the linear and the quadratic terms). We compared the fits of the original model with the two new models including age disparity using Akaike's Information Criterion (AIC) and report the results from the best model here.

1b. Do call exchanges allow females to maintain more social ties than they do through grooming alone?

We next modeled the yearly number of social ties a focal female had as a function of whether the tie was characterized by grooming or by call exchanges (i.e., the yearly number of grooming partners versus the *yearly number of dyadic call exchange partners*). We constructed a LMM that included the following predictors: the type of social tie (grooming or call exchange), unit size (i.e., the maximum number of females in a unit), and an interaction between tie type and unit size. Finally, we controlled for the repeated measures of individual identity, unit, and year.

Question 2: Do call exchanges substitute for grooming?

2a. When are calls used most often?

To examine the relationship between overall call frequency and behavioral state (whether calls were more likely during social or non-social behavioral states), we modeled the total calls for each female-year as a function of the behavioral state (social vs. non-social) of the focal at the time of the call. We constructed a negative binomial GLMM, controlling for the repeated measures of individual identity, unit, and year. Here, we controlled for observation time by offsetting the outcome variable by the log of the time observed in each state (social vs. not social), and limited our analysis to females that had at least 2 focal-hours of observation for the year.

2b. How does the use of call exchanges vary according to restrictions in time budgets? We considered the potential impact of restricted time budgets in two ways: (1) we counted the number of call exchanges a focal female participated in by month (i.e., *individual call exchange frequency*), and (2) we counted the number of call exchange partners a female interacted with each month (i.e., *monthly number of call exchange partners*). In each model, we included the following predictors, which represent potential time constraints due to ecological factors (i.e., seasonal variation in food availability), social factors (i.e., unit size), and individual factors (i.e., energetic requirements). Specifically, we considered the mean temperature over the previous 30 days, the cumulative rain over the previous 90 days (which is highly predictive of the availability of green grass), feeding time (i.e., the minutes spent feeding per focal hour), the maximum number of females in the unit that month (including the linear and the quadratic terms), the maximum number of males in the unit that month, the age of the female, and her reproductive state (cycling, pregnant, or lactating). Each model also controlled for the repeated measures of individual identity, unit, month, and year.

For the number of call exchanges, we first compared the number of “initiator” calls (i.e., where a focal called first) to the number of call responses, and found they were highly correlated (Pearson’s correlation coefficient = 0.76; *p*-value $< 2.2 \times 10^{-16}$). Therefore, we combined both types of calls to obtain the *total call exchanges* for each month. We modeled this number as the outcome variable in a negative binomial GLMM. For the number of call exchange partners, we constructed a GLMM with a Poisson distribution, where the outcome variable was the number of call exchange partners for each female for each month.

RESULTS

Question 1: Do call exchange relationships overlap with grooming relationships?

1a. Who participates in call exchanges?

Three specific features of the dyadic relationship predicted call response frequency: proximity rate, relatedness, and age disparity (Table 5.1). First, females that were often seen in close proximity to one another (within 5 m) were more likely to respond to each other's calls (proximity rate estimate = 0.52 +/- 0.03 SE; *p*-value $<2.0 \times 10^{-16}$; Fig. 5.1a). In contrast, grooming time did not significantly predict call exchange frequencies (grooming rate estimate = -0.02 +/- 0.02 SE; *p*-value = 0.50; Fig. 5.1b). Second, females that were closely related were more likely to reply to one another's calls than were unrelated females (relatedness estimate = 0.05 +/- 0.02 SE; *p*-value = 0.04; Fig. 5.1c). However, rank disparity did not significantly predict the frequency of call exchanges (rank disparity estimate = 0.02 +/- 0.02 SE; *p*-value = 0.33; Fig. 5.1d). Finally, females that were close in age were more likely to respond to each other's calls than females of disparate ages (age disparity estimate = -0.17 +/- 0.03 SE; *p*-value = 6.17×10^{-11}; Fig. 5.2a). Therefore, while females do use call exchanges with a select group of social partners, it appears that call exchange partners do not completely overlap with the strongest, primary grooming partners (who are both close in rank and closely related).

Age disparity significantly predicted both grooming rates and the number of observations in close proximity (Table 5.1). However, the relationships were in opposite directions (Table 5.1): females that spent the most time grooming were further apart in age than females that spent less time grooming (grooming estimate = 49.20 +/- 15.03 SE; *p*-value = 1.13×10^{-3}; Fig. 5.2b), and females that had intermediate age gaps spent the most time grooming of all (grooming^2 estimate = -42.82 +/- 14.80 SE; *p*-value = 3.95×10^{-3}; Fig. 5.2b). In contrast, females that were frequently observed to be in proximity to one another were closer in age than females that were not observed in proximity often (proximity estimate = -20.58 +/- 9.45 SE; *p*-value = 2.95×10^{-2}; Fig. 5.2c). These results support the hypothesis that primary social partners (that spend the most time grooming) are mother-daughter dyads and that secondary social partners (that are often in proximity) are members of the same age cohort, and likely paternal half-siblings.

Taken together, these results suggest that females maintain at least two distinct kinds of social relationships: one with close relatives that share a similar dominance rank but are not close in age, which is primarily characterized by grooming and proximity, and another with close relatives that do not share a similar dominance rank but are close in age, which is primarily characterized by proximity and call exchanges, and occasional grooming.

1b. Do call exchanges allow females to have more social ties than they do through grooming alone?

Females had more social ties through call exchanges than they did through grooming (call exchange estimate = 1.14 +/- 0.08 SE, *p*-value < 2.0×10^{-16}; Fig. 5.3; Table 5.1) and this was even more evident in larger units (call exchange x maximum females estimate = 29.26 +/- 2.53 SE, *p*-value < 2.0×10^{-16}; Fig. 5.3). In contrast, the number of grooming ties a female had showed a significant inverse U-shaped relationship with unit size (grooming x maximum females^2 estimate = -8.04 +/- 2.53 SE, *p*-value = 1.49×10^{-3}; Fig. 5.3), indicating that the number of grooming ties a female had did not increase linearly with unit size (and corresponding with previous analyses reported in Chapter 4).

Together, these results suggest that, like grooming and other prosocial behaviors, female geladas do use call exchanges selectively. However, they may use call exchanges with more than just their primary grooming partners. Instead, call exchanges may reflect an individual’s extended social network, including weak ties between individuals that do not frequently groom together (such as peers close in age).

Question 2: Do call exchanges substitute for grooming?

2a. When are calls used most frequently?

Call rates were significantly more common during non-social than social behavioral settings (Table 5.2). Calls occurred more than six times as often when females were not grooming compared to when they were grooming (non-social state: estimate = 0.13 +/- 0.05 SE, z-value = 2.70, *p*-value = 7.04×10^{-3}; Fig. 5.4). Because these calls are used most often when individuals are not socializing, they have the potential to substitute for grooming.

2b. How does the use of call exchanges vary according to restrictions in time budgets?
Call exchange rates varied significantly across months according to both ecological conditions and individual energetic needs (Table 5.2). First, call exchange rates were highest during the times when females spent the most time feeding (estimate = 0.20 +/- 0.02 SE, z-value = 10.49, *p*-value $<2.0 \times 10^{-16}$; Fig. 5.5a). Mean temperature (estimate = 0.13 +/- 0.06 SE, z-value = 2.36, *p*-value = 1.47×10^{-2}; Fig. 5.5b) and cumulative rainfall (estimate = 0.19 +/- 0.06 SE, z-value = 3.18, *p*-value = 1.47×10^{-3}; Fig. 5.5c) were also positive predictors of call exchange rates. Second, female age and reproductive state predicted how frequently females called (Table 5.2). Older females called more often than younger females (estimate = 0.05 +/- 0.02 SE, z-value = 2.64, *p*-value = 8.21×10^{-3}; Fig. 5.5d), and pregnant females called more often than cycling females (estimate = 0.20 +/- 0.05 SE, z-value = 3.96, *p*-value = 7.45×10^{-5}; Fig. 5.5e) and lactating females (estimate = 0.18 +/- 0.05 SE, z-value = 3.92, *p*-value = 8.71×10^{-5}).

The number of individuals that interacted via call exchanges also varied according to ecological conditions and individual energetic needs (Table 5.2). First, females had more call exchange partners in months that they spent more time feeding (estimate = 0.08 +/- 0.01 SE, z-value = 6.07, *p*-value = 1.27×10^{-9}; Fig. 5.6a), and in months with high cumulative rain (estimate = 0.22 +/- 0.04 SE, z-value = 5.26, *p*-value = 1.42×10^{-7}; Fig. 5.6b). Age did not significantly predict the number of call exchange partners, but reproductive state did: pregnant females had more call exchange partners than cycling females (estimate = 0.07 +/- 0.03 SE, z-value = 2.08, *p*-value = 3.74 x 10^{-2}; Fig. 5.6c). However, the distinction between pregnant and lactating females was not significant (estimate = 0.05 +/- 0.03 SE, z-value = 1.69, *p*-value = 9.18 x 10^{-2}). Social factors also affected the number of call exchange partners: both the number of females in a unit and the number of males significantly predicted the number of call exchange partners (Table 5.2). Females in larger units with more adult females (estimate = 8.97 +/- 2.04 SE, z-value = 4.41, *p*-value = 1.06 x 10^{-5}; Fig. 5.6d) and with more males (estimate = 0.04 +/- 0.01 SE, z-value = 3.29, *p*-value = 1.08 x 10^{-3}; Fig. 5.6e) had more call exchange partners than females in smaller units. Finally, the relationship between call exchange partners and the number of females in a unit displayed a significant quadratic relationship, suggesting that the number of call exchange partners begins to taper off in larger units and does not continue to increase linearly (estimate = -7.06 +/- 1.18 SE, z-value = -5.99, *p*-value = 2.07 x 10^{-9}; Table 5.2).

Together, these results suggest that call exchanges can substitute for grooming. First, females used this type of vocalization more often when they were not already grooming. Second, both the rates of call exchanges and the number of call exchange partners varied in line with predictions: females used call exchanges most frequently when they might be time-constrained due to both ecological reasons (i.e., during the cold-rainy season and the hot-dry season, and during months when foraging rates were higher) and individual reasons (i.e., when pregnant and with age). Females also had more call exchange partners due to ecological factors (i.e., during the cold-rainy season and during months when foraging rates were higher), individual reasons (i.e., when pregnant), and social factors (i.e., in larger units).

DISCUSSION

Our results provide support for the vocal grooming hypothesis and for the role of call exchanges in social bonding (Aiello and Dunbar 1993; Dunbar 1996), albeit in a slightly different way than the original Vocal Grooming Hypothesis may have intended. Call exchanges are used preferentially with preferred social partners, and occur most frequently outside of the context of grooming. Moreover, the frequency of call exchanges and the number of individuals that use them varies month-to-month, tracking changing in time budgets and energetic requirements, suggesting that call exchanges can supplement grooming when time budgets are constrained.

Including call exchanges in analyses of social relationships also reveals a greater range in the types of social relationships female primates have than we typically see through grooming alone. Specifically, we identify two types of social relationships: primary social partners, that are typically mother-daughter pairs and frequently groom together, and secondary social partners, that are age peers (potentially paternal half-siblings) that preferentially interact via proximity, call exchanges, and occasional grooming. Several recent studies have suggested that these types of secondary social relationships are important for individual fitness (Sueur and Maire 2014; Brent 2015; Cheney et al. 2016), but less is known about who forms these kinds of relationships and how they are maintained. Now that we have begun to identify the characteristics of secondary social partners, we can begin to ask whether they provide fitness benefits.

Maintaining relationships with secondary social partners may be particularly important for female geladas, as we know that mid-sized groups are optimal for female fitness, yet are larger than the number of primary social partners a female typically has through grooming. As unit cohesion is a direct result of the number of social ties between individuals (Sueur et al. 2010; Sueur et al. 2011; Sueur and Maire 2014), other behavioral mechanisms, such as call exchanges, may allow unit females to maintain social ties even though they are limited in their grooming relationships. Here, we show that over the course of a year females have more call exchange partners than grooming partners, and the number of call exchange partners increases linearly with unit size, which is not the case for grooming partners (which reach an upper limit between, on average, 2-3 grooming partners).

Including call exchanges in analyses of unit cohesion could increase our ability to predict when and why fissions occur. Previous work focusing on grooming and aggressive interactions found that rates of interactions among group-mates remained the same leading up to a fission, but the identities of individuals that interacted changed (i.e., females focused their grooming on fewer close partners: Larson et al. 2017). If vocal exchanges are key to maintaining unit cohesion in mid-sized units, then changes in vocal exchange behavior may also precede unit fissions, and could also allow us to predict the outcomes of fissions (i.e., identifying which females remain together).

Our results also suggest that variation in social behavior with age may represent shifting priorities instead of reduced overall investment. We know from previous work that older females spend less time grooming with other adult females and have fewer adult grooming partners (Tinsley Johnson et al., in prep). However, older females engage in more frequent call exchanges than younger females, suggesting they may be compensating for reduced grooming time. The use of call exchanges with age peers is also intriguing, and considering when and how these types of relationships are established, and how they change with age, would reveal more about why female geladas invest time and energy into relationships with age peers.

Although female mammals are thought to face their highest energetic demands during early- to mid-lactation (Rosetta et al. 2011), here we found that lactating females did not use call exchanges more often or with more individuals, while pregnant females did. However, pregnant females also face higher energetic demands, so this finding is still in line with the vocal grooming hypothesis. One reason why lactation may not have been significant in this study is because female geladas can nurse their offspring for up to two years (Roberts et al. 2017), and it is currently not clear how much energetic investment they truly contribute toward the end of this period. Therefore, a more specific look at changes in social behavior throughout the period of lactation may pick up on additional variation.

Another avenue of future inquiry should address whether any differences exist between individuals who initiate call exchanges versus those that reply. Here, we found that the rates of initiations and replies were correlated, however there is still room for some variation (i.e., regarding dominance rank, etc.). Moreover, here we only considered dyadic call exchanges, but geladas are also known for long sequences of call exchanges that involve multiple unit members. To what extent are these sequences similar to or different from dyadic call exchanges?

The vocal grooming hypothesis (Aiello and Dunbar 1993; Dunbar 1996) proposes one way that human language could have evolved, and places non-human primate vocalizations and language on a continuum based on their shared social function. If our earliest ancestors evolved the ability for language in response to increasing social challenges, then we would expect to see a greater reliance on vocal contact in primate species faced with similar social demands. Call exchanges represent a potential mechanism by which individuals can maintain social relationships without investing significant time and energy – a supplement for when grooming is not possible. Using the comparative method to investigate the function of vocal contact in the highly social gelada is one way to address long-standing questions on how and why our unique ability for language evolved. Specifically, these results suggest that, at some point during the course of human evolution, vocal grooming may have emerged as an important early adaptation that allowed our ancestors to maintain the social cohesion of increasingly large and complicated social groups.

TABLES

Table 5.1. Effects (ß +/- standard error) of predictors in models addressing Question 1: Do call exchange relationships overlap with grooming relationships?

	Estimate	SE	z-value	*p*-value
Who participates in call exchanges?				
Grooming rate	-0.01515	0.02222	-0.682	0.4953
Proximity rate	0.52097	0.02715	19.188	*** $< 2.00 \times 10^{-16}$
Relatedness	0.04911	0.02431	2.020	* 0.0434
Rank disparity	0.02331	0.02393	0.974	0.3300
Age disparity	-0.16522	0.02526	-6.539	*** 6.17×10^{-11}
Does age disparity predict grooming?				
Relatedness	3.8933	0.4712	8.263	*** 6.66×10^{-16}
Rank disparity	-3.6935	0.5024	-7.351	*** 4.99×10^{-13}
Relatedness x rank disparity	-0.8020	0.4815	-2.892	. 0.096154
Age disparity	49.1966	15.0308	3.273	** 0.001131
Age disparity^2	-42.8151	14.8033	-2.892	** 0.003954
Does age disparity predict proximity?				
Relatedness	2.0192	0.1874	10.777	*** $< 2.0 \times 10^{-16}$
Age disparity	-20.5818	9.4473	-2.179	* 0.0295
Age disparity^2	-6.1013	8.8162	-0.692	0.4890
Do call exchanges allow females to have more social ties than they do through grooming alone?				
Relationship type: grooming	-1.14474	0.07745	-14.781	*** $< 2.00 \times 10^{-16}$
Maximum females	20.93522	2.57099	8.143	*** 3.47×10^{-12}
Maximum females^2	0.11280	2.09629	0.054	0.95711
Maximum females x grooming	-29.26421	2.52618	-11.584	*** $< 2.00 \times 10^{-16}$
Maximum females^2 x grooming	-8.04444	2.52618	-3.184	** 0.00149

Table 5.2. Effects (ß +/- standard error) of predictors in models addressing *Question 2*: Do call exchanges substitute for grooming?

	Estimate	SE	z-value	*p*-value
When is this call type used most frequently?				
State (Not social)	0.13499	0.05009	2.695	0.00704
How do call exchange rates vary according to restrictions in time budgets?				
Feeding rate	0.19684	0.01876	10.493	*** $< 2.00 \times 10^{-16}$
Mean temperature	0.13072	0.05533	2.363	* 0.01814
Cumulative rain	0.19358	0.06087	3.181	** 0.00147
Maximum females	2.77444	2.68938	1.032	0.30225
Maximum females^2	-1.92214	1.70273	-1.129	0.25896
Maximum males	0.02257	0.01978	1.142	0.25364
Age	0.05188	0.01963	2.643	** 0.00821
Reproductive state: lactating	0.01577	0.04221	0.374	0.70870
Reproductive state: pregnant	0.19642	0.04958	3.961	*** 7.45×10^{-05}
How does the number of call exchange partners vary according to restrictions in time budgets?				
Feeding rate	0.204247	0.008138	6.072	*** 1.27×10^{-09}
Mean temperature	0.029438	0.041708	0.706	0.48031
Cumulative rain	0.217984	0.041424	5.262	*** 1.42×10^{-07}
Maximum females	8.972134	2.010841	4.462	*** 8.12×10^{-06}
Maximum females^2	-7.067536	1.170226	-6.039	*** 1.55×10^{-09}
Maximum males	0.041136	0.012586	3.268	** 0.00108
Age	0.008879	0.013797	0.644	0.51987
Reproductive state: lactating	0.016462	0.028164	0.585	. 0.55887
Reproductive state: pregnant	0.068528	0.032937	2.081	* 0.03747

FIGURES

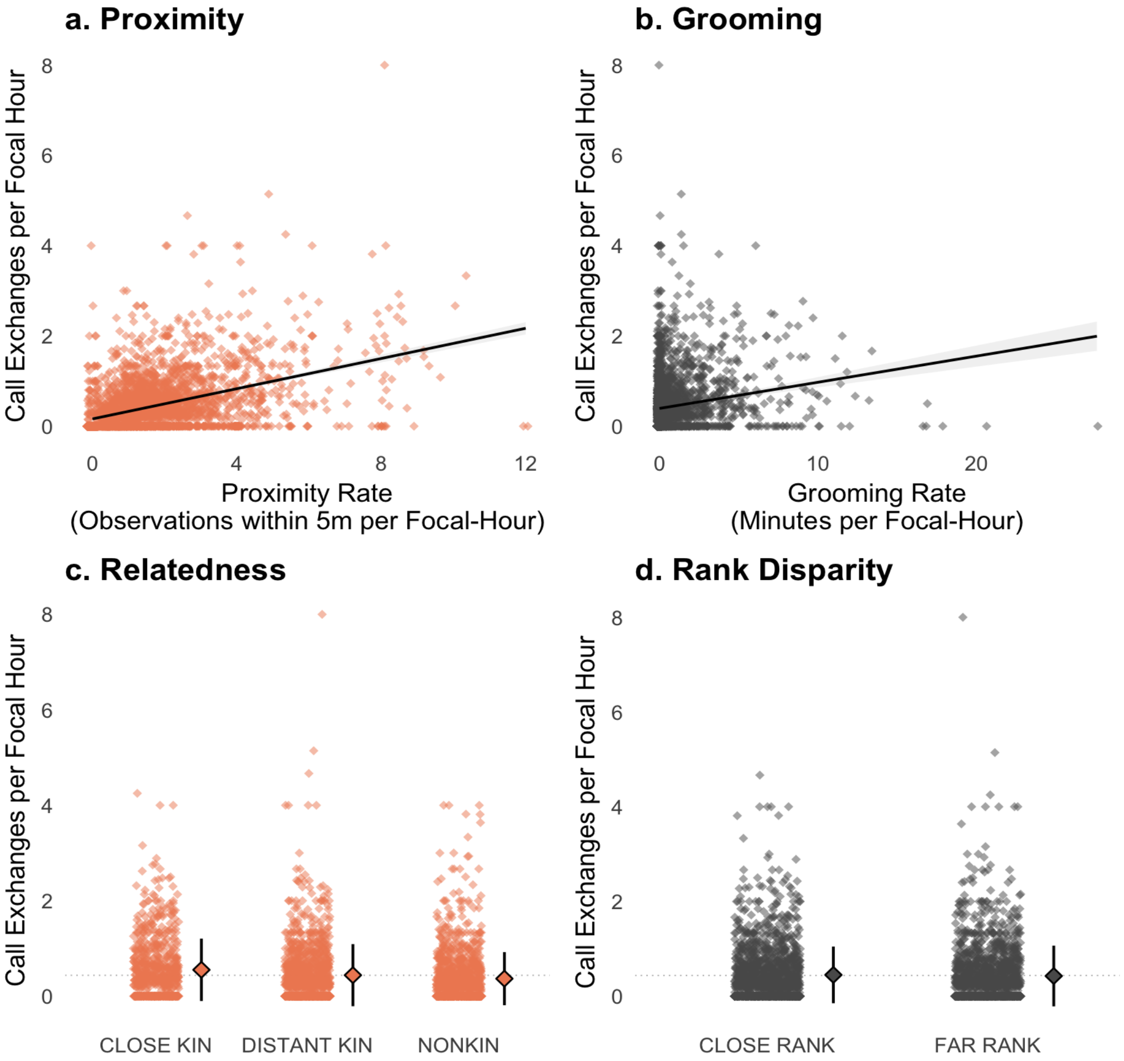
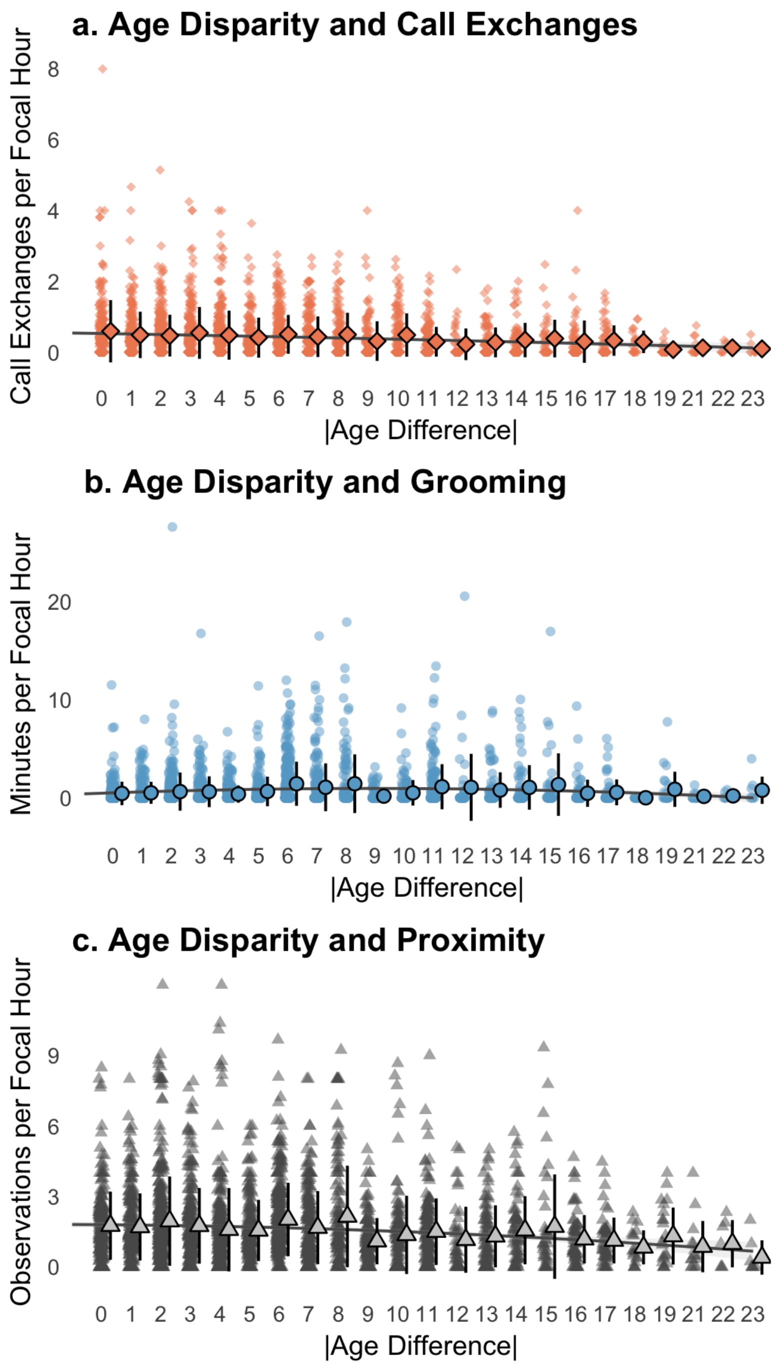


Figure 5.1. Call exchange rates (number of calls per focal hour: y-axes) for each dyad-year by: **(a)** dyadic proximity rates (number of nearest neighbor point samples where the dyad was within 5 meters of one another per focal hour); dyads with higher call exchange rates are in proximity to one another more frequently than dyads with lower exchange rates; **(b)** dyadic grooming rates (minutes per focal hour); grooming rate did not predict call exchange rates; **(c)** dyadic relatedness (categories based on Wang's relatedness estimate (*r*); continuous values were used in all models): close kin: $r >= 0.4$; distant kin: $0.2 <= r < 0.4$; non-kin: $r < 0.2$; close kin exchanged more calls than distant or non-kin; **(d)** dyadic rank disparity (categories based on the absolute value of the difference between individual Elo scores; continuous values were used in all models and categories here reflect the lower 50th percentile and the upper 50th percentile); rank disparity did not predict call exchange frequency. For **(c)** and **(d)** larger points with error bars indicate the mean +/- the standard deviation for each category; dotted grey horizontal lines indicate the overall mean call exchange rates (mean = 0.44).



a. Age Disparity and Call Exchanges

b. Age Disparity and Grooming

c. Age Disparity and Proximity

Figure 5.2. Age disparity (absolute value of age difference, x-axes) and: **(a)** call exchange rates (number of calls per focal hour): dyads close in age exchanged more calls than did dyads of disparate ages; **(b)** grooming rates (minutes of grooming per focal hour): dyads that spent more time grooming were further apart in age than dyads that did not groom; **(c)** proximity rates (the number of nearest neighbor point samples where the dyad was within 5 meters of one another per focal hour): dyads that were more often seen in proximity to one another were closer in age than dyads that were rarely seen in proximity.

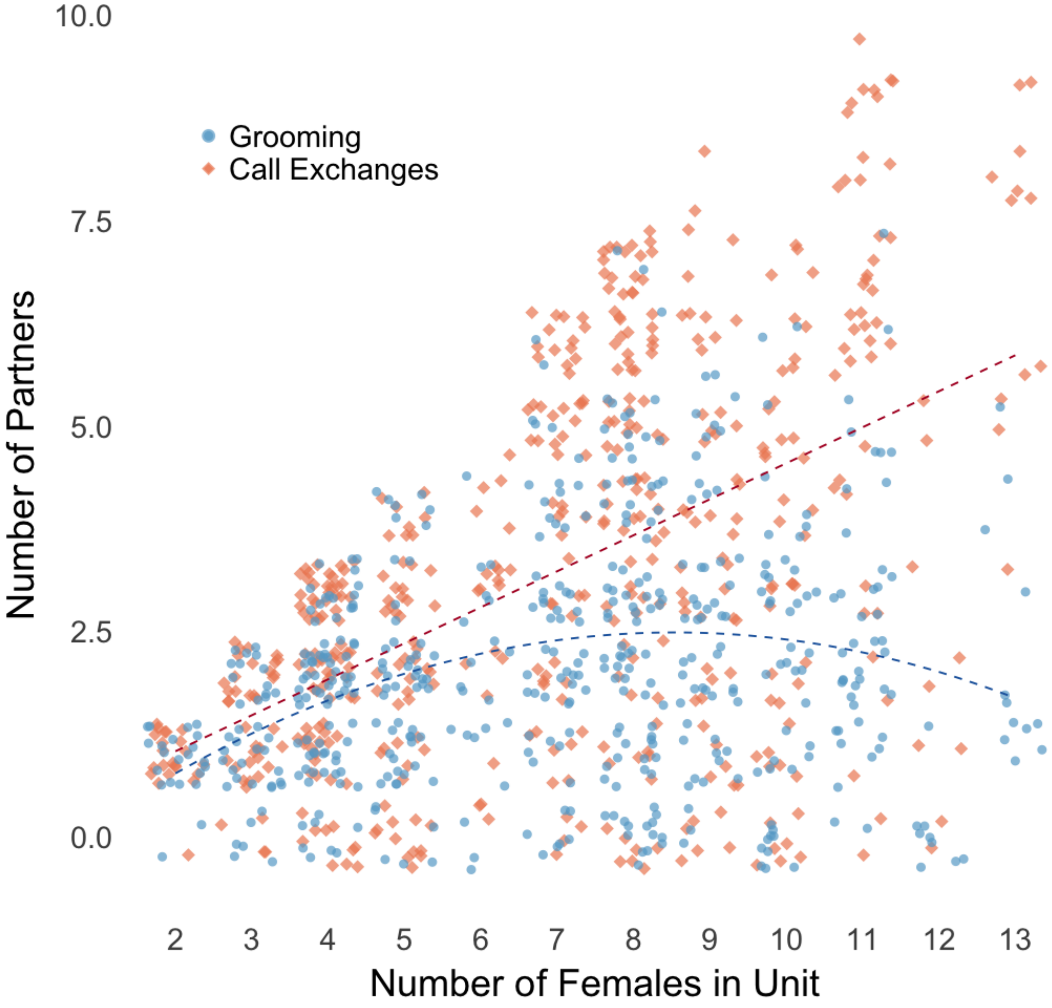


Figure 5.3. The effect of unit size (y-axis) on the number of social partners (x-axis) differed for call exchange partners (orange diamonds) compared to grooming partners (blue circles). Dotted lines = regression lines.

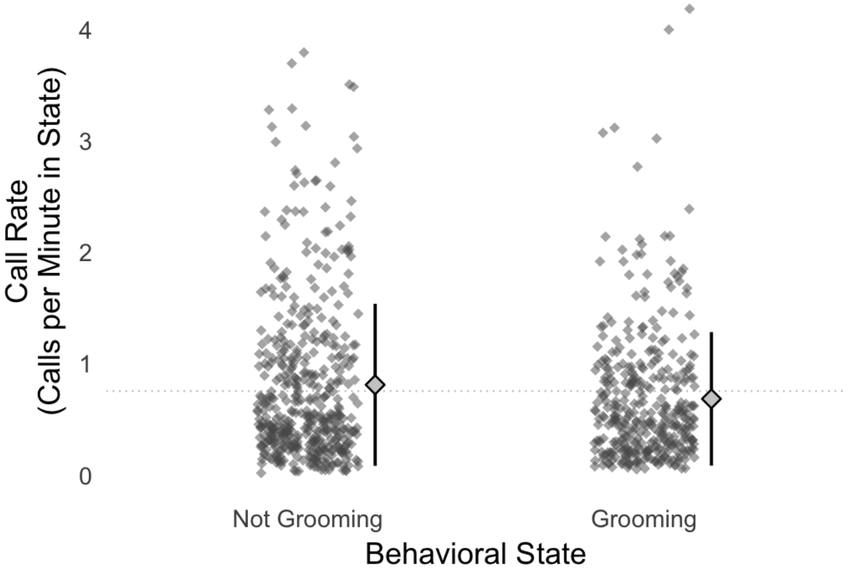


Figure 5.4. Females vocalized more when they were not grooming than they did when grooming. Smaller points indicate overall call rates for each female-year (number of calls per minute spent either grooming or not grooming). Larger light grey points with error bars indicate the mean +/- the standard deviation for each category. Dotted grey horizontal line indicates the overall mean call rate (mean = 0.754).

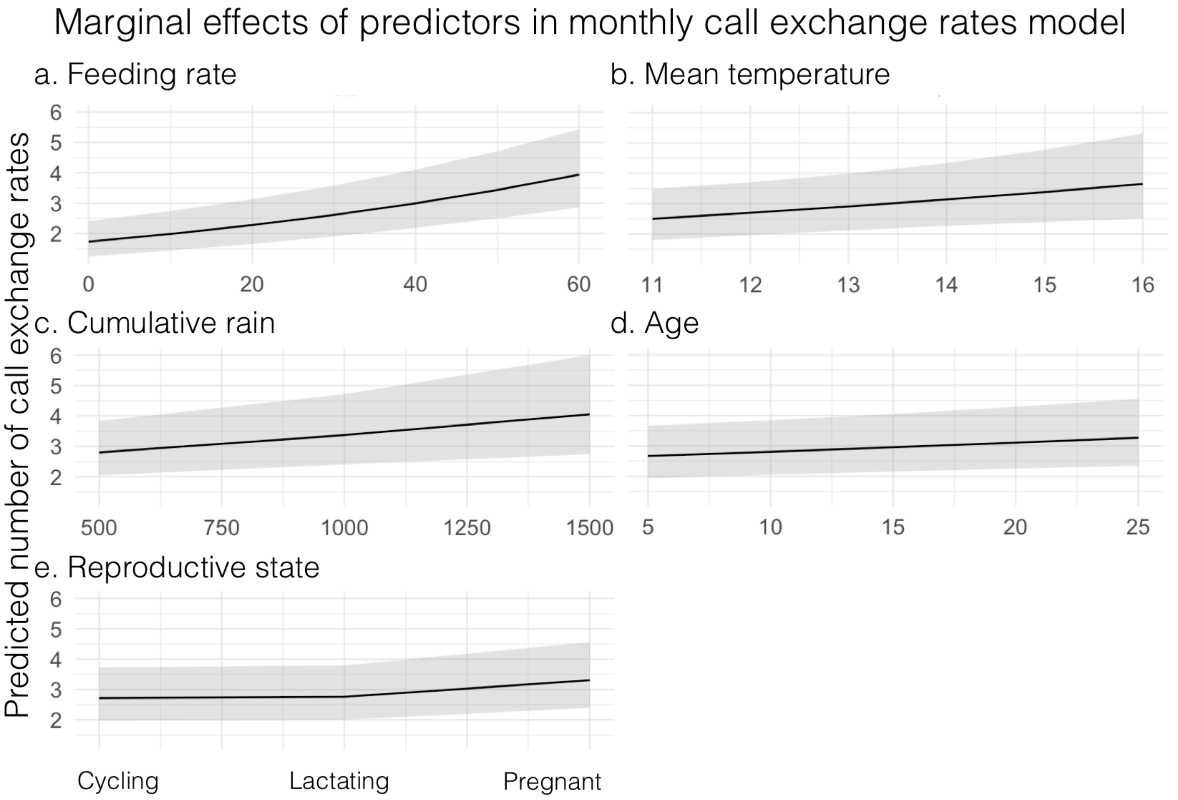


Figure 5.5. Marginal effects plots of significant predictors in the call exchange rates model, showing the predicted change in the monthly number of call exchanges for each unit increase in the fixed effect; shaded regions indicated the confidence intervals. Fixed effects shown: **(a)** feeding rate; **(b)** mean temperature; **(c)** cumulative rain; **(d)** female age; **(e)** reproductive state (note this is a categorical variable). Call exchange rates increased with feeding rates, temperature, rain and age, and were higher for pregnant females than lactating and cycling females.

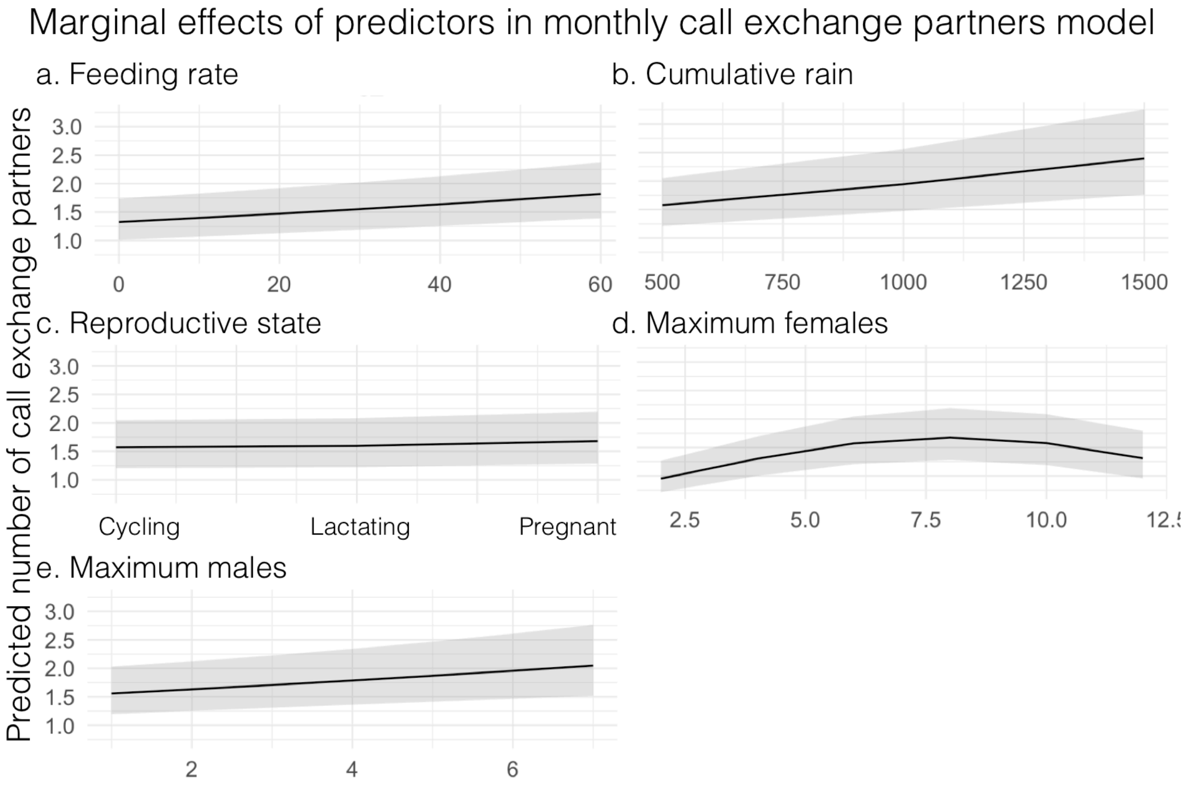


Figure 5.6. Marginal effects plots of significant predictors in the call exchange partners model, showing the predicted change in the monthly number of call exchange partners for each unit increase in the fixed effect; shaded regions indicated the confidence intervals. Fixed effects shown: **(a)** feeding rate; **(b)** cumulative rain; **(c)** reproductive state (note this is a categorical variable); **(d)** maximum females; **(e)** maximum males. Number of call exchange partners increased with feeding rates, rain, number of females, and number of males, and were higher for pregnant females than cycling females.

CHAPTER 6

CONCLUSION

This dissertation has been framed as a test of the vocal grooming hypothesis, a very specific idea positing that human language evolved as a social tool, enabling us to maintain social relationships in spite of increasing ecological and social challenges (Aiello and Dunbar 1993; Dunbar 1996). Addressing this hypothesis required taking a much broader view of the lives of female geladas. Indeed, a thorough test of the vocal grooming hypothesis must establish that: (1) female geladas face specific ecological and social challenges, (2) that these challenges impact individual fitness and time budgets, and (3) that call exchanges are used in response to these challenges. To address these criteria, I combined longitudinal demographic, behavioral, and hormonal analyses in the first test of the vocal grooming hypothesis in a wild primate.

RESEARCH QUESTIONS

Question 1: Do female geladas have preferred social partners?

The main premise of the vocal grooming hypothesis is that vocalizations help maintain social bonds, much in the way grooming does across a number of primate species (e.g., Seyfarth 1980; Henzi and Barrett 1999; Silk et al. 2010a). To be able to test this, we must first identify whether female geladas have preferred social partners, and if so, who forms these kinds of close social bonds. In primates, when we talk about social bonds we refer to social partners that display specific characteristics: individuals are often close relatives, close in dominance rank, and can sometimes be age-mates (Altmann 1979; Smith et al. 2003; J.B. Silk et al. 2006a; Silk et al. 2006b). We recognize these special kinds of relationships because bonded individuals also engage in specific kinds of social behaviors, like social grooming, often at much higher rates than the group mean (Silk et al. 2003). Grooming is a salient social behavior because many primates spend a considerable amount of time grooming one another; indeed, grooming requires a significant investment of time and energy into a social partner. Within the last twenty years, researchers have begun to understand why that is: primates invest in social bonds because social bonds provide fitness benefits, from increased longevity to higher reproductive success (Silk et al. 2003; Schülke et al. 2010; Silk et al. 2010b; Gilby et al. 2013).

In **Chapter 2**, we used longitudinal data on social behavior and genetic sampling to characterize the close social relationships of female geladas. We established that, like many female cercopithecines, female geladas form strong social bonds with other females that are close kin and also share a similar dominance rank. These “primary social partners” spend the most time grooming one another, and are more often seen in proximity to one another than individuals who never groom. In this analysis, we also identified another kind of social relationship, “secondary social partners”: partners that are frequently seen in close spatial proximity to one another, and show intermediate levels of grooming -- less than primary social partners, but significantly more than individuals who never groom. Secondary social partners are also close relatives, but are not close in dominance rank.

Female geladas form strict linear maternally-inherited dominance hierarchies (le Roux et al. 2011). Therefore, females that are close kin and also close in rank are likely maternal relatives -- most likely mother-daughter dyads. In contrast, close kin that are not close in rank may be paternal siblings. In gelada society, leader males monopolize the reproduction within units during their tenure (mean tenure length is around 2 years, (Snyder-Mackler et al. 2012). Therefore, age-mates are likely paternal half-siblings. In other female-bonded primate species, such as baboons, females also socialize with their age peers/paternal half-siblings, more often than would be expected by chance (Altmann 1979; Alberts 1999; Smith et al. 2003). When close maternal kin are not available, females may even form their closest social bonds with paternal kin instead (Silk et al. 2006a; Silk et al. 2006b). Therefore, it is likely that these secondary social partners play an important role in the social lives of female geladas. We return to this possibility in **Chapter 5**.

Question 2: How do ecological and social factors impact female reproductive performance?

The second main premise of the vocal grooming hypothesis is that vocalizations are a more efficient means of socializing than grooming. For humans, the suggestion is that as our lives became larger and more complicated, we increasingly relied on vocalizations to help manage our social relationships. If so, then we would expect to see other primates rely more on vocalizations under challenging conditions. Primate lives can be challenging for a number of reasons, both due to the ecological environment in which they live and their social environment. In **Chapter 3** and **Chapter 4** we focused on how each of these factors represent challenges for female geladas to predict when and how calls might be used.

In **Chapter 3** we combined longitudinal climatological data with behavioral, demographic, and hormonal sampling to characterize how the highly seasonal environment in which geladas live shapes their reproduction and stress physiology. We found that females are cold-stressed, meaning they show the highest levels of fecal glucocorticoid metabolites during the cold-rainy season (Jun-Sep), when maximum temperatures are low and precipitation is high. We identified two separate birth peaks (the “ecological” peak, Aug-Oct and the “social” peak, Dec-Feb), the first of which corresponded with conceptions that would have occurred during optimal high temperatures (during the hot-dry season Feb-May, when we also see the lowest glucocorticoid levels). The second birth peak occurred later in the year, and appears to be the result of disruptive male takeovers “resetting” female reproductive trajectories. These takeovers peak around March every year, and females that experience a takeover at this time show delayed reproduction in comparison to females that do not -- likely due to male-mediated effects on female reproduction, such as the Bruce effect and infanticide (Beehner and Bergman 2008; Roberts et al. 2012). For the vocal grooming hypothesis, these results suggest that the cold-rainy season may be particularly energetically challenging for female geladas, even though this period overlaps with peak food availability. Our results also demonstrate that male takeovers are critical social challenges that impact female reproduction, which we build on in **Chapter 4**.

For geladas, the social environment represents just as many challenges as the ecological one. In addition to living in a complex multi-level society, geladas experience a range of variation within their smaller groups, or reproductive units. Unit size is one characteristic that is particularly relevant for the vocal grooming hypothesis, as maintaining larger units may require more efficient means of socializing. Units range in size (from 1-13 adult females), and in **Chapter 4** we ask if there is an optimal size for female fitness within this range of variation.

Our results demonstrate that mid-sized units (between 5-7 adult females) are optimal for female fitness, for several ecological and social reasons. First, females in mid-sized units have higher reproductive performance, which can be attributed to reduced infant mortality. The main cause of infant mortality in this population is infanticide following male takeovers -- again demonstrating the significant impact these events have on female fitness. Females in larger and smaller units also spend more time feeding than females in mid-sized units. However, despite having more social relationships to maintain, females in larger units do not spend more time socializing or increase the number of grooming partners they have in proportion to the size of their unit. As a result, larger units are less socially cohesive, which in turn makes them more likely to fission.

Mid-sized units still present a social challenge for females: how do these units remain socially cohesive, despite being much larger than the number of primary social partners (1-2) a female typically has? One potential solution is to use calls to maintain social ties, which we address in **Chapter 5**.

Question 3: What is the function of the gelada contact call?

The preceding chapters set the stage for when we might expect to see geladas using calls in the place of grooming. In **Chapter 5** we show that geladas preferentially respond to the contact calls (via call exchanges) of their close relatives and age-mates. Call exchanges may include primary grooming partners, but specifically characterize secondary social partners -- those individuals that occasionally groom and are often in close proximity to one another. Moreover, the way geladas use call exchanges varies according to ecological, social, and individual situations. Specifically, we see higher rates of call exchanges and more call exchange partners during months when females spend more time feeding, especially during the cold-rainy season. Individuals have more call exchange partners in larger groups, and interact with more partners via call exchanges than they do via grooming. We found some evidence that energetically costly periods of female reproduction (specifically, pregnancy, but not lactation) result in both higher frequencies of call exchanges and more call exchange partners. Finally, as females age we see a shift in how they socialize with other adults: older females spend less time grooming with other adults and have fewer adult grooming partners, but use call exchanges more frequently than younger females.

CONCLUDING REMARKS AND FUTURE DIRECTIONS

This dissertation aimed to provide a first comprehensive test of the vocal grooming hypothesis in a wild primate. In doing so, several recurring themes and new questions emerge. First, secondary social relationships appear to play an important role in the social lives of female geladas, but the function of these relationships remains unclear. The importance of the extended social network in primate lives has only recently garnered attention, thanks in part to the use of social network metrics that highlight the ways that weak or indirect connections structure individual social lives (Granovetter 1977; Maryanski 1987; Sueur et al. 2011; Brent 2015; Cheney et al. 2016). To what extent do both primary and secondary social bonds provide fitness benefits for female geladas? One possibility is that primary social bonds provide coalitionary support during foraging competition, while secondary social bonds provide a stable and cohesive social environment. Future work considering the ways social relationships mediate intra-unit conflict and unit stability can help address these questions.

Second, taking a social networks approach to the study of unit cohesion and fissions can help us predict when and why fissions occur. Our results suggest that call exchanges may contribute to social cohesion, which also suggests changes in the vocal behavior of females may predict fissions better than, or in addition to, changes in grooming behavior. Taking this approach will also help us tease apart which of the many costs of group-living (both ecological and social) ultimately trigger a fission -- to what extent does infanticide risk outweigh feeding competition? In addition, to what extent does the pre-fission social network predict the outcome (i.e., which individuals remain together in daughter units)? Do primary or secondary partners tend to remain together?

Third, the impact of male takeovers on female reproductive trajectories, fitness, and social behavior was an important theme. While the focus here was on female-female social relationships, one potential expansion of the vocal grooming hypothesis would be to consider how call exchanges mediate female-male relationships, and the extent to which variation in these relationships predicts the odds of takeovers.

Fourth, our seasonality analysis took a population-level approach to identifying broad patterns in our population. However, and individual-level analysis is required in order to answer a number of remaining questions. For example, how do individual stress hormone levels predict the probability of conceptions? Why do so many females give birth outside of the ecological birth peak? One possibility is that some females (e.g., primiparous females, low-ranking females) may be more constrained to ecological patterns of seasonality than others. A long-standing question for female geladas is why they maintain strict dominance hierarchies, when they presumably do not need to compete over a widely-available and dispersed food resource, grass (Jarvey et al. 2018). However, there is one time of year when geladas rely on very different food resources: in the dry season, underground tubers are time-consumed, valued and monopolizable food resources (Jarvey et al. 2018). Therefore, taking a seasonal approach to the importance of female dominance may help explain not only why we see a dominance hierarchy, but also why some females give birth year-round. Another question raised by the seasonality analysis relates to the costs associated with giving birth out-of-season: if infants are not more likely to die, are there other, more subtle costs to giving birth at different times of year (i.e., interbirth intervals, maternal or offspring condition).

Finally, a number of questions remain regarding the vocal grooming hypothesis, and more broadly relating to the role that vocalizations play in mediating primate social lives. Most notably, do females that use call exchanges experience fitness benefits? How does the use of these call exchanges compare to the longer call sequences that are so characteristic of geladas? Here we show that call exchanges have the potential to substitute for grooming; additional behavioral and acoustic analyses can verify the extent to which vocalizations substitute for grooming.

Together, this analysis of the vocal grooming hypothesis provides insight into how vocalizations could have taken on increasing importance in our own evolutionary history, eventually leading to the multi-faceted tool of language we use today. Specifically, these results suggest that, at some point during the course of human evolution, vocal grooming may have emerged as an important early adaptation that allowed our ancestors to maintain the social cohesion of increasingly large and complicated social groups. It also, more broadly, speaks to the evolution of group-living and the many complications that result from our inextricably social, and undeniably primate, lives.

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