Dispersal and Reproductive Strategies in Wild Male Geladas
(Theropithecus Gelada)

by

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DEDICATION

For my loving family.

To Ma – for everything you have done for me.

To Baba – for teaching me to admire nature as a child.

To Didi – for always having my back and fiercely believing in me.

And Dimma – for all the phuchka, paan, and love growing up.

Thank you for filling my childhood with love, music, good food, laughter, and funny stories.
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Preface

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Abstract

Male reproduction is typically a zero-sum game, where each fertilization by one male comes at the expense of another (Andersson 1994; Darwin 1871). Therefore, in social systems where females can be monopolized, natural selection should favor competitive male reproductive strategies that enhance access to fertile females (Emlen and Oring 1977). In most systems, this is not a singular strategy, but rather comprises many individual decisions facilitated (or constrained) by variation in male quality, development, opportunity, and disposition that subsequently lead to differences in reproductive success.

In this dissertation, I consider two major stages of male life history in a cercopithecine primate, the gelada (Theropithecus gelada): male dispersal “decisions” across development and maturation; and male reproductive strategy “decisions” upon entering a new group as the dominant breeding male. Geladas are an ideal system for this study as juvenile males exhibit individual variation in dispersal “decisions” - starting from the age of dispersal (when), to dispersal patterns (how), and final dispersal destination (where); while dominant adult males exhibit variation in reproductive strategies immediately upon takeover - from killing either all, many, or very few infants on one hand (infanticidal) to not killing any vulnerable infants upon takeover (non-infanticidal).
Using cross-sectional and longitudinal data from Simien Mountains National Park, Ethiopia where long term gelada research (Simien Mountains Gelada Research Project, SMGRP) has been ongoing since 2006, I first investigated how the social environment experienced by males as juveniles leads to variation in male development via androgen production and dispersal decisions. I examined the effect of maternal attributes and group attributes on both these aspects of male development. I found that juvenile males with high-ranking mothers had lower fecal androgen levels compared to males with low-ranking mothers, and that male geladas dispersed earlier in larger groups and when they had more peers in their groups suggesting that maternal resources (via rank) and availability of juvenile partners can alter the pace of male development in geladas.

Second, I investigated factors that drove overall infant mortality rates in our population and immediately following dominant male replacements (takeovers). I found that takeovers drive overall infant mortality in our study population, however, all leader males do not commit infanticide upon takeovers even when the opportunity exists. Higher infant survival following a takeover was particularly attributable to instances when there were already reproductive opportunities present in the unit (in the form of cycling females) and when infants were older at the time of takeover.

Finally, I examined how demographic variables and individual male attributes led to variation in infanticidal behavior during takeovers. I found that the presence of former leaders increased takeover rates and decreased overall leader male tenure length. I found no differences in the attributes of infanticidal vs non-infanticidal leader males (wrt
androgens and glucocorticoid profiles). There was also no effect of killing infants in the first year on overall tenure length suggesting that the reproductive payoffs between infanticidal males and non-infanticidal males might be similar. This study contextualizes how variation in male behaviors can emerge and builds a framework to test future predictions on male reproductive strategies in geladas. Future research will aim at connecting individual male dispersal decisions with subsequent strategies as dominant males and measure paternity success using genetic data.
Chapter 1: Introduction

Overview

Reproduction is the currency of evolution; but in order to reproduce, organisms constantly need to adapt to varying social and ecological conditions (Clutton-Brock 2016; Andersson 1994; Darwin 1871). These condition- and context-dependent adaptations can lead to intraspecific variation in life history patterns and the emergence of multiple reproductive strategies (Rubenstein, 1980; Dunbar 1982; Clutton-Brock 1989; Davies 1991; Lott 1991). We know more about female life history and trait evolution in mammals, because in most social systems, males are the dispersing sex, transferring social groups multiple times throughout their life making them difficult to track. Understanding how males employ contrasting behaviors can provide important clues about social evolution, but examining male life history variation and reproductive strategies in long lived mammals is challenging as it requires even more rigorous tracking efforts than studying females. Using long term data from ongoing research conducted by the Simien Mountains Research Project at the Simien Mountains National Park, Ethiopia, I investigate the different behavioral strategies that male geladas use at two important life history stages: dispersal — which marks the onset of their reproductive trajectory, and takeover — through which males become dominant leader males and begin to monopolize reproduction.
Reproductive strategies

Individual variation in male reproductive strategies is expected to occur when males find different solutions to reproductive competition (Oliveira et al., 2008). Loosely, strategies here encompass a wide range of behavioral, morphological, and physiological traits that have evolved to aid in reproduction (Taborsky et al., 2008). Often, these strategies are termed ‘alternative’ because at any given time there exists more than one way in which males can obtain fertilizations under high levels of intraspecific and intrasexual competition, enabling individuals to “make the best of a bad job”, leading to alternative phenotypes within a population at any given time (Taborsky et al., 2008). These phenotypes can be observed as a discontinuous distribution of traits evolved for reproduction, for example morphological traits like body size dimorphism, color polymorphisms, dimorphic morphological structures as well as behavioral traits such as territoriality, infanticide (Koprowski, 1993; Jordão and Oliveira, 2005; Pusey and Packer, 1994).

Individual variation in reproductive strategies is well documented and generally have focused on organisms with short lifespans and fast life histories (Oliveira et al., 2008). However, for species with long and slow life histories, individuals themselves can switch between these behavioral phenotypes at different life stages by opting for different strategies (Setchell, 2008). This is especially true for non-human primates where reproduction is gradual but the reproductive period itself is prolonged (Bielby et al., 2007). In social systems where reproductive skew is high, multiple reproductive
strategies could emerge during highly influential life-history stages such as dispersal and attainment of dominance rank.

**Dispersal**

Dispersal in socially living organisms has evolved as a mechanism to reduce resource competition and avoid breeding (Greenwood, 1980; Dobson, 1982). Due to difficulty in following individuals after dispersal, we know significantly less about the sex that disperses. In cercopithecine primates, females remain within their natal groups while males emigrate as juveniles (Terborgh and Janson, 1986). During dispersal, males face both ecological challenges in the form of predation risk, as well as social challenges as they navigate a highly stratified social system, where dominance rank plays a major role. Thus, while there are multiple factors affecting a male’s life history, dispersal is likely the pivotal event that sets a male’s reproductive trajectory in motion (Alberts and Altmann, 1995). Males likely rely on key male social partners to disperse with and fall back on male partners again as young adults to climb the social hierarchy upon emigration into a new social group (De Moor et al., 2020; L’Allier et al., 2022; Schoof et al., 2009). In addition to assessing natal group conditions (availability of male partners, social instability), dispersing individuals need to also consider the overall emigration opportunities available to them (in terms of availability groups nearby, the composition of these groups, potential threats from resident males) (Jack et al., 2012; Marty et al., 2016; Wikberg et al., 2014). Since males can adopt variable dispersal strategies even within the same species, examining the *when, where and with whom* type of questions
behind dispersal decisions can give us a critical understanding of evolution of male reproductive strategies.

**Attainment of dominance and infanticide**

In most cercopithecine primates, following dispersal, a male’s ability to mate with fertile females within the group is predicted by his position in the dominance hierarchy. Males in the top position are usually able to monopolize most mating although this is contingent on female reproductive synchrony (van Noordwijk and van Schaik, 2004). Attainment of dominance rank can occur via multiple behavioral pathways that represent variable male strategies spanning from most aggressive to least aggressive (Teichroeb and Jack, 2017). Aggressive strategies include a subordinate male acquiring rank through direct physical contests and ousting the resident dominant male, observed in some neotropical as well as cercopithecine primates (Brasington et al., 2017; Marty et al., 2015; Amann et al., 2017; Packer and Pusey 1983). While less aggressive strategies include acquiring a group of females or subordinate males gradually rising in the male dominance hierarchy following the death or disappearances of higher-ranking males (succession or queuing) observed in male spotted hyenas (*Crocuta crocuta*), and saki monkeys (*Pithecia aequatorial*) (Di Fiore et al., 2007; East and Hofer, 2001).

In social systems with high male reproductive skew, male infanticide is commonly observed (Hrdy, 1979). As a behavior that emerges due to direct intrasexual competition, infanticide increases the reproductive success of the sex engaging in the behavior (Beehner & Bergman, 2008; Bellemain et al., 2006; Brown et al., 2021;
Cheney et al., 2006; Haines et al., 2018; Rosenbaum et al., 2016; Townsend et al., 2007). Infanticide is also a powerful evolutionary force for shaping social systems in mammals (Lukas and Huchard, 2014). While multiple studies have documented the presence of this behavior at the species and population level, very few have examined how variable infanticide is as a male behavioral strategy itself - mainly because such data is really hard to obtain. However, given infanticide can be a costly strategy from a male’s perspective (increasing injury risks from group members or immigrant males, possibly hindering their ability to form social bonds with females, potentially reducing overall reproductive tenure) (Schoof and Jack, 2013; Charpentier and Drea, 2013), it is reasonable to expect that there might be variation in this behavior and males may show variation in this behavior based on social and demographic factors or their own quality.

Factors driving variation in dispersal and rank attainment

Male attributes

Variation in male reproductive strategies can also emerge based on male age and condition (Taborsky et al., 2008). Previous studies from many primates report a strong association between several male attributes (body size, skin coloration, testosterone levels, and vocalizations) that indicate better competitive abilities (reviewed in Setchell, 2008).

Morphological features such as body size or mass plays an important role in multiple aspects of species biology (Bielby et al. 2007). It is also a useful denominator to assess variation in developmental patterns within species and broader macroevolutionary
patterns in paleoanthropological research (Elton and Dunn, 2020; Jungers et al., 2016; Perry et al., 2018). Especially for male primates, body mass and weaponry (such as canine length) can be important predictors determining the outcome of male-male competition (Clutton Brock, 1985; Mitani et al., 1996, McElligott et al., 2001, Wright et al., 2019). Another important attribute that affects male life-history and reproduction are steroid hormones.

Androgens in particular, are a class of steroid hormones that play an integral role in shaping male life history across multiple taxa (Goymann, 2009, Baird and Hews, 2007, Chu and Wilczynski, 2001; Van Loo et al., 2001, Dloniak et al., 2004, Jones, 2019; Rangel-Negrín et al., 2011), bringing a suite of rapid behavioral and physical changes leading to reproductive maturation, and subsequently prepare males to invest in increased mating efforts as they contest other males to gain access to females (Ros et al., 2002; Smith et al., 2005; Wingfield et al., 1990). Glucocorticoids (GCs) are a class of metabolic hormones that allow individuals to respond to ecological and social challenges (Sapolsky et al., 2000; Sheriff et al., 2011). As male cercopithecines experience unstable social periods during dispersal, group transfers, and rank attainment, GCs could be a useful marker to understand how successfully males are able to navigate these social challenges in order to survive and reproduce (Hunninck, Palme, and Sheriff 2020). Both androgens and GCs are responsive to changing social environments experienced by adult males (Higham et al., 2013), but the social environment can in turn also influence critical life history events such as dispersal and rank attainment.
Demographic variables

In the absence of detailed social behavior data, group size can be an important proxy for making predictions about the effect of social groups on male life history and behavior. While the absolute size of the group itself can affect both male and female life history and reproduction (Sterck et al., 1997; Silk 2007; Koenig 2002), specific variables within the group can also lead to individual differences in dispersal decisions and infanticidal behavior. For example, age of dispersal can be affected by the availability of male peers, availability of neighboring groups to disperse to, the sex ratio in these new groups themselves (Schoof et al., 2009). For adult males, presence of other adult males, the number of receptive adult females, and female reproductive synchrony altogether can determine reproductive decisions, rank attainment patterns, and ultimate reproductive success (Boyko and Marshall, 2009; Sterck et al., 1997; van Noordwijk and van Schaik, 2004). Thus, both male attributes and demography can drive variation in male reproductive strategies.

Methodological constraints for studying male reproductive strategies in primates

In primates, variation in morphological and physiological traits is not straightforward to measure in the wild as it requires direct handling of animals and acquiring biological samples invasively. Additionally, measuring payoffs of reproductive strategies also requires paternity data that takes time to generate, and requires accurate demographic and life history information to confirm overall pedigrees. Therefore, it’s not surprising that primatological studies have always heavily relied on long term behavioral observations with continued monitoring of populations and novel non-invasive
techniques (Eberhard and Gutierrez, 1991; Emlen, 1996; Kotiaho and Tomkins, 2001).

Over the past two decades, there has been rapid development of such techniques to measure variation in male traits through i) physiological markers - e.g.: steroid hormones in fecal samples, ii) morphological features - such as body size assessment, coloration patterns, weaponry using digital photogrammetry methods; and iii) reproductive outcomes through rapid paternity assignment using high throughput sequencing methods (Higham, 2016; Rothman et al., 2008; Snyder-Mackler et al., 2016). Each of these methods comes with its own suite of strengths and limitations and needs to be validated in a species-specific manner.

To examine male reproductive strategies in wild primates, we first need a system where observable differences in male strategies exist. Second, we need long term data spanning multiple aspects of species biology including but not limited to life-history, demography, and behavior. Third, reliable non-invasive methods are needed to measure male attributes (using hormones, body mass) and reproductive success (using genetics). Most importantly, we need large sample sizes to make robust statistical tests to quantitatively compare between strategies.

This study

Here, I take an integrated approach to examine causes underlying variation in male strategies in wild geladas (Theropithecus gelada), living in Simien Mountains National Park, Ethiopia (13°15’N, 38°00’E, elevation 3200-4500 m a.s.l) where members of the long-term Simien Mountains Gelada Research Project (SMGRP) have been collecting
data since 2006. The long-term project staff members routinely observe and collect data (demographic data through censuses, life history, behavior, and hormone data) from 14-21 reproductive units in two different bands on a near daily basis. This dissertation incorporates data from natal males (to examine maturation and dispersal) and dominant leader males in the first year of their tenure (to examine reproductive strategies).

Fig 1.1. Map of the Simien Mountains National Park. The Simien Mountains Gelada Research Project is located at Sankaber campsite. Map source: (Ejigu et al., 2020).

Why geladas?

Geladas are an ideal system in which to examine individual variation in male reproductive strategies as they are highly terrestrial making them easily observable. The
core of gelada societies is formed by one male units (hereafter “reproductive units”) that comprise one dominant leader male, 2-12 adult females, 1-5 subordinate follower males, and their related offspring (Snyder-Mackler et al, 2014). Several reproductive units with overlapping ranging patterns may aggregate together to form “bands” and several bands may join together during the day to form “communities” (Snyder-Mackler et al., 2012; Snyder-Mackler et al, 2014). As they live in multileveled societies, males within the same band can still experience varying social conditions as members of different reproductive units each with its own set of social dynamics, giving us a large sample of males to follow at any given time (Snyder-Mackler and Alberts, 2014).

Geladas also form temporary all male units (hereafter “bachelor units”) consisting of 4.7 +/- 1.6 males on an average (Pappano 2013). Bachelor groups are temporary in nature and may contain males of all age classes (Pappano 2013). Females remain in their natal units and males disperse either to join bachelor units or reproductive units. Male geladas in our study population show remarkable variation in the behavioral decisions that they make both during dispersal and upon takeovers.

Upon dispersal, males can join all male units (bachelor units) where they may stay for a few years before taking over a unit and becoming the new leader male, or they can directly join a reproductive unit as a subordinate follower male, or immediately take over a unit to become the new leader male. Paternity analysis in this population has shown that leader males sire 83-100% of offspring in units without and with followers respectively. Even though the second and third options have clear reproductive advantages, we almost always observe natal males dispersing to join bachelor groups
suggesting that this “bachelor stage” plays an important role in the life-history of male geladas. However, the ages at which they disperse and join bachelor groups, and the pattern of dispersal itself (dispersing alone vs with male partners) can vary between males.

Males begin their reproductive tenure after taking over a unit (Barale et al., 2015; Dunbar & Dunbar, 1975; Pappano & Beehner, 2014). The best way to maximize reproductive success is to ensure that they sire offspring at a high rate for a long time. This can be accomplished by increasing the number of fertile females in the unit and/or increasing tenure length. Specifically, leader males can sire more offspring by taking over a larger unit with more adult females. However, larger units are more likely to be taken over by rival bachelor males (Johnson et al., 2018), thereby effectively reducing tenure length for these leader males. Leader males can also sire more offspring by committing infanticide upon takeover to accelerate lactating females’ return to fertility (Beehner & Bergman, 2008). This immediately increases the number of fertile females in their unit. Despite its clear evolutionary benefits, surprisingly, not all leader males commit infanticide upon taking over a new unit.

Over the course of the long-term project, we collected demographic, behavioral, genetic, and hormonal data from 169 individually known natal males and 88 leader males. This provided me with the unique opportunity to take an integrative approach to examine intra-species variation in male reproductive strategies in geladas. In this dissertation, I examine proximate and putative ultimate consequences (when genetic
data was not available) of individual variation in dispersal decisions and infanticidal behaviors in male geladas.

In chapter 2, I examined the social correlates affecting male developmental milestones in juvenile geladas using 14 years of demographic, life-history, behavioral, and hormonal data. I first validated a group specific antibody (epiandrosterone) to measure fecal androgen metabolite levels (fAMs) and quantified the normative pattern of androgen production during development in males. I also reported the population estimates of age of dispersal in male geladas and examine if sudden rise in androgens predict dispersal. Finally, I examined if access to maternal resources and peer resources predict individual variation in fAMs and age at dispersal in geladas. Findings from this study can be summarized as follows: i) juvenile male geladas that have low ranking mothers at birth experience higher age specific androgen levels than juveniles with high-ranking mothers, ii) male geladas do not show any surge in androgen levels before or after dispersal, and iii) male geladas with more peers and living in larger units dispersed earlier than males with few or zero same aged peers living in smaller units. This study sets the stage up for future research on juvenile social relationships and dispersal behavior in a complex multileveled society.

In chapter 3, I focused on infanticide following a takeover as a male reproductive strategy. I first analyzed how overall infant mortality of the population is affected by maternal attributes (dominance rank and parity), unit attributes (unit size) as well as seasonal variables (temperature, rainfall) - all of which are known to affect infant
survival in other non-human primates. I found that takeovers are the most important predictor driving overall infant mortality in our population. However, considerable variation existed in infant mortality post takeover as well (i.e., not all vulnerable infants are killed by new leader males). To examine potential factors contributing to this variation, I zoom in on infant survival strictly following takeovers to identify predictors that positively influence infant survival during a time when infants are most vulnerable (in the presence of adult immigrant males). Post-takeover infant survival analysis shows that younger infants were more likely to be victims of infanticide and that the number cycling females in the units reduced the likelihood of infant death.

In chapter 4, I investigated male strategies during takeovers in three different ways. First, I examined how bachelor males target units with certain demographic characteristics. Second, I examined whether infanticidal behavior in new dominant males affects their overall fecal androgen and glucocorticoid metabolite levels in the first year of tenure. Third, I examined whether infanticide affects tenure length of leader males down the line. I found that bachelors target units with more cycling females and fewer pregnant females and that former leader males in particular make units more susceptible to takeovers. Males that committed infanticide did not have different fecal androgen or glucocorticoid metabolite levels compared to those that did not commit infanticide. Finally, killing infants in the first year did not affect overall tenure length of leader males - instead demographic variables in the first year strongly affected tenure length.
Significance of research

These results will help us contextualize how variation in male behaviors emerge, build a framework to test future predictions, and examine reproductive consequences underlying them. Although variation in male reproductive strategies has been described for different primate species, few studies have quantified the payoffs for many strategies simultaneously (Setchell, 2008). A substantial portion of the research that I conducted also went into validating methods that would allow us to quantify important variables associated with male reproductive strategies in future research.

All field research was conducted with permission from the appropriate authorities in Ethiopia and at the University of Michigan. Additionally, this project has strictly followed guidelines created by the Institutional Animal Care and Use Committee at the University of Michigan (IACUC protocol: PRO10666). We also followed the American Society of Primatologists/International Primatological Society Code of Best Practices for Field Primatology for carrying out this research.
References:


Chapter 2: Social Correlates of Androgen Levels and Dispersal Age in Juvenile Male Geladas


Abstract
Androgens offer a window into the timing of important male life history events such as maturation. However, when males are the dispersing sex, piecing together normative androgen profiles across development is challenging because dispersing males are difficult to track. In this chapter, we examined the conditions that may predict male androgen status (via fecal androgen metabolites, fAMs) and age at dispersal in wild male geladas (*Theropithecus gelada*). Gelada male life histories are highly variable – dispersal may occur before sexual maturation, dispersal itself can be immediate or drawn out, and, due to their multi-leveled society, social conditions affecting dispersal can vary for juveniles living in different reproductive units within the same band. Using longitudinal data from known natal males, we examined how androgen levels and age at dispersal were associated with: (1) access to maternal resources (i.e., maternal rank, birth of a younger sibling, experiencing maternal loss), and (2) access to male peers (i.e., number of similar-aged males in their unit, unit size). We found that androgens
were significantly lower in males with high-ranking mothers (in males >2.5 years of age; infant androgens were unrelated) and that having more male peers in their social group and larger groups overall predicted an earlier age at dispersal. Moreover, dispersal in geladas was not preceded or followed by a surge in androgen levels. This suggests that social environments can cause individual variation in androgens and dispersal age. Whether this variation leads to differences in male fitness in later life remains to be determined.

Introduction

Steroid hormones play a central role in many vertebrate life history trade-offs (Muehlenbein & Bribiescas, 2005). Androgens, in particular, have organizational and activational roles that range from the formation of male reproductive organs and secondary sexual characteristics (e.g., testicular development, spermatogenesis, increase in musculature) to the development of male reproductive behaviors (Alexander, 2014; Dixson & Anderson, 2004; Hau, 2007). Androgens themselves are also modulated by the social environment in a bi-directional relationship (Hirschenhauser & Oliveira, 2006; Rangel-Negrín et al., 2011; Van Loo et al., 2001). For example, reproductive challenges are known to increase androgens (Girard-Buttoz et al., 2015; Ostner et al., 2011; Rincon et al., 2017) while the demand for paternal care is known to decrease them (Gordon et al., 2017; Onyango et al., 2013; Prudom et al., 2008). This androgen-behavior bi-directional relationship has been shown to have fitness consequences for adult males (Oliveira, 2004; Setchell et al., 2008). However,
these bi-directional effects are also expressed prior to adulthood, especially during developmental stages such as puberty.

Puberty, the transition from an immature juvenile state to a reproductively mature adult state, is associated with the release of gonadotropin-releasing hormone (GnRH) leading to gonadal growth and increased secretion of androgens (Alexander, 2014; Perfito & Bentley, 2009; Whitlock et al., 2006). Phenotypic changes in males – such as testicular descent, an increase in body size, development of musculature, development of ornaments (e.g., pelage), development of weapons (e.g., elongated canines or antlers) – closely accompany this surge in androgens (Fuxjager et al., 2018) and set the stage for subsequent life history events. Specifically, in vertebrates, androgen-mediated phenotypic changes have been hypothesized to aid males during one of the riskiest maturational milestones – permanent dispersal from their natal group, which often coincides with the start of a male’s reproductive career (Alberts & Altmann, 1995; Greenwood, 1980). At the species level, the phenotypic changes associated with sexual maturation coincide with dispersal events (Galbany et al., 2015; Holekamp & Smale, 1998). However, at the individual level, the onset of androgen secretion and the timing of dispersal exhibit a high degree of plasticity, which may reflect the ecological and social conditions within their natal group (Jack et al., 2012; Robbins et al., 2019). Here, we investigated social variables that are known to be important for the production of androgens, the timing of dispersal, and the pace of male development in male mammals (Hirschenhauser & Oliveira, 2006; Rutberg & Keiper, 1993) and non-human
primates (Akinyi et al., 2017; Weiß et al., 2016): the social environment provided by their mother and the social environment provided by their peers.

Mothers form an integral component of an offspring's social environment beyond lactation in social mammals (Clutton-Brock, 1991; Maestripieri, 2009). Many studies have examined the role of these non-genetic effects (i.e., “maternal effects”) and their long-term impact on offspring development and fitness (Berghänel et al., 2017; Dantzer et al., 2013; Höner et al., 2010). We focus on the effect of post-natal resources that a mother provides to her offspring that could affect their development. For example, high-rank for many female mammals is associated with direct benefits that extend to their offspring – including better access to food (Fedigan, 1983; Hall & Fedigan, 1997; Koenig, 2002) and stable social positions (Wooddell et al., 2020). Maternal high rank has been shown to predict higher survivability of offspring (Archie et al., 2014; Holekamp et al., 1996; Kalbitzer et al., 2017). Recent studies on free-ranging rhesus macaques (Macaca mulatta) and chimpanzees (Pan troglodytes schweinfurthii) have shown that high maternal rank predicted a later age at dispersal for offspring (Walker & Pusey, 2020; Weiß et al., 2016). Additionally, maternal resources could end abruptly altogether, for example with the birth of a younger sibling or at the death of the mother (Tung et al., 2016). Indeed, both events have been considered “early life adversity” for juvenile yellow baboons (Papio cynocephalus) and were shown to affect the survival and reproduction for these offspring as well as their grand-offspring (Zipple et al., 2021, 2019). Moreover, both of these have been associated with an earlier age at dispersal in several other taxa (red deer (Cervus elaphus) Andres et al., 2013; elephants
(Loxodonta africana) Goldenberg & Wittemyer, 2018; chimpanzees (Pan troglodytes) Stanton et al., 2020). Thus, maternal resources (or lack thereof) that derive from maternal rank, additional siblings, or maternal loss are associated with variation in male development (Bernstein et al., 2012).

Male development can also be impacted by the presence of male peers (i.e., familiar conspecifics that are within a few years of age of one another). In species with stable social groups, juveniles have the opportunity to routinely engage in social interactions with male peers from a very early age. These interactions are critical for facilitating developmental milestones such as independence from their mother, motor-skill acquisition, and socialization skills (Palagi, 2018; Pereira & Fairbanks, 2002). If males are the dispersing sex, male peers can additionally serve as dispersing partners, facilitating parallel dispersal events (Jack & Fedigan, 2004; Jack et al., 2009; Wikberg et al., 2014, 2018) which reduces the risk of predation and harassment from conspecifics during dispersal (Cheney & Seyfarth, 1983; Rutberg & Keiper, 1993). Therefore, males may be able to accelerate or delay their development to maximize the opportunity to disperse alongside a partner; for example, males with older peers in their groups might show higher androgen production or disperse at a younger age; and males with younger peers in their groups might show lower androgen production or disperse at an older age.

Here, we examine whether access to maternal resources or presence of male peers are associated with variation in androgen levels and age at dispersal for young males in a
wild population of geladas (*Theropithecus gelada*). Geladas provide an ideal study system in which to investigate the effects of the maternal and peer social environments on androgen levels and age at dispersal. First, geladas live in multi-leveled societies comprising multiple core social groups, each with their own social dynamics (Snyder-Mackler & Alberts, 2014). The core modular unit of gelada society is the reproductive unit (hereafter “unit”) with one dominant breeding male, 2-12 related adult females, 0-5 subordinate males, and their related offspring (Snyder-Mackler et al., 2012). Prior to maturation, natal males typically disperse into temporary, non-reproductive, all-male groups (“bachelor groups”) (Barale, 2014). Bachelor males can reproduce by either taking over a unit as a dominant leader male (“takeover”) or by joining a unit as a subordinate follower male (Pappano, 2013). Units with overlapping ranging patterns often aggregate together to form a “band” and overlapping bands across the home range are called a “community” (Snyder-Mackler et al., 2014, 2012). This multi-leveled social organization provides the opportunity to observe juvenile males growing up in different social environments, providing us with a comparatively large sample size for a wild primate.

Second, dispersal in geladas is unique in several ways. Juvenile male geladas typically disperse several times (subsequently returning to their natal group) prior to a “final dispersal”. Our observations identify that each of these dispersal events is to a bachelor group for varying amounts of time (from hours to weeks). Due to these multiple dispersal events, gelada dispersals (even “final dispersal”) may not reflect the onset of maturity as for other taxa (Akinyi et al., 2017; Onyango et al., 2013). Furthermore, in
geladas, as with many other non-human primate species, males have been observed to disperse with a male partner (often kin) as this provides an opportunity for dispersing males to form coalitions as they move across unfamiliar ranges (Collevatti et al., 2013; De Moor et al., 2020; Schoof et al., 2009). Male geladas dispersing from the same band often form a resident bachelor group that moves and travels with the natal band (Barale, Beehner, Sen pers obs). Joining a bachelor group may therefore be easier for males that grew up in a band with more male peers.

Using 14 years of demographic and behavioral data from a population living in the Simien Mountains National Park, Ethiopia, we examine whether age-specific androgen levels and/or age at dispersal are associated with the maternal or peer social environment. This is not the first time our study site has reported androgen data across male development for this population. A previous study reported androgen levels for males across all ages (Beehner et al., 2009); however these were only age estimates analyzed at a categorical level. Here, we advance our current knowledge of androgens in male geladas in several important ways. First, after validating a new androgen immunoassay for use in geladas, we establish the trajectory of androgen levels in males with known ages across development (androgen across male ages). Second, we examine how access to maternal resources (i.e., maternal dominance rank, birth of a younger sibling, and experiencing maternal loss) and access to peer resources (i.e., cohort size) predict individual variation in androgen levels. Next, we examine if juvenile males experience a surge in androgen levels around dispersal. Finally, we examine how access to maternal and peer resources affect their timing of dispersal. We predicted that
accelerated male development (e.g., higher age-specific androgen levels, earlier dispersal) would occur when maternal resources within the natal unit were low (i.e., low maternal rank, birth of a younger sibling before the average interbirth interval, or maternal loss) and when peer resources within the natal unit were high (i.e., having many play partners and/or dispersal partners). Based on the bi-directional relationship between androgens and behavior, we make the assumption that variables that pull males away from their natal unit and push them towards extra-unit relationships will accelerate development. Finally, based on the idea that males prefer to disperse with a partner or partners (Schoof et al., 2009), we predicted that the timing of dispersal may be heavily influenced by the presence of male peers around them.
Table 2.1. Summary of predictions for androgen profiles and age at dispersal

<table>
<thead>
<tr>
<th>Predictor</th>
<th>Fecal androgen metabolites</th>
<th>Age at dispersal</th>
</tr>
</thead>
<tbody>
<tr>
<td>Maternal rank</td>
<td>Males with low-ranking moms have higher age-specific androgens</td>
<td>Males with low-ranking moms will disperse earlier</td>
</tr>
<tr>
<td>Early sibling arrival</td>
<td>Males with early sibling arrival will have higher age-specific androgens (not tested due to insufficient sample size)</td>
<td>Males with early sibling arrival will disperse earlier</td>
</tr>
<tr>
<td>Maternal loss</td>
<td>Males experiencing maternal loss will have higher age-specific androgens (not tested due to insufficient sample size)</td>
<td>Males experiencing maternal loss will disperse earlier</td>
</tr>
<tr>
<td>Cohort size</td>
<td>Males with large cohort will have higher age-specific androgens</td>
<td>Males with large cohort will disperse earlier</td>
</tr>
</tbody>
</table>

Materials and Methods

Study site and subjects

This study was conducted as part of the long-term Simien Mountains Gelada Research Project, Ethiopia (13°15’N, 38°00’E, elevation 3200-4500 m a.s.l.). We collected demographic, life history, and behavioral data from 169 males born across 22 reproductive units from 2006-2020. Of these males, the project has known dates of birth for 128 of them. The remaining males were infants when the project began or belonged to units that were not observed routinely in the study area; and we estimated their dates
of birth based on when they were first seen in the unit (estimated with 0-226 days, mean = 33.5 days, SD = 55.6 days). All study subjects were monitored until permanent dispersal from their natal unit. The long-term project collected a total of 1611 fecal samples from 70 natal males from 2011-2020 with known ages at sample collection (age range: <1-10 years; all dates of birth known within 1-15 days) with average of 23 fecal samples per male (range = 1-83, SD = 22) and an average of 134 fecal samples per age group (range = 5-351, SD = 124). Additionally, the project was able to obtain samples 73 samples from 22 natal males three months around dispersal. Details about the sampling distribution are provided in Table 1 (Supp Materials).

**Fecal sample collection, extraction, and storage**

Sample collection, extraction, and storage methods followed protocols previously validated for geladas (Jacinta C. Beehner et al., 2009; Jacinta C. Beehner & McCann, 2008; Pappano et al., 2010). In brief, fresh fecal samples were thoroughly mixed and an aliquot of the sample (~ 0.1 g) was collected in 3 ml of a methanol/acetone solution (4:1, v:v). This mixture was immediately homogenized using a battery powered vortexer and samples remained in the organic solution for 3-4 hours. Once the fecal matter settled to the bottom of the tube, we filtered 2.5 ml of the fecal homogenate solution through a 0.2 \( \mu \)m PTFE filter and washed the filter with an additional 0.7 ml of methanol/acetone solution. We then added 7 ml of distilled water, mixed the solution, and loaded the aqueous homogenate onto a reverse-phase C\(_{18}\) solid-phase extraction cartridge (Sep-Pak Plus, Waters Corporation, Milford, MA). Prior to loading, cartridges were prepared according to the manufacturer's instructions. The loaded cartridge was then washed
with a preservative (2 ml of 0.1% sodium azide solution) and placed inside sealed Whirl-
pak bags with a desiccant (~2g of silica beads). After 3 days at room temperature (to
allow cartridges to dry), samples were transferred to a -20°C freezer. The dry weight of
the extracted fecal sample was measured a few weeks later using a portable scale (to
±0.001 g). Cartridges remained frozen until they were shipped at room temperature to
the Beehner Endocrine laboratory at the University of Michigan for subsequent analysis.

**Fecal androgen metabolite assay**

In the laboratory, steroids were eluted from cartridges with 2.5 ml 100% methanol and
stored at −20°C until the time of assay. We measured fecal androgen metabolites
(fAMs) using a 5α-Androstan-3-ol-17-one (or epiandrosterone) microtiterplate
enzymeimmuno assay (EIA), which is a C17 group-specific enzyme immunoassay that
detects 17 oxo-androgens with 100% cross-reactivity (Möhle et al., 2002; Palme &
Möstl, 1994). The EIA has been used successfully to assess male androgen status from
fecal samples in a variety of primate species (Fürtbauer et al., 2013; Higham et al.,
2013; Rincon et al., 2017) as well as other mammals (Ganswindt et al., 2003; Wolf et
al., 2018). In brief, 50 μl of samples (diluted at 1:20) and standards (range: 3.9-250.0
pg/well) were added to each plate in duplicate followed by the addition of 50 μl biotin-
labeled hormone and 50 μl antibody to each well. Plates were incubated overnight at
4°C, washed three times with PBS wash solution (containing 0.002% Tween 20) the
next day, followed by the addition of 150 μl streptavidin horseradish peroxidase to each
well and incubated in the dark on stirring tables for 1 hour. Plates were washed again
and 100 μl of TMB substrate solution was added to each well and incubated in the dark
for another 30-40 min. The reaction was stopped by adding 50 μl of sulfuric acid to each well and the absorbance measured using an automatic plate reader at a wavelength of 450 nm. The 50% intercept was about 15 pg/well and assay sensitivity was 2.1 pg/well.

**Analytical validation**

We conducted tests for parallelism, accuracy, and precision to check if the epiandrosterone assay could reliably detect fAM levels in gelada fecal samples. Parallelism was measured by running multiple dilutions of a fecal pool (consisting of male samples only) at concentrations that span the assay’s range (250.0-3.9 pg / 50μl). We then back-calculated the concentrations and compared these values with those generated from the standard curve. A visual inspection of the curves for the standards and our pool demonstrated parallelism (Fig. S2.1), a pattern confirmed by the lack of an interaction effect between the concentration and the type of sample (standard vs. male only pool) on percent binding [ANOVA: t-value = 0.155, p = 0.878]. Accuracy was determined by spiking each standard with a diluted aliquot of the gelada fecal extract pool (male-only) and calculating the recovery of each standard sample [mean recovery = 90.54% ± 23.60%] and performing a visual inspection of the curves (Fig. S2.2). Precision was determined by running six different samples four times on the same plate (intra-assay CV). We also ran high (1:20 dilution, 25% binding) and medium (1:80 dilution, 50% binding) concentrations of male-only fecal extract pools on all plates (inter-assay CV). Our inter-assay CV was 16.3% (high concentration pool), 18.1% (medium concentration pool) (N = 61 plates). Average intra-assay CV for these high and medium pools were 10.5% and 11.6% respectively (N = 61 plates).
Comparing RIA and EIA measures

We compared fAM measures between our previous androgen radioimmunoassay (MP Biomedicals Double Antibody Testosterone RIA kit) and the new epiandrosterone EIA using a subset of samples across ages (<1 years - 9 years) that were run for both assays – 1048 samples collected from 49 natal males with an average of 21 samples per male (range = 1-74, SD = 21) and an average of 105 samples per age group (range = 1-262, SD = 90). We found that the epiandrosterone assay has higher biological sensitivity, detected changes in fAMs between age groups during male development which the RIA did not (Fig. S2.3) and that the fAM concentrations obtained from samples run using the two different antibodies were positively but not strongly correlated (Pearson’s correlation test; r = 0.54, p <0.001) (Fig. S2.4). The MP Biomedicals testosterone RIA detects total unconjugated forms of testosterone, whereas the epiandrosterone assay measures downstream metabolites of testosterone (including 17 oxo-androgens). Therefore, we did not expect a strong correlation between the values measured using the RIA and EIA for the same samples as the two antibodies have different cross reactivities with the androgen metabolites in our fecal samples.

Androgens across male ages

We performed a biological validation for the epiandrosterone EIA by quantifying androgen levels for males with known ages. We expected fAMs to exhibit the typical parabolic pattern observed for fecal androgens in other male primates (Bernstein et al., 2012; Conley et al., 2011).
What predicts androgen profiles and age at dispersal in geladas?

After validating the in-house epiandrosterone EIA, we conducted three separate analyses. First, we examined how maternal resources and peer resources affect androgen production in male geladas. Second, we investigated whether males have higher androgen levels right around dispersal. Third, we tested if maternal and peer resources also affect age of dispersal in juvenile male geladas. Each analysis requires slightly different variables (see Data analyses). Here, we describe all variables included in our analyses.

Age at dispersal

Juvenile gelada males move back and forth between bachelor groups and their natal unit before their final permanent dispersal to a bachelor group (Barale, 2014). Because our dataset on early dispersal events is much smaller and less reliable than our dataset on final dispersal events, we focus our analyses on final dispersal only. Age at dispersal, therefore, was the age of the male subject on the last day he was observed with his natal unit. For males without an exact date of dispersal (n = 57,12-224 days of uncertainty), we assigned the date of dispersal as the mid-point between the last date the male was observed with his natal unit and the first date he was either observed in a bachelor group or not observed with his natal unit.

Maternal rank

We calculated maternal rank using ad libitum and focal observation data on displacements, submissive, and aggressive behaviors between adult females living in
the same unit. Daily elo scores (Albers & de Vries, 2001; Neumann et al., 2011) for each female were calculated using the R package EloRating (Bernstein et al., 2008; Bernstein et al., 2012). Elo scores were averaged per month and then converted into proportional scores by taking unit size into account (which could vary each month based on fissions, fusions, female deaths, and maturations). Because maternal rank changes slightly across a male’s lifespan, we had to decide at which point across his life to “assign” him his mother’s rank. We reasoned that androgen profiles would be most likely to be influenced by his mother’s rank while he was highly dependent on her (Bernstein et al., 2008; Bernstein et al., 2012a); therefore, for our androgen analysis, we calculated the mother’s rank at each male’s birth. Each male fecal sample was assigned a corresponding maternal rank calculated as the proportional elo score for the month the male was born. For dispersal however, we expected that immediate maternal rank would be more predictive of each male’s dispersal decision than maternal rank at birth (Alberts & Altmann, 1995). Therefore, for our dispersal model, we calculated a maternal rank for each month that a male was observed. If a male’s mother died during the sampling period, then we used her last available monthly rank for all subsequent months as we expected the effects of maternal rank on offspring development to continue beyond her actual presence (Onyango et al., 2008; Zipple et al., 2021).

**Early sibling arrival**

We scored early sibling arrival as a categorical variable (yes/no) if subjects experienced the birth of a younger sibling before they reached 2.5 years of age – the average interbirth interval for female geladas (Roberts et al., 2017). A “yes” for this variable
would indicate that a male had maternal resources withdrawn earlier than other males in
the population due to the birth of a younger sibling. We added a third category
(“neither”) for males who themselves were under 2.5 years of age during the month of
the data assignment. We were unable to include early sibling arrival in our androgen
model because we did not have a sufficient number of males in each category within
our hormone dataset.

**Maternal loss**

Previous research on this population showed that maternal social integration is related
to male juvenile social networks – males with mothers who were highly socially
integrated within the adult female network had sons that were more centrally located in
the juvenile social network than males with mothers who were poorly socially integrated
(Barale, 2014). Thus, we expected that the presence of mothers can directly or
indirectly impact male dispersal through social integration. We defined maternal loss as
a categorical variable (yes/no), depending on whether the mother was alive or dead in
the unit before the male was 2.5 years of age. Similar to early sibling arrival, we were
unable to include maternal loss in our androgen model because we did not have a
sufficient number of males who lost their mothers.

**Cohort size**

Juvenile male geladas associate with a large cohort of individuals across their band.
However, we do not have sufficiently detailed association data from all juvenile males
within a band to examine the impact that the full cohort has on androgen levels and
dispersal decisions. Instead, we examined one available proxy for cohort size that we had for all immature males: the number of male peers within their natal unit. Growing up in the same unit, males born within the same cohort can serve as play partners, probable social support in juvenile disputes, and possibly dispersal partners (Barale, 2014). We defined peers as any males that were born within +/- 1.5 years from our subjects. We chose 1.5 years as our cutoff as this best captures the males most likely to be paternal half-siblings (average male tenure length for this population is 2.67 years, male infants born within the same leader male's tenure are likely to be half-siblings, Sen et al., 2022). We calculated the total number of peers for each male monthly (cohort size was used in both the androgen and dispersal analyses).

**Unit size**

In line with previous research, we defined unit size as the total number of adult females in each reproductive unit (Feder et al., 2022; Tinsley Johnson et al., 2021) either during the month of sample collection (androgen model) or during the month a male was censored (dispersal model). We include this variable to verify that a larger male cohort is not just a function of a larger unit size (although unit size was moderately correlated with cohort size in our dataset, corr coef = 0.36, t = 32.45, p<0.001). Over and above this justification, we were less interested in unit size as a predictor variable – the number of females in a unit do not present reproductive opportunities for juvenile males since relatedness between all individuals within a unit is high (Tinsley Johnson et al., 2014), and juvenile males are not a threat to a leader male's reproduction in the same way as immigrant adult males or former leader males. Therefore, we do not expect that
leaders of larger units will be more likely to evict juvenile males (and have seen no evidence for this).

**Weather variables**

We controlled for rainfall and temperature by including them as model covariates in our androgen analysis as previous research has demonstrated a positive relationship between rainfall/temperature and testosterone levels for leader males (Pappano & Beehner, 2014), and we found similar trends in androgen levels among juvenile males as well (**Fig. S2.5**). Rainfall (mm) was recorded on a near-daily basis using a rain gauge located in an open area near the field station, and daily minimum/maximum temperatures (°C) were recorded using a thermometer mounted under a shaded location. We calculated cumulative rainfall for each sample collected by summing rainfall measures from the previous 90 days as this measure is positively correlated with green grass availability in this area (Jarvey et al., 2018). Similarly, mean maximum/minimum temperature was calculated as the average maximum/minimum daily temperature across the previous 30 days. In our androgen analysis, we only use mean maximum temperatures and cumulative rainfall as mean maximum temperature was positively correlated with mean minimum temperature (corr coef = 0.65, t = 32.09, p < 0.001), maximum temperature was weakly correlated with cumulative rainfall (corr coef = -0.42, t = -17.3, p < 0.001).

**Data analyses**

**What factors predict androgen profiles?**
All statistical analyses and data visualization was carried out using R v 4.0.3 (R Core Team, 2020). As androgens showed the expected parabolic relationship with male age during development (Fig. 2.1), the first analysis included infant males under 2.5 years ("dependent" males = 29, samples = 126) and the second analysis included males that were above 2.5 years (“independent” males = 43, samples = 771). We picked 2.5 years as the cutoff point because we know that the average interbirth interval for this population is 2.5 years (Roberts et al., 2017) and previous studies on non-human primates has shown that the relationship between fAMs and age becomes linear around the age when infants are independent from their mothers (Bernstein et al., 2012b). Our response variable fAMs (ng/g) was log-transformed because it displayed a right-skewed normal distribution (Fig. S2.6).

We fitted a LMM using the R package ‘lme4’ (Bates et al., 2014; Bolker et al., 2009), with log fAMs as the outcome variable, and the following predictor variables calculated for each hormone sample: male age, cumulative rainfall, maximum temperature, maternal rank in the form of proportional elo score, cohort size, and unit size. A summary of fixed and random effects for androgen analysis and model structure is provided in Table 2. All predictors were z-transformed for ease of interpretation since they were on different scales (Dunbar, 1976). Male ID was entered as a random effect (random slopes) in all our model. Model diagnostic plots confirmed that there were no violations of assumptions (linear relationship between fitted values and residuals, normality, and homoscedasticity) and we also checked for multicollinearity between predictors using vif() function in the car package (Fox et al., 2012). Following model
fitting, we performed model selection using the dredge() function in the 'MuMin' package, which uses an information theoretic multi-model selection approach based on Akaike's information criteria (AIC) (Bates et al., 2014; Burnham & Anderson, 1998). We then performed model averaging across all models by averaging predictions of each model on the link scale as prescribed for linear mixed models and obtained averaged estimates for each predictor using `model.avg()` from the MuMin package in R for all models (Barton & Barton, 2015).
Table 2.2. Description of predictors for fecal androgen metabolite levels in males

<table>
<thead>
<tr>
<th>Fixed/Random variable</th>
<th>Predictor variable</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fixed</td>
<td>Age</td>
<td>Male age in years at sample collection (numeric, continuous)</td>
</tr>
<tr>
<td>Fixed</td>
<td>Maternal rank</td>
<td>Mother’s rank at male’s birth (numeric, continuous)</td>
</tr>
<tr>
<td>Fixed</td>
<td>Cohort size</td>
<td>Number of males in their reproductive unit within +/- 1.5 years of their own age (numeric, discrete)</td>
</tr>
<tr>
<td>Fixed</td>
<td>Unit size</td>
<td>Number of adult females in the reproductive unit at time of sample collection (numeric, discrete)</td>
</tr>
<tr>
<td>Fixed</td>
<td>Cumulative rainfall (mm)</td>
<td>Cumulative rainfall across the 90 days before sample collection (numeric, continuous)</td>
</tr>
<tr>
<td>Fixed</td>
<td>Mean max temp (°C)</td>
<td>Average maximum temperature across the 30 days before sample collection (numeric, continuous)</td>
</tr>
<tr>
<td>Random</td>
<td>Male ID</td>
<td>Male identity</td>
</tr>
</tbody>
</table>

Do males have higher androgen levels surrounding dispersal?

Next, we sought to examine if males have higher fAMs preceding or following dispersal. We approached this question in three ways since we did not have sufficient repeated samples collected from the same males at the cusp of dispersal. First, to identify broader patterns in androgen production surrounding maturational milestones, we visually inspected residual fAMs (after controlling for age) of males (N = 21) during the 3 months before and after dispersal with the expectation that androgens will not rise following dispersal as dispersal is not as risky for geladas as compared to other closely related species. Second, to identify whether dispersal age itself might affect androgen production, we categorized males within this dataset (from whom we had pre- and post-dispersal samples) as “early” (dispersed < 5.5 years), “mean” (dispersed 5.5 - 7.7 years), and “late” (dispersed > 7.7 years). Finally, to further contextualize the results, we performed paired t-tests on fAMs of males dispersed during the 3 months before and after dispersal.
years), or “late” dispersers (dispersed > 7.7 years). Age cutoffs were based on quartile distribution of dispersal age for this population (early = Q1, 5.5 years; late = Q4, 7.7 years; dispersal ages in between assigned as “mean”). We then visually inspected fAM levels for early, mean, or late dispersers during the 3 months before and after dispersal. Finally, we conducted a pairwise non-parametric comparison test using a Wilcoxon’s test for a set of males (N = 7) from whom we had at least one fecal sample during the two months before and after dispersal.

**What factors predict age at dispersal?**

We constructed Cox proportional hazards models to model the dispersal status (yes/no) for each male as a function of maternal and peer social variables, using the Survival package in R (Therneau & Lumley, n.d.). For each male, the observation period extended from his date of birth until his dispersal, death, or the end of the study (whichever came first). Proportional hazards models assume that model covariates have a constant, proportional (i.e., multiplicative) effect on the baseline risk of event (in this case, dispersal) (Therneau & Grambsch, 2013). However, the proportional hazards assumption can be violated when the effect of a covariate (predictor) on the hazard rate changes over time. To test for violations of proportional hazards assumption, we first built a hazard model using the `coxph()` function with age at dispersal (continuous) as our outcome variable, adding covariates to our full model and performed model diagnostics with a scaled Schoenfeld residual test using the `cox.zph()` function. None of our predictors violated the proportional hazards assumptions suggesting that they are time-independent. After performing all checks, we fit a multivariate cox model with the
following predictors: maternal rank at each month (continuous), early sibling arrival (yes/no/neither), maternal loss before 2.5 years (yes/no), cohort size (integer), unit size (integer). We also included male ID as a random effect. Because male dispersal showed no seasonal trends (Fig. S2.7), we did not include seasonal variables in this analysis.

Results

Androgens across male ages

Fecal androgen metabolites in male geladas demonstrated the expected parabolic pattern associated with age. In brief, fAMs were higher in males aged 1-2 years (almost showing adult fAM levels), reached a nadir between ages 2-3 years, and subsequently became higher from ages 3-10 years, becoming rapidly higher each year after the median age of dispersal (6.61 years) and reaching highest levels around 10 years when males reach full sexual maturity (Fig. 2.1).
Figure 2.1. Mean fecal androgen metabolite levels (ng/g) in male geladas with known ages (<1-10 years) with error bars representing the standard error of the mean. The gray rectangle represents the dispersal age range, black solid line indicates median age at dispersal (6.61 years) and italicized numbers represent the number of males sampled for each age category.

What factors predict androgen profiles?

In dependent males (<2.5 years), the only significant predictor for fAMs was male age at sample collection, with males showing lower fAMs as they got older (Fig. 2.2A). In juvenile and subadult males (>2.5 years), age was also a significant predictor but affected fAMs in the opposite direction (a pattern we expected based on known vertebrate male development and from our biological validation in this population) (Fig.
Additionally, we found that maternal rank (at birth) was significantly associated with androgen production, such that males born to high-ranking mothers had lower age-specific androgens (Fig. 2.2 B,C). Specifically, males with high-ranking mothers had 12% lower fAMs compared to males with low-ranking mothers. We did not find any effect of seasonal predictors, cohort size, or unit size on androgen levels. We also ran the androgen model using immediate maternal rank assignment (i.e., maternal rank at the month of sample collection) and found similar results (Fig. S2.8, S2.9). Model averaged coefficients, standard errors, confidence intervals, and significance levels for each predictor variable are presented in Table 2.2 and 2.3 (Supp Materials).
Figure 2.2. Panel A shows a model coefficient plot showing the effect size and direction of estimates for each of the predictors (obtained after model averaging) for male geladas aged <2.5 years old and panel B shows model coefficient plot for male geladas aged >2.5 years old. Estimates are indicated on top of each bar. The gray line indicates an effect size of zero, with points falling on the left indicating lower fAMs for that predictor and points falling on the right indicating higher fAMs. Points here represent
coefficient estimates and error bars indicate the 95% confidence intervals around those estimates. Error bars that do not overlap 0 indicate a reliable effect of the predictor.

Panel C shows the effect of maternal rank on log fAMs values in male geladas aged >2.5 years old. Rank is coded here as a categorical variable by splitting proportional elo scores at the middle: >0.5 High Rank, <0.5 Low Rank.

**Do males have higher androgen levels surrounding dispersal?**

We did not observe higher androgen levels around male dispersal date in geladas (Fig S2.10). Separating individual males into early, mean, and late dispersal categories also did not show any clear patterns (Fig. 2.3). Additionally, we did not have any samples post dispersal from our early-dispersing males. Note, that even though it appears that mean dispersers 3 months prior to dispersal have higher fAMs, we only have one sample each from 3 different males. The same applies for late dispersers 2 months post dispersal when higher fAMs are observed – we have one sample each from 6 different males. Wilcoxon tests showed that fAMs from males 2 months before dispersal were not significantly different from fAMs collected from the same males 2 months after dispersal [V = 14, p = 0.47] (Fig. S2.11).
Figure 2.3. Log transformed fAMs (ng/g) three months around dispersal show no clear surge in androgen levels. We categorized males as early (dispersed at <5.5 years of age), mean (dispersed between 5.6-7.7 years of age) and late dispersers (dispersed at >7.7 years of age). The black line indicates the month of dispersal and numbers at the bottom indicate the number of males sampled at each time point.

What factors predict age at dispersal?

The number of males that dispersed from their natal units for each age category is shown in Fig. 2.4. Median age of final dispersal is 6.61 years for this population [61 males; range = 3.66-8.89 years; std dev = 1.38 years]. Males in this population take an
average of 1.48 years from initial to final dispersal although this period can range from 0-4 years (STD = 1.14 years, N = 11 males). A Cox proportional hazards model showed that the only significant predictor for age at dispersal was the presence of male peers and unit size (Fig. 2.5): males with more peers dispersed at an earlier age than males with fewer peers [hazard ratio = 1.63; CI = 1.01-2.61; p = 0.04], and males from larger units dispersed at an earlier age than males from smaller units [hazard ratio = 1.49; CI = 1.04-2.14; p = 0.03]. Hazards ratios, standard errors, confidence intervals, and significance levels for each predictor variable are presented in Table S2.4 (Suppl. materials).

To inspect the effect of each category of predictor on dispersal age, I generated individual Kaplan-Meier curves adding predictors related to maternal resources (Fig. S2.12) and peer resources separately (Fig. 2.6). Since cohort size and unit size significantly affected dispersal age, we generated Kaplan-Meier curves to visualize the effect of these two continuous variables on dispersal age by converting them into categorical variables: males with few male peers (0-1 male peers) and >1 male peer; males living in small (1-4 females), medium (5-7 females), and large (>8 females) units. Kaplan-Meier curves show that males with 0-1 peers dispersed later than males with more than one peer and males living in large units dispersed earlier than males living in small or medium units (Fig. 2.6). Next, we conducted an additional analysis by splitting up the cohort size variable into the number of older and younger peers and built the same hazards model with the previous set of predictors. We found that having older or
younger peers within the unit did not have an opposing effect on dispersal timing (Fig. S2.13).

**Figure 2.4.** Estimated numbers of males dispersing in each age category. Numbers on top of bars represent the number of males censored for that age category while numbers inside the bar in white represent the actual number of males dispersing in that age category.
Figure 2.5. Proportional hazards ratios for age at dispersal in male geladas. Males with larger cohort (i.e., more male peers in their units) and larger units disperse earlier. Point estimates higher than one indicate an earlier age of dispersal (increased likelihood of dispersal event, indicated in purple) and points lower than one indicate a later age of dispersal (decreased likelihood of dispersal event, indicated in black).
Figure 2.6. Panel A shows Kaplan-Meier curves showing differences in age at dispersal for males with zero or one male peer and with more than one peer in the unit. Panel B shows Kaplan-Meier curves showing differences in age at dispersal for males living in units that were small (1-4 females), medium (5-7 females), and large (>8 females). Juvenile male geladas with more male peers and in larger units disperse at earlier ages. All data are right censored.

Discussion
After validating an in-house epiandrosterone assay for measuring fecal androgen metabolites for use in geladas, I quantified the normative pattern of androgen production in males during development. Androgens were higher (at nearly adult levels) during the first year of life, and subsequently lower in the second year and third year. From the third year onwards, androgens rose steadily each year up to age 10. In addition to age, the only other variable that predicted male androgen levels was
maternal rank; males with high-ranking mothers (at the time of the male’s birth) had slightly lower age-specific fecal androgen metabolite levels than males with low-ranking mothers (the same pattern did not hold true for males below 2.5 years of age). The median age at final dispersal for males in this population is 6.61 years, and, regardless of when males dispersed, they did not exhibit higher androgen levels surrounding dispersal. The only variables that predicted age at dispersal were a male’s cohort size (the number of male “peers” within his natal unit) and unit size (number of females in the unit), with more peers and larger units associated with earlier dispersal.

Age specific androgen production in developing male geladas
Male gelada infants exhibit high androgen levels, which gradually decline shortly after weaning (around 1.5 years, Lu et al., 2017) and reach a nadir when males gain independence from their mothers (around 2.5 years, which corresponds to the mean interbirth interval; Roberts et al., 2017). The high levels of androgens in 1- and 2-year old males is a commonly observed pattern in primates, including humans (Bernstein et al., 2012). The source of elevated circulating androgens in neonates could be attributed to multiple factors, such as the continued organizational activity of testosterone known to kick in during development in male fetuses, the persistent activity of fetal Leydig cells, or due to the cross-reactivities of the antibody with DHEA (Dehydroepiandrosterone) metabolites present in the mother’s milk (Fouquet et al., 1983; Petrullo et al., 2019). The post-weaning period corresponds to the decline in fecal androgens as infants gain independence (Fig. 2.1). After age 3, androgen levels become higher each year and we observe a marked rise in androgens from ages 6-9, which coincide with the arrival of
secondary sexual characteristics (Beehner et al., 2016) and the latter half of the dispersal range for this population. This pattern is consistent with previous studies that have documented an increase in androgens as males transition from juvenile to adults along with changes in dispersal status and mating behavior - hyenas: (Holekamp & Smale, 1998; Holekamp & Sisk, 2003), baboons and geladas: (Beehner et al., 2006; Beehner et al., 2009; Gesquiere et al., 2005). Such an increase in androgens may additionally be associated with other male maturational milestones such as attainment of adult male stature (Setchell et al., 2006), an increase in body mass and musculature, and elongation of canines (Galbany et al., 2015; Setchell & Wickings, 2004); although we do not yet have systematic data on these measures for individual male geladas.

Maternal rank predicts androgen levels in juvenile male geladas
With respect to our androgen analyses, we found some support for the idea that the maternal social environment can alter the pace of male development. Similar to many other cercopithecoids, female geladas form stable linear dominance hierarchies within their units that are inherited from mother to daughter (le Roux et al., 2011; Tinsley Johnson et al., 2014). A recent study on the same population found that low-ranking mothers experience higher glucocorticoids (a steroid hormone that indicates higher metabolic demands; (Sapolsky et al., 2000) during gestation than high-ranking mothers (Carrera et al., 2020). This indicates that maternal rank has the potential to set up offspring for future social conditions even before birth, similar to other mammalian taxa (Berghänel et al., 2017). For post-independence males, we found that males with lower
ranking mothers (at the time of their birth) had higher age-specific androgen levels than males with higher ranking mothers.

This supports our prediction that low maternal rank at birth may push males towards “faster” development (in this case, higher androgen levels at each age). To our knowledge, only one other study on non-human primates has examined the role of rank-related maternal effects on androgen levels in male offspring; in mandrills (*Mandrillus sphinx*), maternal rank was not a significant predictor of free testosterone in young males (0-9 years). However, maternal rank did significantly influence other developmental hormones in this population; males with high-ranking mothers exhibited higher levels of insulin like growth factor-1 (IGF-1) and lower levels of growth hormone binding protein (GHBP) compared to males with low-ranking mothers (Bernstein et al., 2012a). Additionally, the mandrill study found that maternal age affected testosterone levels in males — males with older mothers had higher circulating testosterone than males with younger mothers. Few other studies have examined the direct relationship between maternal rank and androgen production in male offspring, but there have been studies of rank-related maternal effects on other aspects of offspring phenotype. For example, in spotted hyenas (*Crocuta crocuta*), males with high-ranking mothers exhibited higher rates of aggression as adults (Dloniak et al., 2006). Taken together, these studies suggest that mothers can have direct or indirect influence over their son’s developmental timing.

**No observed surge in androgen levels around dispersal in geladas**
It is well known that elevations in androgen levels often accompany dispersal in other species (Akinyi et al., 2017; Holekamp & Smale, 1998; Holekamp et al., 1984). Interestingly, in geladas, we did not observe a similar trend (Fig. 3). We suggest two explanations for this. First, dispersal itself may not be associated with the same risks for geladas as it is for other female philopatric species (Alberts & Altmann, 1995; Jack & Fedigan, 2004; Wolff, 1994) and, therefore, may not require the requisite androgen activation of secondary sex characteristics (e.g., weaponry and musculature, (Galbany et al., 2015; Leigh et al., 2008) and behavior (e.g., willingness to engage in rival challenges or increased vigilance, (Enigk et al., 2020; Harrison et al., 2021) typically associated with dispersal or maturation. Instead, gelada males disperse to, and reside within, the same bachelor group for an average of 1.27 years (range = 0.09-2.41 years, SD = 0.79 years, N = 10 males with known bachelor tenures) where they spend more time resting, foraging, and grooming than adult males in reproductive units (Pappano, 2014). Moreover, aggression is rarely observed between bachelors (personal observation, Sen). Only when bachelor males finally challenge and defeat a dominant male, do they exhibit a significant rise in androgen levels (Pappano & Beehner, 2014).

Second, our dataset did not include sufficient hormone sampling immediately around the time of dispersal, weakening our ability to detect slight elevations in fAMs across this time (although we feel confident that we would have detected any large rises in fAMs). We speculate that this absence of surge in androgens is due to the fact that dispersal is not as risky for geladas as for other cercopithecines. Therefore, we propose that exiting the bachelor group, not entering it, is the life history stage in geladas that is
equivalent to dispersal for other male-dispersing taxa where androgens play a huge role and may even have downstream fitness effects. This is particularly difficult to study in geladas; as it would require tracking developing males as they emigrate from natal units, transfer between bachelor groups, and ultimately join known reproductive units. Currently, we do not have the capacity to study this with the data collected in the last 15 years.

**Male peers and large unit size predicts earlier dispersal in juvenile male geladas**

Male geladas with more peers and those living in large units dispersed earlier compared to those with fewer peers and those living in small units. Previous research has shown that male geladas (compared to female geladas) seek out more play partners, engage in more rough-and-tumble play, and have more play partners outside their units (Barale et al., 2015). Moreover, males with mothers that are less well-integrated into the female social network are more likely to seek out these play-based relationships (Barale, 2014). Because the transition to adulthood for natal males requires them to first navigate entry into an all-male group (bachelor group) followed by entry into a reproductive unit (Barale, 2014; Pappano & Beehner, 2014), close relationships with male peers likely provide young males with important socialization and competitive skills that help prepare them for these transitions. Similarly, male vervet monkeys (*Chlorocebus pygerythrus*) dispersed earlier when they had peers (compared to no peers), possibly indicating a preference for dispersing with another male to reduce the risks of solitary dispersal (Cheney & Seyfarth, 1983).
By contrast, in another multi-level society, the Assateague feral ponies (*Equus ferus*), the opposite result was reported; males dispersed significantly later when they had more peers (Rutberg & Keiper, 1993). The authors suggest that these males remain in the natal group longer because they benefit from peer interactions where they can practice their fighting skills prior to challenging a leader stallion. Although the direction of the results is in a different direction, the selection pressures might be the same. That is, males in both cases benefit from the presence of peers – in geladas this occurs pre and post-dispersal, while in feral ponies this occurs pre-dispersal. Our results support the hypothesis that males will alter their dispersal timing to maximize these male-male interactions and that male peer interactions in social taxa are fundamental for reproductive success (Bekoff, 1977; Berger, 1987).

We found a significant effect of unit size on age at dispersal – males in larger units dispersed earlier than males in smaller units. As larger units are likely to have more juveniles than smaller units, we speculate that the males in these units may be able to form bachelor groups more easily than juvenile males with fewer within-unit peers. These large units may provide a catalyst for males in smaller units to form playgroups, ultimately facilitating their dispersal alongside related and unrelated male peers. Moreover, these results on juvenile male geladas parallel the effect of unit size in female life history. A recent analysis conducted on the same population showed that female geladas in larger groups matured earlier (Feder et al. 2022). Individuals growing up in large groups may benefit from an accelerated life history (faster development) to reduce the risks associated with male takeovers that disproportionately occur in large
units (Tinsley Johnson et al., 2018) and that are known to cause injuries and death for different group members (Schneider-Crease et al., 2020).

Our estimate for cohort size represents the lowest estimate of the number of peers that each male has at any given time as there will always be additional peers available in other reproductive units across the band. Nevertheless, we still found an effect; having more peers predicts earlier dispersal. The two youngest-dispersing males (dispersing at <4 years) dispersed simultaneously from the same unit suggesting that having a dispersing partner may prompt earlier dispersal. As juvenile mortality in this population is extremely low (Sloan et al., 2022), these disappearances are more likely to be dispersal events than deaths, particularly since they were not preceded by any injuries or takeovers. Contrary to expectations, having older peers did not accelerate (and having younger peers did not delay) dispersal timing (Fig. S13). This suggests that just the presence of both categories of peers, regardless of peer age, pushes males to disperse earlier. Additionally, when we broadly categorize cohort size by the number of peers, having more peers predicts an earlier age of dispersal (Fig. 6). In summary, our results suggest that having more peers and living in larger units may: (1) accelerate some aspects of male life history trajectories, (2) provide more potential partners to disperse with, and (3) furnish more potential known partners that have already dispersed creating a bachelor group that is easy to join.

**Dispersal in multi-level social system**
Living in a multi-level society may provide multiple options for dispersing male geladas, and, depending on their current social environments, males may choose to disperse to a bachelor unit within the same band or emigrate to a different band altogether. It is possible that males that disperse with peers from their units form their own bachelor group and continue associating with their natal band. This pattern of context-dependent dispersal strategy has also been observed in wild giraffes (Giraffa camelopardalis tippelskirchi) that live in a multi-leveled society and in feral horses that live in bands (Bond et al., 2021). A comparative analysis of male dispersal patterns across primates indicates that parallel dispersal (dispersing with partners) will be more common in social systems where males form coalitions, since coalitionary behavior aids males during inter-group as well as intra-group encounters (Jack et al., 2009). The gelada system may offer additional support for this result - since we see both parallel dispersal and possible coalitions in geladas. Gelada bachelor males form coalitions during some takeovers when several bachelors simultaneously engage in challenging a single leader male (Pappano, 2013). Therefore, juvenile males may disperse with familiar peers or join up with familiar bachelor groups that associate with their natal band to form such coalitions.

Our study on male gelada development had some limitations. First, we had hormone samples (for the androgen analysis) from only half of the males that were part of the dispersal analysis. The long-term project only started monitoring the demography of juveniles in 2011, and most hormone samples since then were collected opportunistically without targeted sampling. Therefore, we were unable to extend the full
suite of variables to the androgen model, as well as test whether androgen levels predict dispersal timing. Second, we had to use a proxy for cohort size. Although the number of male peers within the unit serves as a coarse estimate for each male's peer social environment, it does not reflect the full suite of social interactions that are available to each juvenile male. A more fine-grained approach should focus on juvenile social network analysis to examine how network statistics and social integration influence androgen levels and age at dispersal (Barale, 2014). Moreover, a network approach would allow us to simultaneously examine the reverse relationship – the influence of androgen levels on social network integration. Third, demographic context almost certainly influences male dispersal timing. Our analyses were based on the age at final dispersal, but we also have some (limited) data on the ages when males first (temporarily) disperse. Males that exhibit the drawn-out dispersal strategy might do so because they cannot find a suitable bachelor group to join, because they are waiting for potential dispersing partners, or because they are building additional social skills during this time. Other social variables – such as presence of probable fathers and group fissions – which are known to influence female development, might similarly influence male development in geladas (Jack et al., 2012; Lu et al., 2021). Finally, although we do not have the data yet to identify whether any form of accelerated development (higher age-specific androgens or early dispersal) is an adaptive response for male geladas in resource-rich or resource-poor environments, we hypothesize that slower development and remaining longer with the natal unit can allow males to fully develop their social skills within the safety of their natal group (similar to what Bekoff 1977 proposed) making it easier to join bachelor groups as fully grown males. Currently, we do not have
longitudinal data on natal males to test this prediction given the difficulty in tracking
males post-dispersal. As the project adds years of data to our study, we will be able to
unravel a more detailed picture of how early social environments affect male
development and quantify the effect of accelerated or delayed male life history
trajectories on male reproductive success.

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This study would not have been possible without the continuing support of our Ethiopian
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References


Barale, Caitlin Laurel. (2014). The effects of early social context and social types on dispersal and reproductive strategies in male geladas (Theropithecus gelada) [Princeton University].


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Supplementary Materials

**Table 2.1.** Sampling distribution for each type of androgen analysis.

<table>
<thead>
<tr>
<th>Analysis type</th>
<th>Age range</th>
<th>Total samples</th>
<th>No of males</th>
<th>Mean samples / age group</th>
<th>SD</th>
<th>Range</th>
</tr>
</thead>
<tbody>
<tr>
<td>RIA vs EIA comparison</td>
<td>0 - 9</td>
<td>1048</td>
<td>49</td>
<td>105</td>
<td>90</td>
<td>1-262</td>
</tr>
<tr>
<td>Biological validation</td>
<td>0 - 10</td>
<td>1611</td>
<td>70</td>
<td>134</td>
<td>124</td>
<td>5-351</td>
</tr>
<tr>
<td>Androgen modelling (males &lt; 2.5 years)</td>
<td>0 - 2.5</td>
<td>126</td>
<td>29</td>
<td>42</td>
<td>38</td>
<td>6-81</td>
</tr>
<tr>
<td>Androgen modelling (males &gt; 2.5 years)</td>
<td>2.5 - 9</td>
<td>771</td>
<td>43</td>
<td>107</td>
<td>65</td>
<td>1-194</td>
</tr>
<tr>
<td>Androgens around dispersal</td>
<td>5.6-8.8</td>
<td>73</td>
<td>22</td>
<td>3</td>
<td>2</td>
<td>1-8</td>
</tr>
</tbody>
</table>
Figure S2.1. The slopes of the standard curve and serially diluted fecal pool sample were parallel. Slopes were obtained by plotting the log-transformed concentration of our standards or our fecal pool as a function of percent binding.
Figure S2.2. Accuracy curves plotting expected log concentrations vs observed log concentrations of hormone values obtained by running pure standards, and standards spiked with male pool at 1:160 dilution.
Figure S2.3. The epiandrosterone EIA assay better discriminates higher androgen levels. Fecal androgen metabolite levels in (ng/g) for samples run using Epiandrosterone EIA and MP Biomedicals Double Antibody Testosterone RIA kit. Italicized numbers represent the number of males for each age category (i.e., 1-9 years old).
Figure S2.4. RIA measures of fecal testosterone metabolites were moderately associated (Pearson's correlation coefficient $r = 0.54$) with EIA measures of fecal immunoreactive epiandrosterone. Log (ng/g) values of fecal androgen metabolites for the same fecal hormone samples (1048 samples from 49 males) run with the RIA and the EIA.
Seasonality of fecal androgen levels in juvenile male geladas.

Figure S2.5. Purple squares and lines represent the mean fAMs from male samples plotted across the year. Upward facing orange triangles represent average maximum temperature (calculated across the previous 30 days). Downward facing orange triangles represent mean minimum temperature (calculated across the previous 30 days). Gray bars represent cumulative rainfall over the previous 90 days. Italicized numbers on top of x axis labels indicate the number of males that we had fecal samples from each month for the duration of the study period (2011-2020).
Figure S2.6. Histogram indicating the distribution of non-transformed fecal androgen metabolite concentrations (ng/g) for our dataset (A). Quantile-quantile plot for the same data (B). Note that the distribution is lognormal (which is typical for hormone values).
Figure S2.7. Final dispersal events in male geladas are higher in July but otherwise not seasonal. Counts of final dispersal events observed in our study population across months (2012-2020) indicate that males disperse in all months of the year, with possibly a slight increase in July. Panel includes males that had estimated final emigration dates within a 30-day range (n = 34 males).
Effect of immediate maternal rank (maternal rank computed each month) on male androgens

To test for activational effect of maternal rank on male androgens, I ran the same set of androgen models by modifying the maternal rank variable from maternal rank at birth to maternal rank at each month of sample collection. In both cases (i.e. when considering monthly maternal rank and maternal rank at birth), higher maternal rank leads to lower fAM levels in males > 2.5 years of age (Fig S8, S9).
**Figure S2.8.** Panel A shows a model coefficient plot showing the effect size and direction of estimates for each of the predictors (obtained after model averaging) for male geladas aged <2.5 years old and panel B shows model coefficient plot for male geladas aged >2.5 years old. Panel C shows the effect of monthly maternal rank on residual fAMs in male geladas aged >2.5 years old. Points here represent coefficient estimates and error bars indicate the 95% confidence intervals around those estimates. Points to the left of 0 indicate a negative effect on fAMs. Points to the right of 0 indicate
a positive effect on fAMs. Error bars that do not overlap 0 indicate a reliable effect of the predictor.
Figure S2.9. Males with low-ranking mothers have higher log fAMs. Panel A shows predicted log fAMs in male geladas aged >2.5 years old with high- and low-ranking mothers at birth. Panel B shows predicted log fAMs in males with high- and low-ranking mothers at each month of sample collection. Predicted log fAMs were obtained by using the predict() in R, holding all other model covariates at their mean value while varying maternal rank.
Coefficient tables for androgen models

Table 2.2. Model averaged coefficients obtained from all LMM models for fecal androgen metabolite levels in males <2.5 years of age (126 samples, 29 males). CI=confidence interval.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Estimate</th>
<th>SE</th>
<th>95% CI</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>(Intercept)</td>
<td>5.90</td>
<td>0.05</td>
<td>5.80 - 6.00</td>
<td>&lt;0.001**</td>
</tr>
<tr>
<td>Age</td>
<td>-0.35</td>
<td>0.08</td>
<td>-0.52 - -0.19</td>
<td>&lt;0.001**</td>
</tr>
<tr>
<td>Maternal rank (at birth)</td>
<td>0.01</td>
<td>0.11</td>
<td>-0.20 - 0.21</td>
<td>&gt;0.90</td>
</tr>
<tr>
<td>Cohort size</td>
<td>-0.15</td>
<td>0.09</td>
<td>-0.34 - 0.03</td>
<td>0.10</td>
</tr>
<tr>
<td>Unit size</td>
<td>-0.06</td>
<td>0.10</td>
<td>-0.25 - 0.14</td>
<td>0.60</td>
</tr>
<tr>
<td>Cumulative rainfall (mm)</td>
<td>0.07</td>
<td>0.09</td>
<td>-0.12 - 0.25</td>
<td>0.50</td>
</tr>
<tr>
<td>Max temp (°C)</td>
<td>0.05</td>
<td>0.08</td>
<td>-0.12 - 0.22</td>
<td>0.60</td>
</tr>
</tbody>
</table>
Table 2.3. Model averaged coefficients obtained from top LMM models for fecal androgen metabolite levels in juvenile and subadult males (771 samples, 43 males). CI=confidence interval.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Estimate</th>
<th>SE</th>
<th>95% CI</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>(Intercept)</td>
<td>5.90</td>
<td>0.02</td>
<td>5.80 - 5.90</td>
<td>&lt;0.001**</td>
</tr>
<tr>
<td>Age</td>
<td>0.38</td>
<td>0.03</td>
<td>0.29 - 0.44</td>
<td>&lt;0.001**</td>
</tr>
<tr>
<td>Maternal rank (at birth)</td>
<td>-0.12</td>
<td>0.05</td>
<td>-0.22 - -0.02</td>
<td>0.014*</td>
</tr>
<tr>
<td>Cohort size</td>
<td>0.01</td>
<td>0.05</td>
<td>-0.08 - 0.11</td>
<td>0.8</td>
</tr>
<tr>
<td>Unit size</td>
<td>-0.05</td>
<td>0.05</td>
<td>-0.15 - 0.05</td>
<td>0.3</td>
</tr>
<tr>
<td>Cumulative rainfall (mm)</td>
<td>0.00</td>
<td>0.04</td>
<td>-0.07 - 0.07</td>
<td>&gt;0.9</td>
</tr>
<tr>
<td>Max temp (°C)</td>
<td>0.05</td>
<td>0.03</td>
<td>-0.02 - 0.12</td>
<td>0.2</td>
</tr>
</tbody>
</table>
Androgens around dispersal

Figure S2.10: Residual fecal androgen metabolite levels in log (ng/g) (controlling for male age) three months around dispersal show no clear pattern. Dashed gray line indicates dispersal.
Figure S2.11. Plot showing log fAMs of samples from 7 males within a window of 2 months before and after dispersal. Wilcoxon’s signed rank test showed that males do not significantly differ in fAMs between the two categories [V = 14, p-value = 0.47].
Coefficient table for dispersal model

Table 2.4. Hazards ratios obtained from cox proportional hazards models. CI=confidence interval.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Hazards ratio</th>
<th>Beta (SE)</th>
<th>95% CI</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Maternal rank</td>
<td>0.84</td>
<td>-0.17 (0.18)</td>
<td>0.60 - 1.19</td>
<td>0.33</td>
</tr>
<tr>
<td>Early sibling arrival = YES</td>
<td>1.04</td>
<td>0.04 (0.35)</td>
<td>0.52 – 2.08</td>
<td>0.91</td>
</tr>
<tr>
<td>Maternal loss = YES</td>
<td>0.54</td>
<td>-0.61 (0.41)</td>
<td>0.24 - 1.21</td>
<td>0.14</td>
</tr>
<tr>
<td>Cohort size</td>
<td>1.63</td>
<td>0.49 (0.24)</td>
<td>1.01 – 2.61</td>
<td>0.04*</td>
</tr>
<tr>
<td>Unit size</td>
<td>1.49</td>
<td>0.40 (0.18)</td>
<td>1.04 - 2.14</td>
<td>0.03*</td>
</tr>
</tbody>
</table>
Figure S2.12. Variables representing access to maternal resources do not affect dispersal in male geladas. Kaplan-Meir curves showing effect of each maternal resource variable (maternal rank, early sibling arrival, maternal loss) on dispersal age in male geladas.
Figure S2.13: Results of a Cox proportional hazards model of male age at dispersal where cohort size was separated by older (males born within 1.5 years before DOB) and younger peers (males born within 1.5 years after DOB). Males with larger units disperse earlier. However, the effect of presence of younger and older peers led to an earlier age of dispersal suggesting that the age of peers might be less important than having peers to disperse with.
Chapter 3: Infanticide is Less Likely in Groups with More Fertile Females
Following Takeovers in Wild Geladas

Sharmi Sen and coauthors Alice Baniel, Amy Lu, Noah Snyder-Mackler, Thore J. Bergman, and Jacinta C. Beehner.

Abstract
Offspring mortality is an important measure of individual reproductive success and can help us examine the evolution of reproductive strategies. Here, we take an integrative approach to examine how maternal attributes, group attributes, seasonal variables, and the arrival of a new dominant male, affect offspring mortality using 14 years of data from a population of wild geladas (Theropithecus gelada) living in the Simien Mountains National Park, Ethiopia. Overall offspring mortality rate (18.2%) for this population is low compared to other cercopithecine primates. Offspring that experienced dominant male replacements before 18 months (age of weaning) have reliably higher mortality than offspring experiencing no takeover. Interestingly, even though takeovers are the key drivers of infant mortality in this population, 46.7% of takeovers did not result in offspring death even when new males had the opportunity to commit infanticide. We examine this variability in offspring survival post takeover by first assessing variability within takeovers themselves and identify factors that might drive infant survival post takeovers. We find that infant age at takeover and number of cycling females are the strongest
predictors of infant survival - infants are more likely to survive if they are older during takeovers and if there are more cycling females available for the new male to reproduce with. Further, former leaders were more likely to be present in the unit after a takeover when there were more vulnerable offspring in the unit. Our results suggest that although takeovers increase offspring mortality overall, new dominant males do not commit infanticide when there are reproductive opportunities already present at takeover. Future research will focus on proximate mechanisms underlying these variation in infanticide strategies for leader males and quantify relative fitness payoffs.

Introduction

Measuring offspring mortality is an important way of assessing evolutionary fitness (Clutton-Brock, 1988; Gadgil & Bossert, 1970; Kaplan et al., 2000; Sibly & Brown, 2009; Stearns, 1992). At the demographic level, offspring mortality (or survival) in a population helps us understand parameters driving growth rates (Altmann & Alberts, 2005), population-specific life-history traits (Charnov, 1991; Clutton-Brock, 1988; Clutton-Brock, 2016; Holliday, 1994), and the evolution of parental care (Clutton-Brock 1991, Vila-Gispert et al., 2002). At the organismal level, offspring mortality can help us identify reproductive strategies within a population by quantifying variation in reproductive success among individuals (Cabana & Kramer, 1991; Descamps et al., 2008; Manguette et al., 2019; Rosenbaum et al., 2016).

Many iteroparous taxa (e.g., many large mammals, including most non-human primates) with slower life histories produce only one offspring per litter, and in these
cases the success or failure of each reproductive event is examined with respect to the individual characteristics of the mother-offspring dyad, the group, and the specific environmental context at the time of the reproductive event (Maestripieri & Mateo, 2009). Because research examining offspring mortality in long-lived taxa that produce only one offspring at a time are limited by small sample sizes, such studies require examining multiple reproductive events across a female’s lifespan and are best conducted with long-term studies of wild populations (Alberts, 2019; Clutton-Brock & Sheldon, 2010; Zipple & Lange, 2021).

One common source of offspring mortality in mammals is infanticide by males (Lukas & Clutton-Brock, 2013; Lukas & Huchard, 2014). Infanticide allows a new immigrant male to reproduce with lactating females earlier than if he had waited for them to wean their offspring. It may also serve to reduce the relative reproductive success of the male’s competitors (van Schaik et al., 2004). In many taxa where infanticide is widespread, infanticide is commonly preceded by the arrival of a new dominant male (van Schaik & Janson, 2000).

Dominant male replacements can occur via multiple behavioral pathways that represent variable male strategies spanning from least aggressive to most aggressive (Teichroeb & Jack, 2017). These include subordinate males gradually rising in male dominance hierarchy following the death or disappearances of higher ranking males (succession or queuing) observed in male spotted hyenas (*Crocuta crocuta*), and saki monkeys (*Pithecia aequatorial*) (Di Fiore et al., 2007; East & Hofer, 2001), males attaining rank
during the formation of a new group or during fission events (Amann et al., 2017), and subordinate males gaining rank through direct physical contests between immigrant or resident males and the dominant male (takeovers) as observed in multiple mammalian species (Amann et al., 2017; Brasington et al., 2017; Marty et al., 2015; Packer & Pusey, 1983). There can be considerable variation within takeovers themselves and the arrival of a new dominant male can lead to cascading events such as females producing deceptive sexual swelling, and an increased risk of infant mortality and injury (Charpentier & Drea, 2013; Schneider-Crease et al., 2020).

Despite how widespread infanticide is, there are surprisingly few studies that examine the factors that keep infants alive in the face of an infanticidal threat. That is, what factors contribute to some infants being more likely to survive than others? Most research on this question has approached it from the perspective of female counterstrategies – the adaptations (behavioral or physiological) that females have in place that can lower the chances of infanticide (reviewed in Palombit 2015; Beehner and Lu, 2013). However, there are mitigating factors that are unrelated to female counterstrategies; for example, the possibly protective presence of the infant’s father, a “dilution effect” that other infants provide, a “distraction effect” that other fertile females provide. We specifically focus on these.

The presence of the putative father can potentially mitigate offspring mortality in situations when offspring experience maternal loss or during the arrival of a new immigrant male (Anand et al., 2022; Chaves et al., 2020; Morrison et al., 2021; Reddy &
Mitani, 2019; Robbins, 1995). Fathers can impact offspring survival in a number of ways – by directly offering protection to vulnerable infants during socially unstable periods (direct paternal care) (Buchan et al., 2003; Sargeant et al., 2016), by forming long term associations with mothers (Städele et al., 2021), or by forming male-male coalitions during intergroup encounters (Cheng et al., 2022; Rosenbaum et al., 2016). Where infanticide by males is a common strategy, a common female counterstrategy among primates is for mothers to form an alliance with the potential father(s) of the offspring (Palombit et al., 1997). These fathers may directly intervene to protect their offspring, or their presence alone may simply serve to deter aggression from the new dominant male (Gubernick et al., 1993).

Larger groups with more females generally attract immigrant males and thus experience more infanticide (Pusey & Packer, 1994; Teichroeb et al., 2012; Tinsley Johnson et al., 2021). Within larger groups itself, multimale groups can have reduced infanticide rates compared to unimale groups, as males do not benefit from killing infants if their ability to monopolize females is low and females adopt counterstrategies by mating with multiple females (Balme et al., 2013; Broom et al., 2004; Robbins et al., 2013). Additionally, the number of other fertile “available” females in the group may also provide sufficient “distraction” for incoming males that they refrain from infanticide. This “distraction effect” may track group size more generally - with smaller groups having fewer available females at any given time. However, to our knowledge, there is very little direct evidence from studies on male infanticide that suggests infanticide is more likely in smaller groups.
The number of other vulnerable infants in the group may also reduce the chance of mortality for any given infant, in what has been called a “dilution effect” for predators (Hamilton, 1971) or increased vigilance by mothers within the group (Bales et al., 2002). Although not yet tested, infants may directly benefit from the presence of multiple same aged infants by reducing their chances of being killed by ecological or social predators such as bachelors (Pappano et al., 2012). In this study, we take an integrative approach to examine offspring mortality and takeovers in a wild population of geladas (Theropithecus gelada). Our goal here is to understand retrospectively which factors predict infant mortality in a wild population of geladas in general, and whether these factors change when examining infant mortality due to the replacement of a dominant male (takeovers).

The gelada system is ideal for this study for several reasons. First, we have a large sample size of multiple “groups” across 14 years of near-continuous monitoring of this population. Geladas live in a complex, multilevel society that includes dozens of core groups (hereafter reproductive units), each comprising one dominant leader male, 1-12 adult females and their related offspring, and possibly 1-5 subordinate follower males that may include a former leader male (Snyder-Mackler et al 2012). Several reproductive units with overlapping ranges aggregate to form bands, and bands often join together across the year to form a community (Snyder-Mackler et al 2012; Snyder-Mackler et al 2014). This multileveled social structure allows us to simultaneously study infants living in different reproductive units independently, each with its own set of socioecological conditions. Second, each reproductive unit undergoes a replacement of
the dominant leader male every few years. Females remain in their natal reproductive units and form matrilineal dominance hierarchies, while males disperse either to join all-male groups known as bachelor groups or attach themselves as subordinate follower males in reproductive units (Sen et al., 2022; Snyder-Mackler et al., 2012; Tinsley Johnson et al., 2014). To gain reproductive access to females in units, bachelors (and possibly follower males) eventually challenge a leader male and if they are successful, they take over as the new leader male (Pappano, 2013; Pappano & Beehner, 2014).

Third, following takeovers, males are known to commit infanticide (Beehner & Bergman 2008). Infanticide appears to be a selective force in many aspects of female reproduction including selecting for male-mediated reproductive changes, such as the Bruce effect (Roberts et al., 2012), male-mediated maturation (Lu et al., 2021), and deceptive sexual swellings (Baniel et al., submitted). Finally, this unusually large dataset of takeovers provides us with variation in the presence of the former leader, the number of vulnerable infants, and the number of fertile females for examining the conditions that may lead to infants being spared from infanticide following a male takeover.

**What factors predict infant mortality in geladas?**

First, we examined the underlying social and ecological drivers of infant mortality. A previous study from this population (Beehner & Bergman 2008) identified that takeovers were disproportionately associated with infant mortality, with the conclusion that sexually selected infanticide is the primary source of infant mortality; however, this was based on only 2 years of data. More recent research has shown that the rate of infant mortality is highest in the largest units (with 8 or more females). This result was
attributed primarily to the effects of takeovers, as larger units were taken over at higher rates than smaller groups, and infanticide was common in the wake of these takeovers (Tinsley Johnson et al., 2021). Additionally, the smallest groups had the highest adult female mortality (and their infants usually died with them) (Tinsley Johnson et al., 2021). This study suggested that smaller groups may be more exposed to predators either because they may be more peripheral within the band or more vulnerable when alone. Here, we update these analyses with 14 years of data from the same population, investigating all known sources of offspring mortality, both within and outside of takeovers, to assess the primary risk factors for gelada infants. We predict that 1) infants with low ranking and primiparous mothers would experience higher mortality rates, 2) infants experiencing takeovers would have higher mortality rates due to infanticide risks, and 3) infants in large groups and/or 4) infants in one-male groups would have higher mortality rates due to increased risk of takeovers (given large number of females attract more bachelors, and followers help extend leader male tenure). Summary of predictions is provided in Table 3.1.

**What factors predict infant survival following a takeover?**

Second, we examined which variables might help keep infants alive post-takeover. Previous analyses of our long-term data demonstrate that not all incoming males commit infanticide, and even among those that do, they do not always kill all vulnerable infants in the unit. Therefore, we investigated the specific circumstances surrounding each takeover *that may spare infants from infanticide*. Here, we seek to identify the common denominators that explain when infanticide is more or less likely to occur.
These factors include those known to affect infant mortality (in general) and infanticide (in particular) in other populations, such as infant age, maternal experience (Blomquist, 2013; Lee et al., 2020), and number of invading males (Engh et al., 2006; Zipple et al., 2017). However, we also examine three specific factors that relate to an incoming male’s opportunity to kill offspring: the presence of the former leader (the putative father of the infant), the number of fertile females (the “distraction effect”), and the number of vulnerable infants (the “dilution effect”). Previous research on this gelada population (Tinsley Johnson et al., 2021) found that infanticide rates were highest in the smallest groups and the largest groups. While the high infanticide rate in the largest groups was attributed primarily to the increase in the number and frequency of takeovers, the high infanticide rate in the smaller groups was largely unexplained. The authors proposed both the dilution and the distraction effect as two possibilities for further investigation (Tinsley Johnson et al., 2021). Here, we predict that infants that are 1) older at the time of takeover, 2) are present in units with more cycling females, 3) in units with former leader male present and 4) in units with fewer immigrant males will experience higher rates of survival. Summary of predictions can be found in Table 3.2.

Methods

Study site and subjects. This research took place in the Simien Mountains National Park, Ethiopia (13°15’N, 38°00’E, elevation 3200-4500 m a.s.l), where the field site of the Simien Mountains Gelada Research Project (SMGRP) is located and long term research on a population of wild geladas has been ongoing since 2006. The dataset for this research comprises the demographic and life history data from 19-21 reproductive
units collected across 14 years (2006-2020). All animals were habituated to observers on foot and were monitored on a near-daily basis.

*Infant births and deaths.* We restricted our dataset to infant births from a total of 163 females where we were able to establish the date of birth within a 2-month window (mean ±SD = 15.2 ±16.8 days, range = 0-62 days, N = 346 infants, 172 males and 169 females). Where the exact date of birth was not known, we assigned the date of birth as the midpoint of the period from which we last saw the female until the time we saw the female again with the new infant. Therefore, all infant ages are known within +/- 2 months. We recorded all infant deaths as the first day a dependent infant (i.e., unweaned infant) was not observed with their mother. Because true weaning is difficult to determine in this population based solely on observations (Carrera et al., in prep), we used the average age at weaning (18 months) ascertained using (i) observations of nursing, (ii) a mother’s resumption of cycling, (iii) gut microbiome analyses, and (iv) C:N isotope ratio analyses (Lu et al., 2017).

*Rainfall and temperature.* We recorded rainfall on a near-daily basis using a rain gauge located in an open area near the field station; we also recorded daily minimum/maximum temperatures using a thermometer mounted under a shaded location. Previous research at this site has demonstrated that rainfall from the previous 90 days accurately reflects green grass availability (the geladas’ primary food resource) (Jarvey et al 2018). Rainfall was also positively related to the number of births (Tinsley Johnson et al 2018). Therefore, we included cumulative rainfall from the previous 90
days as a predictor in all models. Temperature at this site has also been reported to be related to gelada physiology and reproduction – with lower temperatures associated with higher metabolic demands and lower reproduction (Behehner and McCann 2008; Tinsley-Johnson et al 2018). Thus, mean minimum temperature was calculated as the average maximum/minimum daily temperature across the previous 30 days and included as a predictor in all models.

*Maternal attributes.* We assigned maternal parity as a binary category based on whether a female was a first-time mother (primiparous) or had had previous offspring (multiparous). For all analyses, we assigned maternal parity at the time of the infant’s birth (i.e., for a female’s first birth, she would be primiparous). We calculated maternal rank using *ad libitum* behavioral data of adult female dyadic interactions within the same unit that included the “winner” of physical aggression (attacks), non-physical aggression (chases, displacements), and threats (including vocal threats). We used the outcomes of these interactions to calculate elo scores using the R package EloRating (Albers and de Vries 2001; Neumann et al. 2011; Neumann and Kulik n.d.) and our calculations of proportional elo scores have been detailed elsewhere (Baniel et al., 2022; Feder et al., 2022; Sen et al., 2022). For all analyses, we calculated maternal rank at the time of each infant’s birth. Because we do not have accurate maternal rank for our entire dataset, we include this variable in only one model for the overall infant mortality analysis. Further, because this variable does not predict infant mortality in this model (see results), we excluded it entirely from the post-takeover infant survival models.
Group size. Group size for this population (specifically, the number of adult females in a reproductive unit) is associated with many aspects of male and female life history parameters (Feder et al., 2022; Sen et al., 2022; Tinsley Johnson et al., 2021. We therefore included group size in our models on infant mortality and survival, but we did this differently for each model. First, for the overall infant mortality models, we defined group size as the number of adult females present in the unit each month during an infant’s first 18 months. Females were assigned as adults once they exhibited the first signs of sexual swelling on their neck, chest, or perineal region (Roberts et al., 2017). Second, for the post-taking infant survival models, we included two different proxies for group size. Both measures track group size to some extent, but with important differences that will help us identify why males might not kill offspring.

(i) Number of cycling females. The number of cycling females in the unit is the number of females that are not pregnant or lactating at the time of takeover. These females may be actively fertile (exhibiting sexual swellings on their chest, neck, and/or perineal area) or they may be between swellings. The number of cycling females serves as a proxy for an incoming leader male’s reproductive opportunities.

(ii) Number of infants. The number of infants in the unit is the number of dependent infants up to 18 months of age. The number of infants serves as a proxy for the costs of an incoming leader male not committing infanticide, since the number of infants represents the number of lactating females that the male cannot mate with.
Takeovers. We recorded 94 takeovers in 36 reproductive units from 2006-2020. We assigned a start date for takeovers when we first observed a bachelor male or group of bachelors trailing the target unit, with the leader males exhibiting defensive behaviors such as initiating chases, engaging in vocal displays and vocalizing, and sometimes physically fighting the challenger males. Takeovers were deemed successful when a challenger male mated with almost all adult females in the unit and resident leader males began showing submissive behaviors (fear grimace, fear bark) towards the new male. The end date of the takeover was assigned when there was a clear dominant leader in the unit and all females were presenting and/or mating with the new male. For takeovers that occurred when the units were missing for more than 21 days (N=16), we assigned the date of takeover as the mid-point of the missing observation period (mean ± SE= 71.06 ± 10.77 days of uncertainty, range= 22-252 days). In the overall infant mortality models, we included takeover (yes/no) as a predictor based on whether a takeover occurred between the infant’s conception and when the infant reached 18 months of age (the average age at weaning for this population, Carrera et al in prep). Using adlib data and behavioral observations we report descriptive statistics on how takeovers unfold in our study population to provide further demographic context on why certain takeovers do not lead to infant death and help identify male strategies that might be at play.

Likely father / Former leader present. There is evidence from other primates that the presence of a father (even in species with little direct paternal care) can improve survival outcomes for their infants (Rosenbaum & Silk, 2022). Moreover, in this gelada
population, genetic evidence suggests that the leader male is the biological father for 100% of the infants in one-male units (the leader male is the sole male) and 83% of the infants in multi-male units (with 1 or more follower males) (Snyder-Mackler et al., 2012). Therefore, in the absence of paternity data (which is forthcoming), we assigned the leader male as the “likely father” at the time of the infant’s conception. Following a takeover, the presence of the former leader (i.e., the infant’s likely father) may provide some protection against infanticide by the new leader male. In cases where the former leader / likely father is defeated and subsequently disappears, we suspect that he was killed during the challenge (and we have witnessed these deaths several times). However, for about half the takeovers, we have observed that former leaders / likely fathers remain in the unit. Therefore, we expected the presence of a likely father might have some consequences for infant mortality, especially following a takeover.
### Table 3.1. Predictions for infant mortality overall

<table>
<thead>
<tr>
<th>Variable</th>
<th>Type</th>
<th>Prediction</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rainfall</td>
<td>Continuous (mm)</td>
<td>Decreased rainfall → Higher infant mortality</td>
</tr>
<tr>
<td>Minimum temperature</td>
<td>Continuous (°C)</td>
<td>Decreased min temp → Higher infant mortality</td>
</tr>
<tr>
<td>Maternal parity</td>
<td>Categorical (primi/multi)</td>
<td>Primiparous mothers → Higher infant mortality</td>
</tr>
<tr>
<td>Maternal rank</td>
<td>Continuous (elo)</td>
<td>Low maternal rank → Higher infant mortality</td>
</tr>
<tr>
<td>Group size</td>
<td>Discrete (# females)</td>
<td>Larger group size → Higher infant mortality</td>
</tr>
<tr>
<td>Takeover</td>
<td>Categorical (yes/no)</td>
<td>Experienced takeover → Higher infant mortality</td>
</tr>
</tbody>
</table>
Table 3.2. Predictions for infant survival post-takeover

<table>
<thead>
<tr>
<th>Variable</th>
<th>Type</th>
<th>Prediction</th>
</tr>
</thead>
<tbody>
<tr>
<td>Former leader absent</td>
<td>Categorical (yes/no)</td>
<td>Absence of former leader → Lower infant survival</td>
</tr>
<tr>
<td>Number of cycling females</td>
<td>Discrete (# females)</td>
<td>Fewer cycling females → Lower infant survival</td>
</tr>
<tr>
<td>Number of infants</td>
<td>Discrete (# infants)</td>
<td>Fewer infants → Lower infant survival</td>
</tr>
<tr>
<td>Infant age</td>
<td>Continuous</td>
<td>Younger infants → Lower infant survival</td>
</tr>
<tr>
<td>Parity</td>
<td>Categorical (primi/multi)</td>
<td>Primiparous mothers → Lower infant survival</td>
</tr>
<tr>
<td>Number of immigrant males</td>
<td>Discrete (# males)</td>
<td>Many males → Lower infant survival</td>
</tr>
</tbody>
</table>

Data analyses

All data analyses were conducted using R (version 4.2.2, R core team 2022). We outline the nested nature of each dataset below with sample sizes (number of infants) for each model (Fig. S3.1).
**What factors predict overall infant mortality in geladas?**

To examine which factors predict overall infant mortality, we constructed multivariate Cox proportional hazards models in the *survival* package of R (Therneau and Grambsch, 2013). Our outcome variable was infant death (yes/no) for each infant month. Predictors for the first model (*infant mortality model 1*) included the following variables calculated for each infant month: cumulative rainfall (mm, summed across previous 90 days), mean minimum temperature (˚C, averaged across previous 30 days), maternal parity (primiparous / multiparous), group size (number of adult females in the unit), and whether infant experienced a takeover in that unit (yes/no). In a second model (*infant mortality model 2*), we included all the previous predictors plus one additional predictor, maternal rank (the proportional elo score of mothers) (*Fig S3.1B*). For categorical variables, maternal parity and takeover, we set the reference category to multiparous mothers, and did not experience a takeover respectively. We then built a multivariate hazard model with infant death as our outcome variable and these predictors while controlling for maternal ID as a random effect using `cluster()`. Following model fitting, we plotted model coefficient plots using the `plot_model()` in sjPlot package in R (Lüdecke, n.d.).

Cox proportional hazards models are ideal for this analysis as they allow us to simultaneously test the effect of multiple predictors over time. However, these models assume that proportional hazard rates are fixed, and these assumptions can be violated when the effect of a covariate (predictor) on the hazard rate changes over time. To test for violations of proportional hazards assumption, we performed model diagnostics with
a scaled Schoenfeld residual test using the `cox.zph()` function. Scaled Schoenfeld residuals test showed that there was a significant deviation for proportional hazards for the takeover variable in the first infant mortality model (Fig S3.2). We therefore fit a time-varying coefficient for this variable by using `tt()` function available in the survival package to fit time-dependent covariates (Therneau & Grambsch, 2010). We did not have maternal ranks for the early years of the long-term dataset, therefore, to maximize our dataset we fitted two survival models – one without rank as a predictor (N = 59 infant deaths) and one with rank included (N = 45 infant deaths). All models were right censored until infants reached the age of weaning (18 months) or died (whichever came first).

**Takeovers in gelada society**

Using 14 years of long-term data spanning 94 takeovers, we describe general patterns of takeovers observed in our study population. We took ad libitum observations of male-male, male-infant, and male-female interactions during takeovers. We assigned takeovers as successful when we observed the following suite of changes in the unit: (i) adult females started presenting to the new leader male and the new male copulated with one or all females in the unit producing copulation calls, and (ii) the former leader began to interact submissively and associated mostly with juveniles in the unit. We categorized takeovers as “messy” or drawn out if they went on for more than a week before a clear leader emerged in the unit, if there were multiple males trailing the unit and fighting among each other at the same time, if females were mating with more than one male, and if it appeared that the unit was about to fission (increase in frequency of
female-female fights). A “clean” takeover on the other hand was when the unit had a clear dominant leader male within the span of a week or less. Any infant that was under 18 months of age at the time of takeover was considered to be vulnerable and infant disappearances that occurred within 12 months of new leader male’s tenure was attributed as an infanticide. Since we had a few messy takeover cases where there were multiple leader males within a short period of time and units underwent fission/fusion, we left out these takeovers (n = 6) as it was not possible to determine which male had committed infanticide. We seek to explain this variation in infant survival when faced with the threat of infanticide following a takeover in two different ways.

**What factors predict infant survival following a takeover?**

To predict which variables are associated with increased infant survival following a takeover (**post-takeover infant survival model**), we used binomial generalized linear mixed effects models (GLMMs) (Bolker et al., 2009). We employed a fixed approach because our dataset, including only cases where a takeover occurred and with vulnerable infants present, was too small for a time-varying Cox proportional hazards model (with only 41 events in our data and 6 predictors of interest). We also ran survival models with this same dataset to confirm that both models yielded similar results (**Fig S3.4**). We examined each takeover and the subsequent infant survival/mortality from the perspective of the infant. Our dataset included all infants that experienced a takeover, measuring predictors of interest at infant-month following a takeover for up to 12 months (n = 121 infants, 893 infant-months). Our outcome variable was binary - whether an infant died (yes/no) each month during the follow up time. Our predictors
included former leader presence (yes/no), number of cycling females (integer), number of immigrant males (integer), parity of the mother (primi/multi), age of infant at takeover (integer), and total number of infants within the unit each month(integer). We did not include unit size (total number of adult females in the unit) as in our previous model because we reasoned that the number of cycling females represents a male’s reproductive opportunities (possibly deterring infanticide in a *distraction effect*); and the number of infants represents alternative targets (possibly deterring infanticide in a *dilution effect*). We included the ID of the takeover (as infants could have experienced multiple takeovers within the same unit) as a random effect in our model. Including male ID and infant ID as additional random effects did not improve overall model AIC score.

Prior to model fitting, all continuous variables were scaled and standardized for ease of interpretation (Gelman, 2008) and multicollinearity between predictors was checked by measuring variance inflation factors from a simple linear model containing our predictors using the *vif()* function within the package car in R (García et al., 2015). As unit size and number of cycling females was positively correlated ($r = 0.55$), we did not use these two predictors in the same model. We fitted GLMMs using a binomial error structure and logit link function as our outcome variable was binomial and used the “bobyqa” optimizer setting the number of iterations to 100,000 to give the model more time to converge (Nash & Varadhan, 2011). After fitting models, we employed model comparison using AIC values and performed model selection and model averaging with functions in the MuMin package in R (Barton & Barton, 2015). We present results from
our model averaged coefficients using the package *sjplot* and plot model predictions using the package *effects* in R (Fox & Hong, 2010; Lüdecke, n.d.).

**Are former leaders more likely to stay if there are vulnerable infants in the unit?**

We modeled former leader presence as a function of total vulnerable infants (infant protection), number of cycling females (reproductive opportunity), and number of immigrant males (male competition/infanticide risk) to investigate which of these demographic variables strongly predicts the likelihood of former leaders remaining the unit. We fitted a binomial GLMM (similar to the infant survival post-takeover infant survival model) with former leader presence as our outcome variable (yes/no) and as covariates: total vulnerable infants (infant protection), number of cycling females (reproductive opportunity), and number of immigrant males (male competition/infanticide risk) predictors mentioned above. After model fitting, we followed the same procedure for this analysis as done in the model described above (post-takeover infant survival).

**Results**

**What factors predict overall infant mortality in geladas?**

Overall, we observed 81 infant deaths (71 infants with accurate date of deaths) of 445 infants born in our dataset (370 infants with accurate date of births), with an average infant death rate of $6.14 \pm 3.78$ / year. Thirty of 217 infants died outside of takeovers (22 with an accurate date of death) and 51 of 153 infants that experienced a takeover died following takeovers (39 with an accurate date of death). Survival analysis using multivariate Cox proportional hazards models showed that experiencing takeovers was
the most important predictor driving overall infant mortality in geladas. Both sets of survival models (i.e., models with and without maternal rank at birth as a covariate) showed that infants experiencing takeovers were more likely to die than infants not experiencing takeovers [infant mortality model 1: HR = 1.24, CI = 1.13-1.36, p <0.001; infant mortality model 2: HR = 1.20, CI = 1.07-1.34, p <0.01] (Fig. 3.1). Estimates, standard errors, and confidence intervals for all covariates in each model are presented in Tables S3.1 and S3.2 (Suppl. materials). Kaplan-Meier survival curves modeling infant mortality as a function of takeover shows that infants experiencing takeovers between ages 4-18 months had higher mortality compared to infants that did not experience takeovers (Fig. 3.2).
Figure 3.1. Coefficient plots from Cox proportional hazards model showing that takeovers are the most reliable predictors of infant mortality. Panel A (without maternal rank as a covariate) shows that experiencing a takeover is associated with an increase in infant mortality (hazards ratio > 1) while having primiparous mothers is associated with a decrease in infant mortality. Panel B (i.e., the model including maternal rank as a covariate) shows that only experiencing a takeover led to an increase in infant mortality (hazards ratio > 1).
Figure 3.2. Kaplan Meier survival curves illustrate that post-takeover infants were more likely to die than those that did not experience a takeover.

**Takeovers in gelada society**

Bachelor challenges against leader males resulting in takeovers lasted from one day to several weeks (94 takeovers, mean = 29.08 days, SD = 47.39 days, range = 0-252 days). We observed 28 messy and 66 clean takeovers (see methods for definitions). All messy takeovers involved multiple bachelor males (1-7) temporarily immigrating into the unit for short periods of time. Deposited leader males remain in units following 45 out of 94 takeovers (this included takeovers where we did not observe the takeover directly as the unit was missing but when we found the unit later on, the deposed former leader was a follower). Out of 94 takeovers, 22 takeovers led to unit fissions and one takeover.
led to unit fusion – out of these 23 fusion/fission events, 14 were known to be messy takeovers.

**Infanticide following takeovers**

Outside of takeovers, most infant deaths occurred between the ages of 0-6 months; however, following takeovers, the infant deaths (attributed to infanticide) were far more spread out across infant age (Fig S3.6). While we cannot definitively attribute each of these post-takeover infant deaths to infanticide, theoretically, the rates of infant mortality following takeovers should continue to remain higher than outside of takeovers until infants reach 14.76 months of age (Fig 3.3). This is only slightly lower than a previous estimate for this population based on 2 years of data (15.2 months of age; Beehner & Bergman 2008). Furthermore, this previous study only considered infant mortality within 4 months of a takeover, but our updated analysis suggests that infant mortality (presumably due to infanticide) is elevated for up to 11 months post-takeover (Fig. 3.4). Therefore, this updated dataset indicates that our window of infanticide vulnerability is for infants up to 18 months of age, and infants up to 12 months post-takeover.
Figure 3.3. Linear regression between infant age at death (on x-axis) and the subsequent female interbirth interval (on y axis). Each point represents one female interbirth interval/infant death. Note that this interbirth interval is from the birth of the infant that died to the birth of the next infant (this is not the typical interbirth interval). This regression line suggests that males should stop killing infants at 14.76 months (this is when infanticide will no longer be advantageous to the male).
Figure 3.4. Distribution of infant death rates according to time since takeover (in months). Italicized numbers on the x-axis show the total number of vulnerable infants during that time point and numbers adjacent to the points indicate the number of infant deaths observed at that time point. The horizontal dotted line represents the average monthly non-takeover death rate for infants.

What factors predict infant survival following a takeover?

Although we confirmed that infant mortality was highest following takeovers, we are intrigued that not all males that took over a unit were infanticidal, and not all infanticidal
males killed all vulnerable infants in their unit. Indeed, of 75 takeovers with vulnerable infants present, 40 (53.3%) of these males were infanticidal (i.e., killed at least one infant) and males only killed *all infants* 3 times, representing 7.5% takeovers (not including units with only 1 infant). Moreover, infanticidal males do not universally kill all infants in the unit; of 40 infanticidal males with more than one infant present, only 13 (32.5%) of these males killed more than one infant and only 6 (15%) killed all infants (including units with only 1 infant). Therefore, many of the infanticidal males in this population are not completely infanticidal. For the remaining 35 takeovers, males did not kill any infants even when the opportunity existed (with 1-7 infants present under 18 months). Ultimately, we are interested in identifying whether different gelada males have different reproductive strategies. However, as a foundation for future analysis, here we first identify whether this variation in infanticide can be attributed to variation in *opportunities* - based on a combination of variables such as infant age, cycling females, other vulnerable infants, presence of other males, and the putative father.

The post-takeover infant survival model results showed that infant age at takeover and number of cycling females present in the unit were the strongest predictors of infant survival following a takeover - older infant age at takeover and more cycling females present in the unit each month post-takeover leading to higher infant survival (Fig 3.5). Each additional month of infant age at takeover led to a 64% decrease in infant mortality [$\beta = 0.36, \text{CI} = 0.28-0.46$]. Similarly, the likelihood of infant death decreased by 31% with each additional number of cycling females in the unit [$\beta = 0.69, \text{CI} = 0.51-0.93$].
Model averaged coefficient plots along with predicted curves showing the effect of both infant age and number of cycling females is shown in Fig 3.5.

**Figure 3.5.** Post-takeover infant survival model results showing that as the infant age at takeover increases, the probability of infant death is reduced. Similarly, a higher number of cycling females within the unit also reduces the probability of infant death. Panel A shows the model averaged coefficient plot from dredged GLMMs. Panels B and C show model predictions for the effect of age at takeover and number of cycling females on infant death respectively. Shaded areas in both plots (B & C) represent standard errors.

Since former leader presence did not affect offspring survival following a takeover, we examined what factors predicted whether a former leader male remained in the unit following a takeover. We acknowledge that when a former leader male disappeared, we
did not know whether he was killed or dispersed to another group (i.e., a reproductive unit or an all-male group) as former leaders are hard to track longitudinally. We found that when controlling for time since takeover, deposed leader males were most likely to be found in units following a takeover when there are multiple vulnerable infants in the unit \[\beta = 6.33, \text{CI} = 3.32-12.07\].

**Figure 3.6.** Model coefficient plot showing that probability of a former leader being in the unit following a takeover is significantly higher when there are more vulnerable infants (<18 months old) at takeover. Panel A shows the model coefficient plot and Panel B shows model predictions. Shaded areas in Panel B represent standard errors.

**Discussion**

This study examined infant mortality using 14 years of data from the gelada population living in Simien Mountains National Park, Ethiopia. The leading cause of infant mortality
was suspected infanticide, accounting for more than half of all mortality (62.9%). Indeed, in the 12 months after a takeover, there was a 42.8% increase in infant mortality compared to infant mortality outside of takeovers. But not all takeovers resulted in infanticide. When there were vulnerable infants in the group, new leader males only committed infanticide 44.2% of the time, suggesting that other factors offer infant protection during takeovers. Our analyses indicated that in addition to older infants being less likely to be killed than younger infants, units with more cycling females were less likely to have an infanticidal male than units with fewer cycling females. Contrary to expectations, neither the number of vulnerable infants nor the presence of the likely father had an effect on the likelihood of infanticide. These results point to an important factor that has not received enough attention in the sexual conflict literature, which is the presence of fertile females as a “distractor” to the potentially infanticidal male.

**Takeovers predict overall infant mortality in geladas**

Infant mortality was overwhelmingly driven by takeovers in geladas. In line with many other taxa from mammals (Lukas & Huchard, 2014), new breeding males in gelada society very often commit sexually selected infanticide. Takeovers are the primary way in which males can gain dominance over other breeding males in a reproductive unit in geladas. Takeovers are socially challenging events, where the challenge for dominance can last from less than one day to several months; a process that can cause severe injuries and infant death (Baniel et al., 2017; Borries et al., 2017; Schneider-Crease et al., 2020). Both takeovers and infanticide are costly for females and has led to the selection of multiple female counterstrategies in geladas with pregnant females aborting
fetuses during takeovers (Bruce effect) (Roberts et al., 2012), immature females showing early signs of maturations (Vanderbergh effect) (Amy Lu et al., 2021), and lactating females showing fake sexual swellings (Baniel et al 2023, submitted).

Previously, paternity analysis from this population has shown that reproductive skew is high with dominant leader males siring 83–100% of the offspring in units with and without followers respectively (Snyder-Mackler et al., 2012). Socioecological theory predicts that when reproductive skew is high, intense sexual selection would select for more aggressive behaviors in males (Kappeler & van Schaik, 2004). Therefore, while infanticide is extremely costly for females and the potential father of infants, the cost of not committing infanticide for male geladas is also not trivial - as marauding bachelor groups pose a constant threat to leaders acting as “social predators” and female geladas have long lactation periods and interbirth intervals compared to other cercopithecine primates (Lu et al., 2017; Pappano et al., 2012; Roberts et al., 2017). Therefore, it is very interesting that all new leader males do not commit infanticide even when presented with the opportunity.

Overall infant mortality outside of takeovers is extremely low in geladas (18.2% of total deaths occurring outside of takeovers, and monthly infant mortality rate is 0.07% in this population). This rate is lower than other closely related taxa and could be due to the fact that geladas do not have many predators in the Simien Mountains National Park. However, this monthly infant mortality rate goes up to 3.96 % in the 12 months following
a takeover indicating takeovers are the primary source of infant mortality in our study population.

There is variation in takeovers and infanticide in gelada society

Once a leader male has been targeted by bachelors, he almost always loses his dominance status due to the coalitions formed by bachelors, with multiple bachelors taking a turn chasing and tiring out the leader male until he is exhausted (Pappano, 2013). It is therefore difficult (to impossible) for a leader male to defend his unit against the attacks from multiple bachelor males simultaneously. This problem may be additionally compounded by the seasonal timing of most takeovers – the majority occur at the end of the dry season when green grass availability is low (Tinsley Johnson et al 2018). Thus, bachelors might be targeting leader males when they are most energetically constrained as leader males have to expend more energy in vigilance behaviors than bachelor males. And, indeed, in another study from this population of geladas, it was found that leader males were generally in an inferior energetic condition (i.e., lower C-peptide levels) compared to bachelor males (Perlman 2021); possibly because they must consistently expend more energy maintaining social relationships with females within their units and being vigilant to prevent takeovers. Bachelors on the other hand, spent the majority of their time resting and feeding and had higher energy balance overall (Perlman, 2021).

Although most takeover attempts were successful in the long run, some took longer to complete than others. The “messy” takeovers (i.e., takeovers that took longer than a
week to decide the new leader male) were most likely to occur when units were large (more than 8 females) and often led to unit fissions. Of all 94 takeovers, 22 takeovers led to unit fissions and one takeover led to unit fusion – out of these 23 fusion/fission events, 14 were known to be messy takeovers. Examining how these fissions occur in geladas is a topic for future analyses. Even messy/drawn–out takeovers ultimately result in one of the bachelors becoming the successful dominant male. This suggests that bachelor males have means of assessing the quality of leader males even before challenging them using multiple signals (chest patch color, loud calls) (Bergman et al. 2009; Benítez et al. 2017).

In this study, we individually examined cases when males do not commit infanticide. Despite the success of this male strategy, only 53.3% of all gelada males with the opportunity to commit infanticide actually carried it out (40 males of 75 total). Moreover, of these 40 infanticidal males, only 3 of the 37 males with more than one infant in the unit (8.1%), killed all of them. When visualizing infant deaths across the unit, we first find that most infant deaths occurred within 0–6 months of a takeover although a non-trivial number of infants also died in the 6–12-month period following a takeover (Fig S3.6). Post-takeover infant mortality rates return to baseline levels around 12 months following a takeover (Fig 3.4) and maximum observed infant age at death following a takeover is 18 months suggesting that infants are vulnerable at ages up until 18 months - infants older than 6 months also dying during the first 12 months following a takeover (Fig S3.6). We speculate that there might be some long-term benefits of not committing infanticide for incoming leader males that outweigh potential short term reproductive
costs. For example, infanticidal males may erode their potential to socially bond with the unit’s females, which could lead to a reduction in their tenure length. We plan to follow up on this in future analyses.

The number of cycling females predict infant survival following a takeover

Unsurprisingly, infant age at takeover emerged as the strongest predictor for infanticide (Fig 3.5). Sexually selected infanticide is a successful strategy for males when it reduces the time for females to resume fertility and mate with the perpetrator, as found in other primate studies where females lost their infants to infanticide (Borries 1997; Crocket & Sekulic 1984; Sommer 1994; Struhsaker & Leland 1985; Cords & Fuller, 2010). Therefore, there is an infant age where it may no longer be advantageous for males to kill them – even if they are not yet weaned (as per Crocket & Sekulic, 1984; van Schaik 2000). In this population of geladas, we calculated this theoretical infant age to be 14.8 months (Fig 3.3). And, based on our analyses, we observed that infanticide tapered off at 12 months following a takeover (Fig 3.4). This theoretical age as well as the maximum age of infant death post-takeover is higher than what we would have expected. One possibility is that older infants may be more likely to be targets of infanticide based on other influential factors, such as the number of cycling females.

In addition to infant age, the number of cycling females in a unit at the time of a takeover emerged as a reliable predictor of the likelihood of infanticide; more cycling females in the unit reduced the likelihood that any given infant in that unit was killed (Fig 3.5). We are calling this the “distraction effect” based on the hypothesis that when an
incoming male takes over as the primary breeding male, his infanticidal tendencies will be mollified when he has more females to mate with and heightened when he has fewer females to mate with. To our knowledge, this effect has only been examined in one previous study (Cords & Fuller, 2010) on blue monkeys (Cercopithecus mitis). However, in this previous study, the authors did not find that the number of females to mate with had an effect on infanticide – although the sample size was extremely small.

Note that the cycling females in this study were designated based on the absence of pregnancy and the absence of an infant. This is an important distinction because we have observed that lactating females can exhibit deceptive sexual swellings after takeovers as a counterstrategy to infanticide (Baniel et al., in review). However, none of these deceptive sexual swellings were “counted” in the cycling female category. Therefore, over and above this (successful) deceptive strategy by lactating females to prevent infanticide of their own infant (Baniel et al., in review), having many other females cycling in the unit also helps prevent infanticide by the incoming male. Because females in the unit are closely related (Snyder-Mackler et al., 2012), this new result raises several intriguing questions related to kin selection and possible selection for reproductive synchrony.

Evidence for the “distraction effect” (i.e., that more cycling females reduces the number of infanticides) may explain the high rate of infanticide in the smallest sized units. In a previous study on this population (Tinsley Johnson et al., 2021), the highest rates of infanticide were found in the largest and smallest reproductive units. The high rate in the
largest units was tentatively explained based on the high rate of takeovers, each one associated with a potentially infanticidal male. However, the high rate in the smallest units remained unexplained in the 2021 study. We suggest that because these units have a very limited number of adult females, it stands that there will by definition be very few cycling females at any given takeover. Therefore, to the extent that the number of cycling females causes the distraction effect, smaller units will have less ability to do so.

Contrary to our predictions, the number of vulnerable infants in the unit did not predict likelihood of infanticide for an individual infant. Our initial reasoning was based on the theory behind the dilution effect in predators (Bumann et al., 1997; Hamilton, 1971) or the bachelor threat hypothesis in polygynous mating systems (Pappano et al., 2012) where having more individuals in the group in turn reduces the likelihood that any one of them is the selected target. However, unlike the dilution effect or the bachelor threat hypothesis where a kill or a takeover leads to satiation in the predator (he has his meal) or the bachelor (he has taken over the alpha position), there is no reason that an infanticidal male should not kill all infants given that each one essentially frees up one more female to mate with. Indeed, the opposite could be argued – that having more infants statistically leads to more infants (not fewer) getting killed as has been reported in studies on howler monkeys and hanuman langurs (Borries & Koenig, 2000; Van Belle et al., 2010). But, we do not observe this in our study system. The number of infants in a unit does not predict the likelihood of infanticide for any infant in either direction. Therefore, we suggest that for this population of geladas, large units have high rates of
infanticide due to a high rate of takeovers and small units have high rates of infanticide due to a small number of cycling females in the units at takeover.

Contrary to what we expected, the presence of former leader males (the putative father of vulnerable infants in the unit at the time of takeovers) did not increase infant survival in the wake of a takeover. The average length of time that former leaders remain in their reproductive units after their overthrow is 17.84 months +/- 15.15 months (range: 0.13-52.6 months). We have observed that when former leaders remain attached to their reproductive unit after a takeover, they exhibit shifts in their social behaviors: they are submissive to the new leader male, they continue to associate with the females, and they spend some (although limited) time with infants and juveniles (Sen and Beehner, personal observations).

Therefore, if males are not helping keep their infants alive, why do they remain in their groups (keeping in mind that this may not be strategic – it may just be the default if they are not killed by their challenger). The main factor associated with former leader attachment was the number of vulnerable infants. It may be that the overthrown males with the shortest tenures that sired no offspring do choose to exit the unit to try their luck elsewhere (either heading back to an all-male group, or to take over a new reproductive unit). The overthrown males that did sire offspring in the unit remain whenever possible and exit only when either killed or forced out. We do not yet have a good grasp of whether former leaders are enacting one or more reproductive strategies once they are no longer the leader male.
**Conclusion**

In this study, we have identified that (1) infant mortality is driven overwhelmingly by infanticide following takeovers, and (2) the best way to mitigate infanticide after a takeover is to be in a unit with a lot of cycling females. This is the first research to identify the importance of a possible distraction effect in mitigating sexually selected infanticide in a social group. Our results establish a framework for male *opportunities* for infanticide. However, given the high variation in infanticide across males, there is a critical step that we will focus on next: modeling individual male reproductive strategies. For example, controlling for the number of cycling females, a new leader male can maximize his net reproductive opportunities by killing all dependent infants and evicting (or killing) the former leader male (non-tolerant strategy). An incoming male may kill only some infants and may or may not evict (or kill) the former leader male (intermediate strategy). Or at the other end, an incoming male may not kill any dependent infants and “tolerate” the presence of the former leader male (tolerant strategy). The presence / absence of the former leader male in the unit may not constitute any strategy on the part of the male and may simply be the outcome of circumstances beyond a leader male’s control. The next step is to identify if infanticide is just a by-product of any given male’s *opportunities* (as identified here) or if each male demonstrates flexibility in the face of different opportunities (male strategies).

**Acknowledgements**

We would like to thank our Ethiopian collaborators, the former and current wildlife wardens (Berhanu Gebre, Maru Biadglegn, Abebaw Azanaw Haile) and wildlife experts
at the Ethiopian Wildlife Conservation Authority (EWCA). This research would not have been possible without our wonderful team of long-term Ethiopian research assistants and staff (Esheti Jejaw, Ambaye Fanta, Setey Girmay, Yeshi Dessie, Dereje Bewket, Atirsa Aduga, Tariku W/Aregay, Shifarew Asrat), former camp managers (Clay Wilton, Julie Jarvey, Levi Morris, Tara Regan, Patricia DeLacey, Peter Clark, Megan Gomery, Liz Babbitt) and research assistants (Caitlin Hawley, Evan Sloan, Laura Morrissey, Emily Downey, Eddy Wild, Maddie Melton, Anna Cryer) who have assisted with the collection of demographic, behavioral, and life history data from our study population. SS would also like to thank Andrew J. Marshall for helpful feedback on the statistical analyses for this study.
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Pappano, D. J. (2013). The Reproductive Trajectories of Bachelor Geladas. https://deepblue.lib.umich.edu/handle/2027.42/102358


https://doi.org/10.1098/rspb.2016.2561
**Fig S3.1.** Panel A shows the distribution of infant births and deaths within and outside of takeovers in the study (only includes infants with accurate DOBs and DODs (i.e. dates estimated within 0-62 days if event was not directly observed). Panel B shows the nested nature of the dataset and individual models tested with each dataset.
**Fig S3.2.** Schoenfeld residual plots for each predictor in infant mortality model 1 (model without maternal rank).
**Fig S3.3.** Kaplan-meier survival curves showing the effect of each predictor on overall infant survival. Note, none of these predictors were statistically significant in the multivariate cox proportional hazards model.
Fig S3.4. Survival model for post takeover infant survival shows that only age of infant at takeover matters.
Table S3.1. Hazards model tables (Infant mortality analysis 1)

<table>
<thead>
<tr>
<th>Predictor</th>
<th>Beta (SE)</th>
<th>HR (95% CI)</th>
<th>P value</th>
</tr>
</thead>
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<tr>
<td>Primiparous moms</td>
<td>-0.68 (0.35)</td>
<td>0.50 (0.24-1.08)</td>
<td>0.08</td>
</tr>
<tr>
<td>Takeover = Yes (time transformed)</td>
<td><strong>0.22 (0.04)</strong></td>
<td><strong>1.24 (1.13-1.36)</strong></td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Number of females</td>
<td>0.08 (0.13)</td>
<td>1.08 (0.82-1.42)</td>
<td>0.56</td>
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<tr>
<td>Uni-male units</td>
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<td>0.87 (0.43-1.74)</td>
<td>0.69</td>
</tr>
<tr>
<td>Min temp (°C)</td>
<td>0.06 (0.13)</td>
<td>1.06 (0.84-1.35)</td>
<td>0.61</td>
</tr>
<tr>
<td>Cumulative rainfall (mm)</td>
<td>0.06 (0.12)</td>
<td>1.06 (0.81-1.39)</td>
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Table S3.2. Hazards model tables (Infant mortality analysis 2)

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<td>Maternal rank</td>
<td>-0.09 (0.15)</td>
<td>0.92 (0.70-1.19)</td>
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<tr>
<td>Primiparous mother</td>
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<tr>
<td>Takeover = Yes</td>
<td><strong>0.20 (0.04)</strong></td>
<td><strong>1.22 (1.11-1.33)</strong></td>
<td>&lt;0.001</td>
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<tr>
<td>Number of females</td>
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<td>1.06 (0.78-1.44)</td>
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<td>Uni-male units</td>
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<td>0.81 (0.36-1.82)</td>
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<td>Min temp (°C)</td>
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<td>0.85 (0.60-1.22)</td>
<td>0.39</td>
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<tr>
<td>Cumulative rainfall (mm)</td>
<td>0.11 (0.13)</td>
<td>1.12 (0.85-1.48)</td>
<td>0.42</td>
</tr>
</tbody>
</table>
**Figure S3.5.** Number of infant deaths within and outside takeovers at each infant month (x-axis).
Fig S3.6. Distribution of infant deaths according to time since takeover. Bar colors indicate the age at which infants died in each time category. Most infant deaths occurred for infants in the youngest age category (0-6 mos) AND within 0-6 months of a takeover. There were also a large number of infants between 6-12 months of age killed within 0-6 months of a takeover.
Chapter 4: Male Reproductive Strategies in Wild Geladas

Sharmi Sen and coauthors Eden Kim, Alice Baniel, Amy Lu, Thore J. Bergman, Noah Snyder-Mackler & Jacinta C. Beehner

Abstract

Infanticide is an important evolutionary force shaping animal societies. However, we know very little about factors that contribute to variation in whether and how males commit infanticide. Here, we examine the causes and consequences of variation in infanticide behavior in male geladas (Theropithecus gelada) living in Simien Mountains National Park, Ethiopia. Male infanticide in this population is common (accounting for 63% of overall infant mortality) yet highly variable across males. Using over 14 years of data on life history, demography, behavior, and hormones, we answer three questions: First, which units do males target for takeover? We examined the demographic conditions within units that make them targets for bachelors and subsequent takeovers – the prelude to all infanticidal behavior. We found that units with more cycling females, fewer pregnant females, and units with multiple males had an increased likelihood of being taken over. We suggest that this latter result may simply emerge because former leaders are typically only present in the early days of a takeover, which is also a vulnerable time for new leaders for other reasons. Second, once males takeover a unit, we know from chapter 3 that the number of cycling females decreases the likelihood
that any male will commit infanticide, but beyond this general prediction, are there male traits that make it more likely that he commits infanticide? For this question, we examined the relationship between steroid hormones and male infanticide behavior. Fecal androgen and glucocorticoid metabolite levels (measured in the first year of takeover) did not differ between new leader males that committed infanticide versus those that did not. Finally, given the variability in male infanticide, what are the payoffs for the different degrees of infanticide (e.g., from killing all infants to killing no infants)? To answer the last question, we compared the reproductive payoffs of infanticide versus non-infanticide behavior by examining overall male tenure length (a proxy for reproductive success in male geladas). We found that killing infants did not decrease overall leader male tenure length. However, other demographic variables measured in the first year of male tenure significantly affected tenure length.

**Introduction**

As a sexually selected strategy, infanticide increases the reproductive success of the sex engaging in the behavior (Hausfater and Hrdy 2017). Male infanticide is particularly common in social systems where females can be monopolized spatially or temporally and is suggested to have evolved as a result of direct male-male competition (the sexual selection hypothesis) (Hrdy 1974; Emlen and Oring 1977; Clutton-Brock and Parker 1995). As a male strategy, infanticide can simultaneously reduce the fitness of male competitors and accelerate the time taken for lactating females to return to fertility (Hrdy 1977, 1979). By committing infanticide and targeting unweaned offspring, new immigrant males are able to reset lactating females’ reproductive cycle, accelerating
their return to a sexually receptive state so that they are able to conceive after mating with the new immigrant male (Balme and Hunter 2013; van Schaik and Janson 2000).

Phylogenetic comparisons show that the risk of infanticide in a population can lead to the evolution of monogamous pair bonds between males and females (Opie et al. 2013; Lukas and Clutton-Brock, 2013). Infanticide also shapes grouping patterns - decreasing female group size or leading to the formation of multimale multifemale groups within populations (Robbins et al. 2013; Sicotte et al. 2017; Borries and Koenig 2000). It also leads to the selection of behavioral counterstrategies in males and females (Deschner 2000; Parmigiani et al. 1989; Kahlenberg et al. 2008; Manguette et al. 2019; Singh et al. 2014), and affects overall male and female life-history strategies (Borries et al. 2001). Infanticide is therefore an important factor driving the evolution of different social and mating systems across the animal kingdom (Lukas and Huchard 2014; van Schaik and Janson 2000). Especially in systems where females are monopolizable and male reproductive skew is high, it is unusual for infanticide *not to occur*. In other words, when infanticide is clearly advantageous for a male’s reproductive success, why don’t all males commit infanticide when given the opportunity? Plausible explanations for this variation in infanticide behavior must take the costs associated with the behavior along with the reproductive opportunities present for males (so that males can forego infanticide and still benefit in evolutionary terms) into consideration. Here we examine the causes and consequences of variation in male infanticide behavior.
One possible explanation could be that infanticide is a costly mating strategy - not only for females who lose their offspring, but also for males committing infanticide as it involves risk of fatal injuries from resident group members (Feder et al. 2019; Charpentier and Drea 2013; Smith et al. 2022). Furthermore, committing infanticide does not guarantee the infanticidal male’s future offspring success, as another male may soon replace him if male turnover rates are high (Widdig et al. 2004; Dyble and Clutton-Brock 2023). Most importantly, in species with stable social groups, infanticide might hinder a male’s ability to form close social relationships with adult females or drive the evolution of strong male-female social bonds to reduce the risk of infanticide (Van Schaik and Kappeler 1997; Palombit 2000). This can further impact a male’s long-term reproductive success.

To date, nearly every study on male infanticide has focused on the presence/absence of infanticide within any given species and on explanations for the variation in this behavior among species. We do not know a lot about variation in infanticide among males within any given species. There are several reasons contributing to this dearth of information. First, infanticide is often not always directly observed in wild populations and thus infanticide is usually inferred when an increase in deaths follows the arrival of a new male. Second, since infanticide occurs during chaotic, socially unstable periods (alpha male replacements, group fissions, intergroup encounters), it is extremely difficult to obtain fine grained data on events and circumstances that lead to infanticide. To our knowledge, there has been only one study that has focused on the variation in male infanticidal behavior (Cords and Fuller 2010). This study reported that infants were less
likely to be targets of infanticide if they were older when immigrant males first arrived in the group or if their mother had previously mated with the immigrant male. This study also found that male identity was the most influential predictor of infanticide with some males being more infanticidal than others. Here, we seek to understand variation in male infanticidal behavior in a wild population of geladas (*Theropithecus gelada*) living in the Simien Mountains National Park, Ethiopia. Specifically, we ask the following questions:

1. Which units do males target for takeover?
2. Once males takeover a unit, we know from chapter 4 that the number of cycling females decreases the likelihood that any male will commit infanticide, but beyond this general prediction, are there male traits that make it more likely that he commits infanticide?
3. Given the variability in male infanticide, what are the payoffs for the different degrees of infanticide (e.g., from killing all infants to killing no infants)?

**Why geladas?**

Geladas are an ideal system for this study as male geladas show remarkable variability in infanticidal behavior. In this population, 44.12% males do not commit infanticide even when the opportunity exists, with males killing all vulnerable offspring only 3.41% of the time. Males commit infanticide during takeovers which are periods of intense physical challenges between resident males and immigrant males, following which the new male becomes the dominant breeding male of a one male unit. These one male units (hereafter “units”)—comprising one dominant leader male, 2-12 adult females, 1-5
subordinate follower males, and their related offspring–form the core of the gelada’s complex multilevel society, allowing researchers to study the strategies of new leaders from multiple units within the same band (Snyder-Mackler et al. 2012; Snyder-Mackler et al. 2014). Males emigrate from their natal groups between ages 4-9 years to join all male units (*bachelor units*) and begin to reproduce either by taking over a unit and becoming the new leader male or by submissively joining a unit as a follower male (Pappano 2013; Sen et al. 2022). In gelada society, leader males sire 100% of the offspring in units without followers and 83% of the offspring in units with followers (Snyder-Mackler et al., 2012). Overall, leaders yield higher fitness than the follower tactic. Males that commit infanticide should gain a reproductive advantage over those that do not, since they are able to mate with the females in their unit more quickly (Beehner and Bergman, 2008). Although the adaptive significance of infanticide remains very clear, we still don’t know a lot about the proximate mechanism underlying the variation in this strategy in geladas. A recent study from the same population has shown that infant mortality following a takeover (within the first 12 months of a new male’s tenure) is lower when there are more cycling females in the unit and when infants themselves are older in the units (Sen et al in prep 2022). While incoming leader males might weigh these reproductive opportunities during takeovers, here, we examine if there are certain male attributes that influence male strategy. We take an integrative approach to understand how variation in this important reproductive strategy is maintained in this population. We test proximate mechanisms and ultimate explanations that might allow us to understand why such variation in infanticide exists in the first place.
Takeovers in gelada society

The effect of takeovers in shaping male and female life history and behavior in gelada society has been reported previously (see Lu et al. 2021; Tinsley Johnson et al. 2021; Tinsley Johnson et al. 2018; Snyder-Mackler et al. 2012; Beehner and Bergman 2008; Schneider-Crease et al. 2020; Pappano and Beehner 2014). What has yet to be described is the variability of takeovers or how takeovers themselves unfold in this population. Understanding both these aspects of takeovers is important to gauge the presence of multiple strategies. Here, for the sake of simplicity we consider sources of variability in gelada takeovers that can arise in multiple ways via: (i) the outcome - successful vs unsuccessful takeovers, (ii) duration of takeovers - quick takeovers drawn out process prior to takeover ("short" vs "drawn-out"), (iii) whether the sequence of events during takeover was observable ("clean" vs "messy"), (iv) the nature of challenges imposed on resident leader male (single bachelor vs coalition of males attacking leader male), and finally, (v) the outcome of each takeover in terms of the demographic changes within the unit (death of resident male, group fission/fusion events, former leader male remaining as a follower and infant mortality following takeovers). All of these can be difficult to observe directly, as groups can disappear from view for days to weeks and even when they are around observers, it is not always possible to record all social events when unknown males appear in the group and chaos ensues for weeks. Therefore, we take a parsimonious approach and exclude all cases where a study group disappeared for an extended period and was later found with a new leader male. Using a combination of demography, life history, and ad lib behavioral data, we first describe the general sequence of events that we have consistently seen
across the years during takeovers, the types of takeovers, and the general patterns associated with each type.

**Which units do males target for takeover?**

Next, to answer our first question, we examined takeovers to understand if bachelor males preferentially target units with certain attributes. In line with our results from chapter 4, we make the following predictions for this question. We predict that units with more cycling females will experience more takeovers and units with more pregnant females will experience fewer takeovers because they represent fewer reproductive opportunities for bachelor males. Second, we predict that the presence of additional immigrant males and/or the former leader will decrease the likelihood of takeover based on previous results suggesting that leader males concede to allow followers in their units as former leaders and followers might help prevent takeovers, in line with the “concessions model” (Snyder-Mackler et al 2012). Third, we predict that units with fewer vulnerable infants present will be more likely to be taken over because fewer infants could be an indirect measure of more cycling females within the unit.

**Are there traits that make it more likely that a male commits infanticide?**

Male attributes could be a determinant of infanticidal behavior (i.e., some males could be more aggressive than others or males that kill one infant are more likely to kill the next one). One mechanism mediating this aggressive behavior could be the rise of androgens or glucocorticoids in the males. Androgens in particular modulate social behaviors that lead to mating opportunities, therefore, it is possible that surges in
androgens can precede extremely forms of aggressive behavior such as infanticide (Dixson 1980; Muller et al. 2021; Beehner et al. 2006). Multiple studies on vertebrates have documented the increase in androgen levels during time periods when males face challenges from conspecifics via multiple ways - to either gain access to females and/or rise in rank within the dominance hierarchy (challenge hypothesis) as well as during intergroup encounters where males protect territory or resources (Schoof and Jack 2013; Cheng et al. 2022; Mitani and Watts 2005; Rosenbaum et al. 2016). Therefore, it is reasonable to expect that males that commit infanticide might exhibit higher levels of androgens compared to males that do not. Similarly, biological signals of periods of instability and risks experienced by animals can be reflected in the HPA axis through the production of glucocorticoids - a class of metabolic hormones that help animals mitigate social challenges by mobilizing energy and resources towards immediate needs (Sapolsky 2021; Sapolsky 1982; Sheriff et al. 2011; Raulo and Dantzer 2018). Such periods of social instability and increased levels of male-male competition that lead to surges in androgens can also cause higher GC production as documented in other species (Higham et al. 2013; Bergman et al. 2005; Beehner et al. 2006; Dantzer and Newman 2022). Here, we expected that males that commit infanticide will exhibit higher androgen and glucocorticoid levels than males that don’t. Second, we expected variation in infanticide behavior (in terms of the degree to which males commit infanticide) to be reflected in male hormone levels in the first year of tenure when infanticide typically occurs in this study system.

*What are the payoffs for the different degrees of infanticide?*
One possible explanation about why males do not commit infanticide could be attributed to social relationships - males are risking their ability to socially integrate within the unit with adult females by committing infanticide. Gelada males transfer from their natal unit to a bachelor unit, to a reproductive unit where they can reproduce. Each of these transitions requires social skills to integrate into the social network of their new group. In particular, most leader males seek to establish social bonds with adult females in their unit (Ohsawa & Dunbar, 1984; Gustison et al., 2012; Barale et al., 2015, Gustison and Bergman, 2016). It has been suggested that females with strong social bonds with their leader male may choose to support them during attempted takeovers (Dunbar & Dunbar, 1975, Mori 1979). Thus, males who invest time and energy in establishing and maintaining social relationships with resident females instead of committing infanticide may forestall takeovers, have higher reproductive success, and longer tenure. Here, we measure reproductive payoffs emerging from variation in infanticide by assessing tenure length - a proxy for male’s reproductive success. We expect that males that commit infanticide will have shorter tenure than males that do not as infanticide might impede a male’s ability to socially integrate with females in the unit.

Methods

Study site

This study took place at Simien Mountains National Park, Ethiopia, where the long term field site of the Simien Mountains Gelada Research Project has been collecting data from wild geladas since 2006. All animals were habituated to observers on foot. We routinely observe and collect data from approximately 300 animals from 19 units in two
different bands. The long-term project collects demographic data through daily
censuses and life history data on female maturations, female deaths, takeovers, infant
births, infant deaths on a near daily basis. We used data on life history, demography,
hormones, and behavior from 2006-2020 in all our analyses. Observation time for each
unit differed across the years as we dropped/added units throughout this time period.

Rainfall and temperature. We recorded rainfall and minimum temperature on a near-
daily basis using a rain gauge located in an open area near the field station and a
thermometer mounted under a shaded location. Since we know from previous studies
that rainfall and temperature play an important role in gelada physiology and
reproduction – rainfall from the previous 90 days accurately reflects green grass
availability (primary food resource) and lower temperatures are associated with higher
metabolic demands (Beehner and McCann 2008; Tinsley-Johnson et al 2018, Jarvey et
al 2018), we included cumulative rainfall from the previous 90 days and mean minimum
temperature averaged across the previous 30 days to obtain residual fAMs and fGCMs
first and then used these residual fAMs and fGCMs for subsequent analyses (see Data
analysis).

Unit attributes

Number of cycling and pregnant females. We estimated the number of cycling females
in the unit as the number of females that may be fertile by either actively exhibiting
sexual swellings on their chest, neck, and/or perineal area or between swellings. We
assigned pregnancy states to females based on infant birth dates and known gestation length for this population (Roberts et al 2017).

*Total infants.* The number of infants in the unit is the number of dependent infants up to 18 months of age which is roughly the average age of weaning in this population (Lu et al 2017).

*Number of follower males and former leaders.* Previous research on this population suggested that leader males may benefit from having followers in the unit to help prevent takeovers (Snyder-Mackler et al. 2012). Therefore, we included follower males in all our models with one important distinction - we took into account *follower identity* (for our takeover and tenure length models) as we wanted to examine if former leaders and immigrant males have an opposing effect on these two outcome variables. We do not expect androgens to be affected by follower identity but by the total number of followers in the unit as any follower male represents competition for the leader male irrespective of their identity. SMGRP data suggests that units that have resident followers (not floating males) are actually older former leaders that remain in the unit after a takeover; immigrant males that join as subordinate followers are usually early-mid prime males that do not remain as followers for long periods of time (presumably try to take over a different unit) (Beehner et al 2016). As former leaders are the true *follower males* in gelada society and based on the concessions model previously proposed for geladas, we would expect leader males with former leaders present to have lower takeover rates and higher overall tenure lengths. We test this prediction in
this study with an additional 12 years of data since the original concessions study which proposed that leader males potentially allow follower males to remain in their units at the cost of sharing reproduction as followers help increase tenure length of leaders by helping leaders defend their unit (Snyder-Mackler 2012).

Fecal hormone sample collection, extraction, and storage
All fecal samples were collected, stored and extracted following laboratory protocols previously validated for geladas (Beehner and McCann 2008; Pappano et al. 2010; Beehner et al. 2009). All samples were obtained from known individuals within minutes of defecation. Briefly, in the field fecal samples were mixed and ~0.1g of the sample was transferred to a tube containing 3 ml of a methanol/acetone solution (4:1, v:v) and the mixture was homogenized using a battery powered vortexer immediately. Samples settled to the bottom of the tube within 3-4 hours in the field, after which we performed sample extraction by filtering 2.5ml of the clear homogenate solution through a 0.2 μm PTFE filter and washing the filter with an additional 0.7ml of methanol/acetone solution. To the filtered homogenate we then added 7ml of distilled water and the solution was mixed by gently inverting the tube several times. This solution was then loaded onto a reverse-phase C_{18} solid-phase extraction cartridge following the manufacturer’s instructions (Sep-Pak Plus, Waters Corporation, Milford, MA) and washed with 2ml of 0.1% sodium azide solution. After this step, cartridges were transferred to a sealed Whirl-pak bag with ~2g of silica beads and kept at room temperature for three days to dry out, following which they were kept frozen in a -20°C freezer until they were ready to be shipped to the laboratory.
**Fecal androgen and glucocorticoid EIA**

In the laboratory, steroids were eluted from cartridges with 2.5ml 100% methanol and stored at −20°C until the time of assay. We measured fecal androgen metabolites (fAMs) using a 5α-Androstan-3-ol-17-one (or epiandrosterone) assay and fecal glucocorticoid metabolite levels (fGCMs) using a 11β-hydroxyetiocholanolone (or 69-a). Both assays have been successfully used in a variety of primate species (CITE), their cross-reactivities have been reported elsewhere (Möhle et al. 2002; Palme and Möstl 1994; Frigerio et al. 2004). Both assays have been also previously validated for measuring fecal androgen metabolite and glucocorticoid levels in wild geladas respectively (Sen et al. 2022; Carrera et al. 2020), and both epiandrosterone and 69-a assays has been previously biologically and analytically validated for measuring fecal androgen metabolite and glucocorticoid levels in wild geladas respectively (Sen et al. 2022; Carrera et al. 2020). Briefly, 50μl of samples (diluted at 1:30 for androgen assays and 1:40 for glucocorticoid assays) and standards (range: 3.9-250.0 pg/well) were added to each plate in duplicate, followed by 50μl biotin labeled hormone and 50μl of antibody to each well after which plates were incubated overnight at 4C. The following day, plates were washed three times with PBS wash solution (containing 0.002% Tween 20), 150 μl of streptavidin horseradish peroxidase added to each well and incubated in the dark on a shaker for 1h. Plates were washed again after this step, 100 μl of TMB substrate solution added to each well and plate was incubated in the dark for 30-40 mins. We stopped the reaction by adding 50 μl of sulfuric acid to each well and measured absorbance at 450 nm using an automatic plate reader. For epiandrosterone assays, 50% binding was at 15 pg/well and assay sensitivity was 2.1 pg/well. For 69-a
assay, 50% binding was at 13 pg/well and assay sensitivity was 1.9 pg/well. In total, we ran 169 assays measuring fecal androgen metabolite levels in 2469 samples from 62 males (mean = 39.82 samples/male, range = 1-120, SD = 30.81). And 118 assays measuring fecal glucocorticoid metabolite levels in 2252 samples from 63 leader males (mean = 35.75 samples/male, range = 1-121, SD = 29.13).

**Takeovers and tenure length**

Takeovers were categorized as successful once we observed a new male copulating with adult females in the unit. We labeled leader males as infanticidal or non-infanticidal depending on whether an infanticide was assigned during the first 12 months of tenure (as a previous study showed that infant deaths occurred up until 12 months of post takeover) (Sen et al in prep). The takeover analysis dataset included monthly demographic variables measured across 43 units following 75 leader males in total from the start of their tenure to the end of tenure or observation time and had 55 takeover events. Observed takeover counts across the study period is provided in the supplementary materials (Fig S4.1). The tenure length analysis dataset consisted of 54 males with known tenure lengths in total. Median tenure length of leader males in our population was 26.27 months (range= 3.06-105 months, SD=28.7 months, n = 54 leader males) (Fig S4.2).

**Data analysis**
All data analyses were performed using the statistical software package R (v. 4.2.2). Below we outline our main research questions and provide details about the statistical modeling approach taken.

**Takeovers in gelada society**

We present the summary statistics for the number of successful takeovers, how many were short vs drawn-out, how many were clean vs messy, how many resulted in fissions, and how many ended with the former leader male remaining with the unit.

**Takeover model (GLMM): Which units do males target for takeover?**

To ascertain which demographic parameters increase the likelihood of takeovers in our population, we used binomial generalized linear mixed effects models (GLMMs) (Bolker et al. 2009). Our dataset included all predictors of interest at unit-month starting from three months following a takeover (n = 43 units). We chose three months as our cutoff as we wanted to exclude the time immediately following a takeover as this period can be quite chaotic with many random males trailing the unit. Instead, we chose to start the observation time for all our units 3 months post takeover once there was a clear leader male in the unit. Our outcome variable of interest was whether takeover occurred (yes or a no) during each month of observation in units and our predictors included the number of cycling females (integer), the number of pregnant females (integer), the number of immigrant males (integer), whether the former leader was present or absent (yes/no), and the total number of infants measured every month (integer). We included the male ID as a random effect in our model. Prior to model fitting, we scaled
continuous variables for ease of interpretation (Gelman 2008). We fitted GLMMs using a binomial error structure and logit link function as our outcome variable was binomial and using the “bobyqa” optimizer setting the number of iterations to 100,000 (Nash and Varadhan, 2011). We also tested for multicollinearity by measuring variance inflation factors using the \texttt{vif()} function within the package \texttt{car} in R (García et al., 2015). After fitting models, we employed model comparison using AIC (\textit{Akaike information criteria}) values and performed model selection and model averaging with functions in the MuMin package in R (Barton and Barton 2015). We present results from our model averaged coefficients using the package \texttt{sjplot()} in R and plot model predictions using the \textit{effects} packages in R (Fox and Hong 2010; Lüdecke n.d.).

\textbf{Hormone model (LMM): Are there traits that make it more likely that a male commits infanticide?}

To detect whether there are any underlying hormonal mechanisms affecting infanticide behavior, we visualized our dataset in a few different ways. First, we examined the variation in the distribution of fAMs (39.82 ± 30.81 samples/male) and fGCMs (mean = 35.75 ± 29.13 samples/male) across the full length of male tenure based on the total number of infants that they killed during the first year of a takeover. To examine the relationship between androgens, glucocorticoids, and infanticidal behavior in new leader males, we subsetted our dataset from part 1 by only including units that had infants at the time of takeover and restricting the window of sample collection to the first year of tenure from new leader males. In other words, we are only testing those scenarios where a leader male had the option of committing infanticide upon takeover. Second,
we zone in to the first 12 months post takeover where infants are most vulnerable to infanticide in this population and visualize overall patterns of fAMs and fGCMs. We had samples from a total of 39 leader males (androgens: total = 895 samples, range = 1-86 samples per male, mean = 22.94 samples, SD = 20.21; glucocorticoids: total = 891 samples, range = 1-86 samples per male, mean = 22.84 samples, SD = 20.69) where takeovers occurred with units containing vulnerable infants.

Both fAMs and fGCMs are affected by temperature and rainfall (Fig S4.3 & S4.4). Therefore, to model the respective relationship with only our predictors of interest while controlling for these influential seasonal variables, we fitted two separate linear mixed models (LMM) with log transformed fAMs and fGCMs (as hormone levels followed log-normal distribution, Fig S4.5) as our outcome variable respectively and male identity as a random effect. In both models, we used z-transformed cumulative rainfall and minimum temperature as fixed predictors. The residuals obtained from these two models were used as outcome variables for all subsequent analyses (hereafter “residual fAMs” and “residual GCMs”). We again used LMMs with male ID set as a random effect for this analysis. All LMMs were fitted using the lme4 package in R (Bates et al. 2014).

In our androgen model, the mean monthly residual fAMs of leader males was our outcome variable and the number of follower males (integer), total number of infants present in the unit (integer), number of cycling females (integer), and total number of infant deaths (integer) occurring up until sample collection date as our predictor variables. We calculated mean residuals because our sample collection was
opportunistically done, and we did not necessarily have samples during the month of an infant death for all infant deaths post takeovers. Neither did we have a large number of samples across the weeks preceding or following infant deaths to measure modulation (differences between high and low hormone values) that could capture surges in androgens or glucocorticoid levels during infanticide. Since our overall prediction is that males that kill more infants (show more infanticidal behaviors) will exhibit higher levels of androgens, we used the cumulative number of infant deaths (0-4) directly attributable to infanticide up until the point of sample collection as a measure for degree of infanticidal behavior.

In our GC models, the mean monthly residual fGCMs of leader males was our outcome variable and the number of follower males (integer), total number of infants present in the unit (integer), number of cycling females (integer), and cumulative number of infant deaths (integer) occurring up until sample collection date as our predictor variables. Male identity was added as a random effect in both models. We z-transformed all our numeric predictor variables before fitting models and checked for multicollinearity issues again.

After fitting these two models, we employed model comparison methods using AIC values and performed model selection using the `dredge()` function, followed by model averaging with functions in the MuMin package in R (Barton and Barton 2015). We present results from our model averaged coefficients using the package `sjplot()` in R (Fox and Hong 2010; Lüdecke n.d.).
Tenure length GLM model: What are the payoffs for the different degrees of infanticide?

We examined whether mean measures of demographic variables as well as mean residual androgens and glucocorticoids averaged over the first year of tenure (or shorter if male tenure itself was <12 months) predicted overall male tenure length of leader males. Our demographic variables included average number of cycling females in the first 12 months (integer), average number of followers in the first 12 months (integer), proportion of time the former leader was present in the unit the first 12 months of tenure (continuous 0-1), and the total number of infants killed (integer). Our hormone measure variables included the mean measure of residual fAMs and GCMs calculated across the year for each male. We had accurate tenure lengths from 54 males - but not all of these fit into our category of infanticidal /non-infanticidal males as some males did not have infants in their units at takeovers. This restricted our dataset further to 38 males. In the first tenure length model, we only included demographic variables as our predictors (38 males) since we did not have hormone samples from all these males. In our second model, we included all demographic variables along with the mean measures of residual fAMs and fGCMs calculated in the first year of tenure, this dataset consisted of 28 males. As our outcome variable (tenure length) was not normally distributed, and each row in our dataset represented a leader male with averaged values of our predictors calculated over the first year, we fitted a generalized linear model (GLM) with a Poisson distribution.

Results
Takeovers

We observed 94 successful out of 96 takeovers during the study period. The duration of takeovers ranged from short (n = 38, range = 0-7 days; mean = 3.16 days, SD = 2.99 days) to drawn out (n = 56 takeovers, range = 8-252 days; mean = 49.19 days; SD = 56.82 days) and 28 out of 94 takeovers were messy, with only 9 challenges imposed on resident leader male by a single bachelor, the rest all being groups of bachelor males vs coalition of males attacking leader male. 23 out of 94 takeovers led to group fission/fusion events and former leader male remained as a follower in the unit 45 out 94 takeovers.

Takeover analysis

Number of pregnant females in the unit decreased the likelihood of takeovers [β = 0.42, CI = 0.33-0.54] while the number of cycling females increased the likelihood of takeovers [β = 1.35, CI = 1.17-1.56]. With each additional pregnant female and cycling female in the unit, we observe an approximately 58% decrease and 35% increase in the odds of takeover respectively. Former leader presence and number of followers both increased the likelihood of takeovers [former leader presence: β=23.07, CI=14.64-36.36; followers: β = 1.44, CI = 1.30-1.59] (Fig 4.1). With each additional follower in the unit, there is a 44% increase in the odds of a takeover while the presence of former leaders in units leads to a 22.07 increase in the log odds of a takeover. We conducted an additional set of cox proportional hazards model with takeover as our outcome variable and same set of predictor variables to confirm our results from the binomial model. Even though the number of followers was time transformed in this model as it
violated the proportional hazards assumption, the results from the cox proportional hazards model are identical to the one presented in the GLMM (Fig S4.6).

**Figure 4.1:** GLMM results showing that probability of takeover of a unit at any time increases significantly with the presence of a former leader, more followers, and more cycling females in the unit. The probability of takeovers decreases with the increasing number of pregnant females within the unit. Panel A shows the model coefficient plot from full binomial GLMM. Points represent coefficient estimates and error bars the 95% confidence intervals. Points to the left of 1 indicate decreased likelihood of takeover occurrence while points to the right indicate increased likelihood of takeover. Panels B-E shows model predictions for each predictor that came out significant in our model respectively.
Hormone analysis

Visualizing fAMs and fGCMs values across the full length of male tenure based on the total number of infants killed seems to suggest that overall, there might be a sharp decline over male tenure in hormone levels in males that kill more infants (although this pattern doesn’t necessarily hold true for the category of males that kill three infants) (Fig S4.7). Plotting residual fAMs and fGCMs across the first 12 months post takeover also suggests that there are no differences between males that kill infants and those that don’t kill infants (Fig 4.2). Our first two LMMs with seasonal predictors as fixed effects and male ID as a random effect show that increase in rainfall leads to lower fAM and fGCMs while increase in min Temp leads to higher fAMs and fGCMs (a pattern that we expected based on previous reports from this population) (Fig S4.8). Number of cycling females, cumulative number of infants killed up until sample collection month, and number of follower males did not reliably predict residual fAMs and fGCMs in our LMMs (Fig 4.3).
**Figure 4.2:** Panel A shows no difference in overall mean androgen and glucocorticoid residuals between leader males (that commit infanticide and that do not, despite having the opportunity to do so). Panel B shows no difference in mean residual fAMs and fGCMs in the two categories of males when observed across 12 months following a takeover.
Figure 4.3: LMM results showing that both residual fecal androgen metabolite levels (fAMs) and residual glucocorticoid levels (fGCMs) in leader males in the first year of tenure are not affected by the number of infants killed. Panel A & B show the model averaged coefficient plot from dredged LMMs. Points represent coefficient estimates and error bars the 95% confidence intervals. As all error bars overlap 0, the effect of predictors on both fAMs and fGCM is not reliable.

Tenure length analysis

We modeled tenure length in two different ways. First, we examine the effect of demographic variables and infanticide behavior only - so that we can include more males in this analysis. Here, we found that former leader presence in the first year decreases the overall tenure length of males by 18% [$\beta=0.82$, CI=0.80-0.84] and with each additional cycling female in the unit, the overall tenure length of leader males reduces by 23.6% [$\beta=0.76$, CI=0.74-0.79]. The number of followers in the first year increased tenure length by 7% [$\beta=1.07$, CI=1.03-1.11] (Fig 4.4A). Interestingly, the total
infants killed does not predict tenure length overall in males [β=1.03, CI=1-1.05] suggesting that demographic variables in the first year of tenure (such as cycling females and presence of former leaders) more strongly influence tenure length of leaders (Fig S4.9).

Next, using a reduced dataset consisting of 28 males, we modeled tenure length with mean measures of fAMs and fGCMs along with the same set of demographic variables (as in the previous analysis) from the first 12 months of male tenure. This analysis showed that high residual fecal androgen metabolite levels (fAMs), high residual glucocorticoid levels (fGCMs), more cycling females and the presence of former leaders in the first year of tenure all reduce overall tenure length of males. On the other hand, the only variable increasing tenure length was the number of followers. Specifically, having followers increases overall tenure by 12% [β=1.12, CI=1.08-1.16] and with each infant killed in the first year, tenure length of leader males increases by 12% [β=1.12, CI=1.08-1.16]. With increasing cycling females in the unit, tenure length reduces by 28% [β=0.72, CI=0.69-0.74] (Fig 4.4B). Similarly with each an increase one SD of mean residual fAMs and fGCMs in the first year, tenure length decreases by 25.7% [fAMs: β=0.74, CI=0.70-0.78] and 5% [fGCMs: β=0.95, CI=0.91-0.99] respectively (Fig S4.10).
**Figure 4.4:** Panel A showing model coefficient plot (29 males) showing that high residual fecal androgen metabolite levels (fAMs), high residual glucocorticoid levels (fGCMs), more cycling females and presence of former leaders all reduce overall tenure length of males while more follower males and killing more infants increases tenure length. Panel B showing the model coefficient plot from Poisson GLMM (38 males) without hormone predictors shows similar results (except for the effect of infants killed which is no longer statistically significant). Points represent coefficient estimates and error bars the 95% confidence intervals.
Discussion

In this study, we take an integrative approach to examine infanticide in geladas by simultaneously assessing proximate mechanisms and reproductive payoffs of infanticide as a strategy. Overall, our research provides evidence that reproductive opportunities as well as presence of male followers can have important implications in shaping male strategies during takeovers. Specifically, we find no evidence that infanticide is mediated by surges in hormone levels in new leader males. More cycling females in the unit in the first year of male tenure can increase the likelihood of takeovers and reduce tenure length of leader males, while more pregnant females in units lead to decreased likelihood of takeovers. On the other hand, the presence of former leaders both increases the likelihood of takeovers and presence of former leaders in the first year reduces tenure length of leader males. The presence of other followers (non-former leaders) in the unit might increase the likelihood of takeovers, but leader males with more followers in the first year of tenure also had longer tenure lengths.

Cycling females and former leaders increase likelihood of takeovers

A previous set of analysis of demographic data from the same gelada population found that unit size (total number of adult females in the unit) drives overall takeover rates (Tinsley Johnson et al. 2021) and followers in units increases leader male tenure length (Snyder-Mackler et al. 2012). We re-analyze the long-term data with two important considerations that previous studies have not made mainly because data was not available at the time. First, we take into consideration the reproductive state of females.
We find that female reproductive state is an important parameter driving takeover rates as well as infanticide in gelada units. Infant survival is higher post takeover when there are more cycling females in the unit (Sen et al in prep 2023). While unit size is expected to generally track with the number of available fertile females in the unit, the presence of lactating or pregnant females in the unit might have opposing effects on male takeover decisions as they represent reduced opportunities or costs. Here, by adding the number of cycling and pregnant females along with the number of vulnerable infants in our models, we tease apart the opposing effect that females in different reproductive states might have on takeover rates. We find that the number of cycling females increases the likelihood of takeovers while the number of pregnant females reduces it (Fig 4.1).

Second, we consider follower male type in units - as followers in gelada units could either be older deposed former leader males remaining with the unit after a takeover or young immigrant males i.e. adult males that are early-mid prime (8-12 years) that join the unit for short periods of time (Beehner et al 2016). We found that both categories of follower males increase the likelihood of takeover in our study population. This result was unexpected because we know from previous studies that followers share a small percentage of paternity with leader males in units (Snyder-Mackler et al. 2012). Therefore, we would expect that follower males provide protection against takeovers in units; especially more so for former leaders, who are essentially extending their reproductive tenure in the unit by remaining in it post-takeover. Therefore, our results showing former leaders having the strongest effect in driving likelihood of takeovers in our study site is surprising (Fig 4.1). But, considering what we know now about male
social dynamics in our population from field observations, former leaders might actually have little incentive to defend gelada units for two reasons. First, most former leaders who remain as followers have vulnerable offspring and have well established social bonds with females in their units. Second, former leaders might also be physically weaker and have lower energy reserves to aid in competitive challenges (for example, former leaders have lower subscapular skinfold measure - indicative of peripheral body fat measures and lower fAMs, Sen in prep 2023). We speculate that bachelors may target units with multiple adult males and females as these units are more conspicuous in the band and male-female connections in multimale-units might be weaker. However, we cannot be sure if presence of these males is causing these takeovers, as these two factors could also be more prevalent in the wake of a takeover.

*Infanticidal males do not show high levels of androgens of GCs*

Both fecal androgen and glucocorticoid metabolite levels did not reflect infanticidal behavior in leader males within the first year of tenure (Fig 4.2). LMMs showed that when controlling for seasonal and other demographic variables, infanticidal males did not have high residual mean fAMs or fGCMs. This absence of a pattern observed could be due to our low sample resolution - as samples are mostly collected opportunistically, our samples might not accurately capture the time frame when infanticide could have most likely occurred. We also suspect there could be methodological issues with this analysis (using mean residuals to control for seasonal effects) that are interfering with our ability to detect a signal of fAMs or fGCMs. When we broadly categorize males based on the total number of infants that they killed and visualize raw values of fAMs and fGCMs across overall tenure, we do see some differences emerging based on the
slope of the regression line for hormone levels across male tenure (with males that kill more infants have a steeper downward slope) \((\text{Fig S4.7})\). So, it might be worth examining hormonal attributes over the entire male tenure instead of just the first 12 months (or even less if they were taken over between 3-12 months following their takeover date).

**Former leaders and follower males have opposing effects on male tenure length**

We examined if killing infants reduces overall tenure length in leader males. We included number of cycling females, total number of infant deaths attributed to infanticide, number of follower males, and proportion of time former leader was present - all averaged over the first year of tenure in our models. We found that demographic variables have a stronger and more reliable effect on male tenure length than infanticide, and that number of infants killed does not affect tenure length \((\text{Fig 4.4})\).

First, leader males that had more cycling females in their units in the first year had overall shorter tenure lengths. Second, leader males that had followers in their units (that are non-immigrant males) in the first year had increased male tenure. Third, having former leaders in the first year themselves do not increase tenure length of males \((\text{Fig S4.9})\). Although our tenure length analysis that included fAMs and fGCMs showed males with overall high levels of these residual steroid hormones in the first year had lower tenure length, this analysis included only 29 males - and therefore the effect of these predictors might be less reliable because of a limited dataset.

**Conclusion**
With the accumulation of more long-term data on leader males and takeovers in our study population, we were able to revisit some previously published analysis investigating how multimale groups in gelada society affect leader male tenure. When we take follower male identity into consideration, former leaders do not help lengthen leader male tenure. This result is somewhat surprising as we would expect former leaders to help resident leader males defend the unit. However, former leaders in our study site that have long tenures as followers actually are older leader males (that had greater than median tenure length). We speculate that these males remain in units simply because, a) emigrating at their body condition and age is riskier, b) the chances of them taking over another unit is too low and c) they already have established social connections with females in the unit. Furthermore, leader males that have overall long tenures do not have former leaders present throughout their tenures (as former leaders eventually disappear and are presumed to be dead). Therefore, we think the ability of leader males to stick on for longer periods of time could be driven by demographic variables and/or his ability to maintain social bonds with unit females.

Male-female social behavior is one important aspect of male strategy that we have not considered here. Although we had initially proposed a tradeoff between the “aggressive” strategy (infanticide), maximizing immediate mating success by increasing the number of fertile females, versus the “affiliative” strategy (social bonds with females), maximizing unit cohesion and possibly male tenure, our results show that infanticidal males might be the ones that have a higher reproductive tenure. This suggests that these males are also able to quickly integrate themselves within the unit and form social
bonds with females. Thus, investigating social integration between males and females in the first year of tenure and during overall tenure will be a critical next step to examine if males can switch between extreme strategies.

Finally, we need to examine how leader males that follow these two strategies (infanticidal versus non-infanticidal) differ in their overall reproductive success. Indeed, this was a main focus of this study but due to methodological constraints (shutting down of fragment analysis core at UM, validating a new sequencing protocol and bioinformatics pipeline to generate the genetic data) and complications due to the COVID-19 pandemic, this analysis was delayed. Paternity data which is forthcoming will help us understand if these males have higher paternity success.

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Supplementary materials

Figure S4.1. Number of takeovers across the year in our study population. Colors represent the distinct season categories observed in the Simien Mountains (as published in Tinsley Johnson et al 2018).
Figure S4.2. Panel A showing tenure length distribution of 54 leader males with known start and end dates in our study population.
Figure S4.3. Seasonality of fecal androgen levels in adult male geladas from different social status. Closed circles and lines represent the mean fAMs from male samples plotted across the year. Upward facing orange triangles represent average maximum temperature (calculated across the previous 30 days). Downward facing orange
triangles represent mean minimum temperature (calculated across the previous 30 days from sample collection date). Gray bars represent cumulative rainfall over the previous 90 days from sample collection date. Italicized numbers on top of x axis labels indicate the number of males we had fecal samples from each month for the duration of the study period (2006-2020).
Figure S4.4. Seasonality of fecal glucocorticoid levels in adult male geladas from different social status. Closed squares and lines represent the mean fGCMs from male
samples plotted across the year. Upward facing orange triangles represent average maximum temperature (calculated across the previous 30 days). Downward facing orange triangles represent mean minimum temperature (calculated across the previous 30 days from sample collection date). Gray bars represent cumulative rainfall over the previous 90 days from sample collection date. Italicized numbers on top of x axis labels indicate the number of males we had fecal samples from each month for the duration of the study period (2006-2020).
**Figure S4.5.** Histogram showing the distribution of fecal androgen metabolite levels (A) and fecal glucocorticoid metabolite levels (B) measured from adult male samples.
Figure S4.6. Cox model hazards ratio for takeover analysis shows the same results as takeover analysis in this study.
Figure S4.7. Plotting mean fAMs (panel A) and fGCMs (panel B) across tenure for males that killed 0-4 infants during the first 12 months of takeover.
Figure S4.8. Coefficient plot from LMMs showing the effect of rainfall and min Temp on fecal androgen levels and fecal glucocorticoid levels. Points here are estimates for each predictor with horizontal lines representing the 95% confidence interval around each estimate. The vertical gray line indicates no effect with each point estimate falling on the right side indicating a positive effect of the predictor on the outcome variable and points falling on the left indicating an overall negative effect.
**Figure S4.9.** Plot showing model prediction results from tenure length analysis for each predictor of interest. Tenure length decreases when leader males have more number of cycling females in the first year and if former leaders are present for greater proportion of time in the first year of leader male’s tenure (panel A & C). While tenure length increases with more infants killed in the first year and with more followers in the unit in the first year of male’s tenure (panel B & D).
**Figure S4.10.** Mean residual fGCMs and fAMs in the first year plotted against tenure length of males. High first year residual fGCMs and fAMs in the first year of tenure shows a trend towards shorter tenure lengths.
Chapter 5: Conclusion

Significance of research

This dissertation focused on reproductive strategies in wild geladas (*Theropithecus gelada*) living in the Simien Mountains National Park, Ethiopia. I examined two distinct and risky life history stages where male geladas are faced with unique social challenges - dispersal and takeovers - during which males are known to show variability in the decisions they make. In cercopithecine primates, successful emigration from natal groups and subsequent rank attainment are two critical factors that determine male reproductive success (Kappeler and van Schaik, 2004; van Noordwijk and van Schaik, 2004). Although typical male strategies to acquire dominance rank in a new group include aggressive behaviors that facilitate competition (e.g., male contests, female coercion, and infanticide), they can also include affiliative behaviors (e.g., male-female friendships, male-male coalitions) (Clutton-Brock, 2021; Clutton-Brock and Harvey, 1978; Goffe et al. 2016; Danish and Palombit, 2014). Interestingly, both aggressive and affiliative strategies can be found within the same species, and possibly even the same individuals. Although male geladas ostensibly fall on the aggressive side of the male behavior spectrum (due to high male reproductive skew, high degree of sexual dimorphism in both body size and canine size (Clutton-Brock, 1998; Setchell et al. 2005), this research suggests that males may employ/rely on affiliative strategies to meet their reproductive goals. My research goals first required that I validate methods to
reliably measure male attributes. I then laid particular emphasis on the proximate mechanisms underlying these variations and developed a foundation for testing future predictions on how these variations in male decisions may lead to differences in male reproductive success. Below, I summarize the main findings from my dissertation and provide new insights about dispersal patterns and infanticidal behavior in geladas.

**Dispersal and male maturation in geladas**

In Chapter 2, I validated an in-house biotin labeled microtiterplate enzymeimmunoassay (epiandrosterone assay) for measuring fecal androgen metabolite levels in wild geladas. In this study, I first assessed the age specific normative androgen profiles and dispersal ages of males in this population. I then examined social correlates of androgen levels and dispersal age in natal males. I found that for juvenile males, maternal rank was the only influential predictor of fecal androgens - males with low-ranking mothers having higher age specific androgen levels than males with high-ranking mothers. These results suggest that maternal effects (via rank) can affect the pace of male development in geladas. Although we did not see a similar effect of maternal rank on age of dispersal (i.e. males with low-ranking mothers did not disperse earlier), there was a trend in the data towards this direction. I expect this trend to become clearer as we acquire more long-term data confirming a pattern also reported in male rhesus macaques and female chimpanzees (Weiβ et al. 2016; Walker and Pusey, 2020).

I found that male gelada dispersal was influenced by other social factors; juvenile males with more male peers and males residing in larger groups dispersed earlier than males...
with few peers and males in smaller groups respectively. The effect of peers and group size on dispersal age may be due to the multileveled social structure of gelada society and the formation of temporary all male groups. Male geladas that disperse from natal groups with peers disperse at an earlier age but may remain in their natal bands, as they can easily form bachelor groups with known peers. This joint dispersal pattern is common in cercopithecine primates as dispersing with a partner may reduce risks associated with this life history milestone. However, unlike other cercopithecine primates, the timing of dispersal and male maturation are not closely linked in geladas, as shown by the lack of surges in androgens preceding or following dispersal. In fact, both androgen data and teeth emergence data suggest that male geladas continue to grow and mature even after dispersal. These results suggest that dispersal may not pose as serious a risk in geladas compared to other cercopithecine primates, particularly for males that disperse with known individuals and remain in their natal bands; we speculate that emigrating from these bachelor groups (instead of emigrating from natal groups) is the life history stage that is equivalent to dispersal in other male-dispersing taxa. Taken together, these results suggest that juvenile males benefit from having same aged social partners both during and after dispersal. Future research will identify how affiliative male-male interactions in juveniles impact their dispersal decisions and future reproductive success.

**Variation in infanticide behavior in geladas**

Across nearly every major mammalian taxon, sexually selected infanticide is a highly successful male reproductive strategy. However, although multiple theoretical models
have demonstrated the conditions under which infanticide should emerge, very few empirical studies have had sufficient data to test these models. In Chapters 3 and 4, I examined variation in infanticidal behavior in male geladas using 14 years of data.

In Chapter 3, I first examined drivers of overall infant mortality in the Simien Mountains population of wild geladas. I found that infants that experienced takeovers before 18 months (mean age of weaning, (Baniel et al. 2022) have reliably higher mortality compared to infants that do not experience takeovers. Infant mortality rates also remained high up until 11 months post takeover suggesting that infants are vulnerable to infanticide for a longer period of time compared to other cercopithecine primates. Interestingly, even though takeovers are the key drivers of infant mortality in this population, 44% of takeovers did not result in offspring death even when new males had the opportunity to commit infanticide. Upon examining infant survival post takeover, I found that infant age at takeover and number of cycling females were the strongest predictors of infant survival. Infants are more likely to survive if they are older during takeovers and if there are more cycling females available for the new male to reproduce with. I also found that former leaders were more likely to remain with the unit when there are more vulnerable offspring in the unit, however the presence of former leaders themselves do not reduce the risk of infanticide. These results suggest that although takeovers increase offspring mortality overall, new dominant males do not commit infanticide when there are reproductive opportunities already present at takeover suggesting variation in infanticide occurrence is best explained by demographic variables and not former leader presence. Whether or not this variation observed in
males is directly caused by males pursuing alternate reproductive strategies still needs to be statistically tested.

**Male attributes and reproductive tenure of infanticidal and non-infanticidal males are similar**

In Chapter 4, I quantitatively assessed the conditions under which takeovers occur in our population and examined the factors that make units susceptible to takeovers - the prelude to all infanticidal behavior. I found that bachelor males target units with more cycling females, fewer pregnant females, and multimale units. The presence of former leaders in units had the strongest effect of increasing the likelihood of takeovers. Fecal androgen and glucocorticoid levels of new leader males were not affected by the number of infants they killed when controlling for all seasonal and demographic predictors suggesting that there are no physiological differences between males committing infanticide. However, this lack of relationship between steroid hormones and infanticide could also be due to our coarse sampling regime - as samples are mostly collected opportunistically, our samples are not always collected within the nearest time point when infanticide could have most likely occurred, and/or there are methodological issues with this analysis (using mean residuals instead of actual values) that are interfering with our ability to detect a signal of fAMs or fGCMs. Contrary to expectations, I found that killing infants does not decrease overall leader male tenure length.

In this study, I took advantage of the accumulation of long-term data on leader males and takeovers in our study population to revisit previously published analyses.
investigating how multimale groups in gelada society affect leader male tenure. My analysis suggests that having followers (that are non-immigrant males) in the first year overall does help increase male tenure, however former leaders themselves do not increase tenure length. This result is somewhat surprising as we would expect former leaders to help resident leader males defend the unit as predicted by the male concessions model. Closer inspection of our long-term data indicates that most former leaders that have long tenures as followers are older leader males (that had greater than median tenure length themselves). We speculate that these males remain in units simply because a) emigrating at their body condition and age is riskier, b) the chances of them taking over another unit is too low and c) they already have established social connections with females in the unit. Leader males that have overall long tenures (>3 years) do not have former leaders present throughout their tenures (as former leaders eventually disappear, and presumably die). Thus, we think the number of reproductively available females and/or the ability to maintain social bonds with unit females predict the ability of leader males to remain with a unit longer rather than the presence of followers.

**Future research**

While this research examines putative mechanisms underlying differences in male dispersal and infanticide strategies in geladas, examining male affiliative behaviors in the future will be an important next step in piecing together the male life history puzzle. Specifically, we need to closely examine if male-male affiliative relationships help juveniles disperse and form bachelor groups that form coalition to takeover units, and
whether infanticide truly impedes a male’s ability to form social bonds females. Male-female social bonds are an important predictor of male reproductive success in primates as long-term data from the wild suggests that males can form strong affiliative bonds to attain their reproductive goals (Ostner and Schülke, 2014; Ebenau et al. 2019; van Schaik et al. 2006; Young et al. 2014). Understanding how males employ these affiliative behaviors can provide important clues about social evolution. In this dissertation, I followed 11 leader males and 4 former leader males during 2018-2020 for my dissertation fieldwork where I collected detailed hormonal, behavioral, and demographic data. I had originally planned to examine dominant male-female social bonds and how new males form social relationships at the very start of their reproductive tenure by establishing a dense behavioral data collection protocol in the field and focusing on takeovers. I was not able to analyze this data for my dissertation as a) I ran out of time because of funding issues, b) I observed only two takeovers during the 14 months of fieldwork, and c) because of the pandemic and subsequent war in Ethiopia, our behavioral data collection was stalled significantly even though there have been five takeovers in the past two years. However, all hope is not lost! The SMGRP has coarse data on male-female dyadic interactions, and once routine data collection restarts in the field, the project will be able to collect dense behavioral data (using the protocol I established) from units undergoing takeovers and in the first year of male tenure. My future research will focus heavily on this important aspect of male reproductive strategy and incorporate both sparse and dense behavioral data to examine broader patterns in how males socially integrate in units in their first year.
In primate behavioral ecology, a lot of focus has been put on aggressive reproductive strategies aiding male-male competition and males have traditionally been thought to be less social than females. However, recent studies using long-term data suggest that males in some species can also form strong affiliative bonds with one another as well as with females and infants (Rosenbaum et al. 2011; Feldblum et al. 2021; van Schaik et al. 2006; Ostner and Schülke, 2014). For example, in chacma baboons (closely related to geladas) males show distinct age-based behavioral patterns where older adult males exhibit more parenting and affiliative behavior towards females than younger adult males (Silk et al., 2020). Although former leader males do not provide direct protection to infants from infanticide in geladas, we still need to examine if former leaders transition from a mating to a parenting role in geladas.

Finally, the use of genetic data has provided valuable insight into the evolution of primate social systems - ascertaining reproductive payoffs and skew, sex-specific dispersal patterns, social structure, effect of kinship on social behavior to name a few (Di Fiore 2012). Traditional methods have relied on fragment analysis, which is time consuming, expensive, and not comparable between labs. Using a universal panel of microsatellite markers that was developed and published in 2020, I modified and validated a novel and cost-effective research pipeline to genotype geladas using Next Gen Sequencing methods. Data from this study is forthcoming, and once genotypes are obtained, I will be able to measure and update paternity measures previously reported in Snyder-Mackler et al 2012 with an additional ten years of demography and life history data.
Despite our knowledge of the existence of reproductive strategies in primates, detailed and rigorous studies have yet to address (a) proximate mechanisms underlying these strategies, (b) individual fitness consequences of these strategies, and (c) how they impact the genetic structure of a population as a whole. My research sets up the foundation for addressing all these equally crucial components to better understand the evolution of male reproductive strategies in wild primates.
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