

## Social correlates of androgen levels and dispersal age in juvenile male geladas

Sharmi Sen<sup>a,\*</sup>, Sofia C. Carrera<sup>b</sup>, Michael Heistermann<sup>c</sup>, Caitlin Barale Potter<sup>d</sup>, Alice Baniel<sup>e,f</sup>, Patricia M. DeLacey<sup>b</sup>, Lauren Petruccio<sup>b</sup>, Amy Lu<sup>g</sup>, Jacinta C. Beehner<sup>a,b</sup>

<sup>a</sup> Department of Anthropology, University of Michigan, Ann Arbor, MI 48109-1107, USA

<sup>b</sup> Department of Psychology, University of Michigan, Ann Arbor, MI 48109-1107, USA

<sup>c</sup> Endocrinology Laboratory, German Primate Center, Leibniz Institute for Primate Research, 37077 Göttingen, Germany

<sup>d</sup> Cedar Creek Ecosystem Science Reserve, University of Minnesota, St. Paul, MN 55108, USA

<sup>e</sup> Center for Evolution and Medicine, Arizona State University, Tempe, AZ 85281, USA

<sup>f</sup> School of Life Sciences, Arizona State University, Tempe, AZ 85287, USA

<sup>g</sup> Department of Anthropology, Stony Brook University, Stony Brook, NY 11794-4364, USA

### ARTICLE INFO

#### Keywords:

Juvenile development  
Male life history  
Androgens  
Dispersal  
Individual variation  
*Theropithecus gelada*

### 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. Here, we examined the conditions that may be associated with 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). 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. Taken together, results suggest 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.

### 1. Introduction

Steroid hormones play a central role in many vertebrate life history trade-offs (Muehlenbein and 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; Dixon and Anderson, 2004; Hau, 2007). Androgens themselves are also modulated by the social environment in a bi-directional relationship (Hirschenhauser and 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 and Bentley,

\* Corresponding author at: 101 West Hall, 1085 South University Avenue, Ann Arbor, MI 48109, USA.

E-mail address: [sharmisn@umich.edu](mailto:sharmisn@umich.edu) (S. Sen).

<https://doi.org/10.1016/j.yhbeh.2022.105264>

Received 5 April 2022; Received in revised form 6 September 2022; Accepted 9 September 2022

Available online 22 September 2022

0018-506X/© 2022 Elsevier Inc. All rights reserved.

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 and Altmann, 1995a, 1995b; Greenwood, 1980). At the species level, the phenotypic changes associated with sexual maturation coincide with dispersal events (Galbany et al., 2015; Holekamp and Smale, 1998). However, at the individual level, the onset of androgen secretion and the timing of dispersal can 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 and Oliveira, 2006; Rutberg and 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 and 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 and 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., 2019, 2021). Moreover, both of these have been associated with an earlier age at dispersal in several other taxa (Andres et al., 2013; Goldenberg and Wittemyer, 2018; Stanton et al., 2020). Thus, maternal resources (or lack thereof) that derive from maternal rank, additional siblings, or maternal loss can be associated with variation in male development (Bernstein et al., 2012a).

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 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 and Fairbanks, 2002). If males are the dispersing sex, male peers can additionally serve as dispersing partners, facilitating parallel dispersal events (Jack and Fedigan, 2004; Jack et al., 2009; Wikberg et al., 2014, 2018) which reduces the risk of predation and harassment from conspecifics during dispersal (Cheney and Seyfarth, 1983; Rutberg and 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 accelerate androgen production/disperse earlier; and males with younger peers in their groups

might decelerate androgen production/disperse later.

Here, we examine whether access to maternal resources or 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 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 et al., 2014). The core modular unit of gelada society is the reproductive unit (hereafter “unit”) with one dominant breeding male, 2-12 related adult females and their related offspring, and 0-5 subordinate males (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 (Papano, 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., 2012, 2014). This multi-leveled social organization provides the opportunity to observe juvenile males growing up in relatively 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 their “final dispersal”) may not reflect the onset of maturity, as found for other taxa (Akinyi et al., 2017; Onyango et al., 2013a, 2013b). 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 of geladas 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 we have 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 (*androgens 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 male geladas experience *a surge in androgen levels around dispersal*. Finally, we examine how access to maternal and peer resources affect their *timing of dispersal* (Table 1). We predicted that accelerated male development (e.g., higher age-specific androgen levels and/or 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 be associated with accelerated development. Finally, based on the idea that males prefer to

**Table 1**  
Summary of predictions for androgen profiles and age at dispersal.

	Predictor	Fecal androgen metabolites	Age at dispersal
Maternal resources	Maternal rank	Males with low-ranking moms will have higher age-specific androgens	Males with low-ranking moms will disperse earlier
	Early sibling arrival	Males with early-sibling arrival will have higher age-specific androgens (not tested due to insufficient sample size)	Males with early-sibling arrival will disperse earlier
	Maternal loss	Males experiencing maternal loss will have higher age-specific androgens (not tested due to insufficient sample size)	Males experiencing maternal loss will disperse earlier
Peer resources	Cohort size	Males with larger cohort will have higher age-specific androgens	Males with a larger cohort will disperse earlier

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.

## 2. Materials and methods

### 2.1. Study site and subjects

This study was conducted as part of the long-term Simien Mountains Gelada Research Project in Simien Mountains National Park, 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 to 2020. Of these males, we have known dates of birth for 128 of them. The remaining males belonged to units that were not observed routinely in the study area or were infants when the project began; and we estimated their dates of birth based on when they were first seen in the unit (estimated with 0–226 days uncertainty, mean = 33.5 days, SD = 55.6 days). All study subjects were monitored until permanent dispersal from their natal unit. We collected a total of 1611 fecal samples from 70 natal males from 2011 to 2020 with known ages at sample collection (age range: <1–10 years; all dates of birth known within 1–15 days) with an 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, we were able to obtain 73 samples from 22 natal males during the three months around dispersal. Details about the sampling distribution are provided in Table 1 (Supp Materials).

### 2.2. Fecal sample collection, extraction, and storage

Sample collection, extraction, and storage methods followed protocols previously validated for geladas (Beehner et al., 2009; Beehner and McCann, 2008; Pappano et al., 2010). In brief, fresh fecal samples collected from known individuals were thoroughly mixed with a spatula 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 h. 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 µm 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<sub>18</sub> 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 (~2 g 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 analyses.

### 2.3. 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 enzyme-immunoassay (EIA), which is a C17 group-specific enzyme-immunoassay that detects 17 oxo-androgens with 100 % cross-reactivity (Möhle et al., 2002; Palme and 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 the next day with PBS wash solution (containing 0.002% Tween 20), followed by the addition of 150 µl streptavidin horseradish peroxidase to each well and incubated in the dark on shaker for 1 h. 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 was 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.

### 2.4. 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/50 µl). 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. S1), 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). 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).

### 2.5. 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 (<1–9 years of age) 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 had

higher biological sensitivity, detected changes in fAMs between age groups during male development which the RIA did not (Fig. S3), 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. S4). 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.

## 2.6. 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., 2012b; Conley et al., 2011).

## 2.7. 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 are associated with androgen production in male geladas. Second, we investigated whether males have higher androgen levels in the months surrounding dispersal. Third, we tested if maternal and peer resources are associated with 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.

## 2.8. Age at dispersal

Juvenile gelada males typically 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.

## 2.9. 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 and de Vries, 2001; Neumann et al., 2011) for each female were calculated using the R package EloRating (Neumann and Kulik, 2014). 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 (Albers and Altmann, 1995a, b). 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).

## 2.10. 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 suggests that a male had maternal resources withdrawn earlier than other males in the population due to the birth of his 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.

## 2.11. Maternal loss

We know from previous research on this population that maternal social integration is related to male juvenile social networks — males with mothers that 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 that were poorly socially integrated (Barale, 2014). Thus, we can expect 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 that lost their mothers.

## 2.12. 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  $\pm 1.5$  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, (Sen et al., 2022)). We calculated the total number of peers for each male monthly (*cohort size*) and this variable was used in both the androgen and dispersal analyses.

## 2.13. 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 are 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).

2.14. Weather variables

We controlled for rainfall and temperature in our androgen analysis as previous research has demonstrated a positive relationship between rainfall/temperature and testosterone levels for leader males (Pappano and Beehner, 2014), and we found similar trends in androgen levels among juvenile males as well (Fig. S5). 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 in 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,  $t = -17.3$ ,  $p < 0.001$ ).

3. Data analyses

3.1. What factors predict androgen profiles?

All statistical analyses and data visualization was carried out using R v 4.0.3 (R Core Team, 2020). Because androgens showed the expected parabolic relationship with male age during development (Fig. 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 have shown that the relationship between fAMs and age becomes linear around the age when infants are

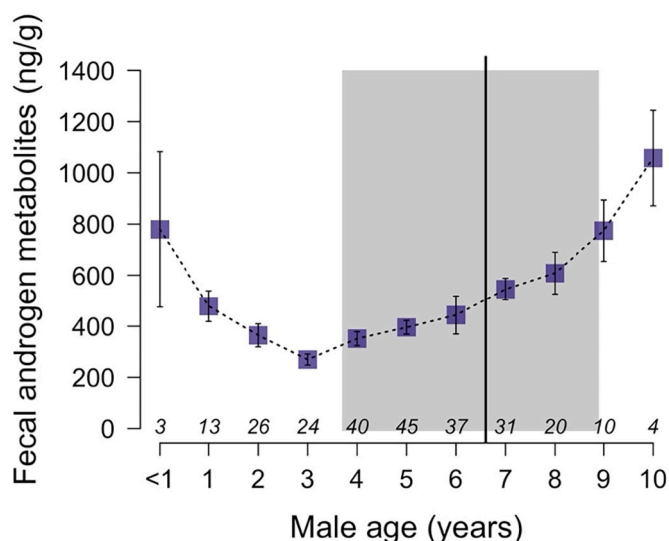


Fig. 1. Mean fecal androgen metabolite levels (ng/g) in male geladas with known ages (<1–10 years) with error bars representing the standard error of the mean. The gray rectangle represents the dispersal age range, black solid line indicates median age at dispersal (6.61 years) and italicized numbers represent the number of males sampled for each age category.

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. S6).

We fitted a linear mixed model (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 (Gelman, 2008). Male ID was entered as a random effect in all models. 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 multi-collinearity between predictors using the 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 and Anderson, 1998). We then performed model averaging across all models by averaging predictions of each model on the link scale as prescribed for LMMs and obtained averaged estimates for each predictor using model.avg() from the MuMin package in R for all models (Barton and Barton, 2015).

3.2. 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), 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

Table 2 Description of predictors for fecal androgen metabolite levels in males.

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

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.

### 3.3. 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, 2015). 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 and 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. S7), we did not include seasonal variables in this analysis.

## 4. Results

### 4.1. Androgens across male ages

Fecal androgen metabolites in male geladas demonstrated the expected parabolic pattern associated with age. In brief, fAMs were higher

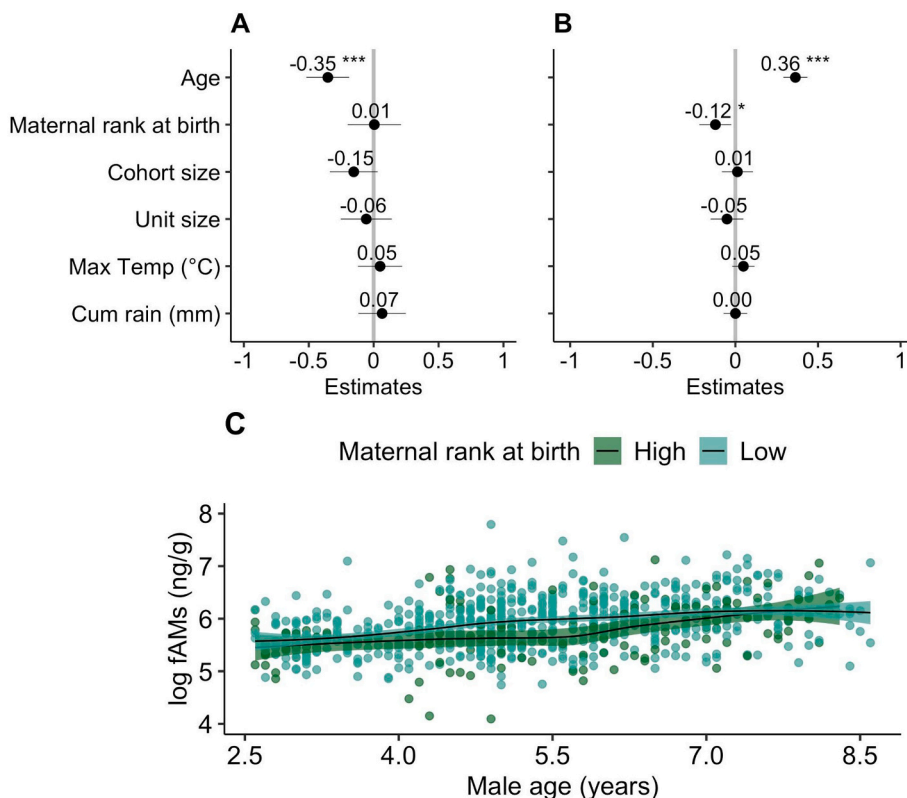
in males aged 1–2 years (almost showing adult fAM levels), reached a nadir between ages 2–3 years, and subsequently became higher from ages 3–10 years, becoming rapidly higher each year after the median age of dispersal (6.61 years) and reaching highest levels around 10 years when males appear to reach full sexual maturity (Fig. 1).

### 4.2. What factors predict androgen profiles?

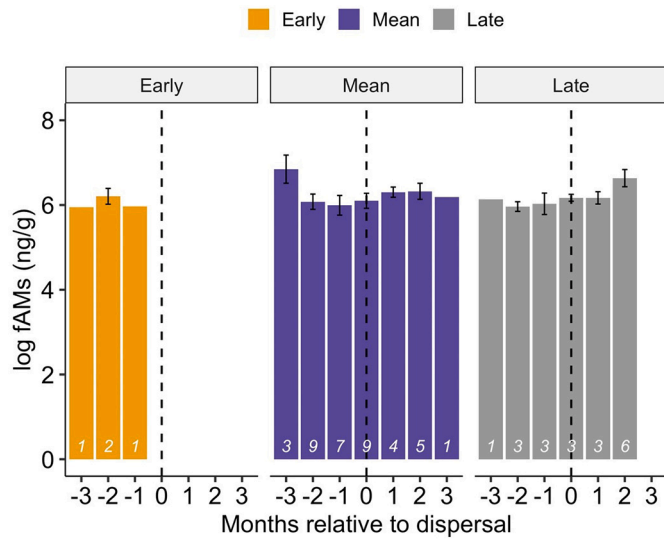
In our youngest, dependent males (<2.5 years), the only significant predictor for fAMs was male age at sample collection with males showing lower fAMs as they got older (Fig. 2A). In the older juvenile and subadult males (>2.5 years), age was also a significant predictor but affected fAMs in the opposite direction (a pattern we expected based on known vertebrate male development and from our biological validation in this population) (Fig. 2B). However, for the older group, we also found that maternal rank (at birth) was significantly associated with fAMs, such that males born to high-ranking mothers had lower age-specific androgens (Fig. 2B, 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 fAMs. 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. S8, S9). Model averaged coefficients, standard errors, confidence intervals, and significance levels for each predictor variable are presented in Tables 2 and 3 (Supp Materials).

### 4.3. Do males have higher androgen levels surrounding dispersal?

We did not observe higher fAMs around male dispersal date in geladas (Fig. S10). Separating individual males into early, mean, and late dispersal categories also did not show any clear patterns (Fig. 3). Additionally, we did not have any samples post-dispersal from our early-dispersing males. Note, that even though it appears that mean dispersers have higher fAMs 3 months prior to dispersal, we have only one sample



**Fig. 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 and panel B shows model coefficient plot for males aged >2.5 years. Estimates are exponentiated in log(ng/g) and the exact value is 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. 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.

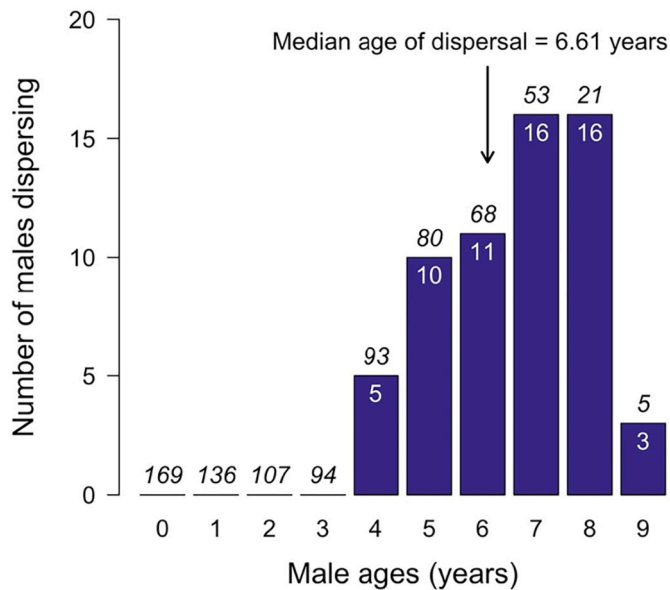


**Fig. 3.** Log transformed fAMs (ng/g) three months around dispersal show no clear surge in androgen levels. We categorized males as early (dispersed at <5.5 years of age), mean (dispersed between 5.5 and 7.7 years of age) and late dispersers (dispersed at >7.7 years of age). The black line indicates the month of dispersal and numbers in white at the bottom of each bar indicate the number of males sampled at each time point.

each from 3 different males. The same applies for late dispersers 2 months post dispersal when we see higher fAMs, where we have only 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. S11).

**4.4. What factors predict age at dispersal?**

The number of males that dispersed from their natal units for each age category is shown in Fig. 4. Median age of final dispersal is 6.61 years for this population [61 males; range = 3.66–8.89 years; std. dev =



**Fig. 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.

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 to 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. 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 4 (Supp Materials).

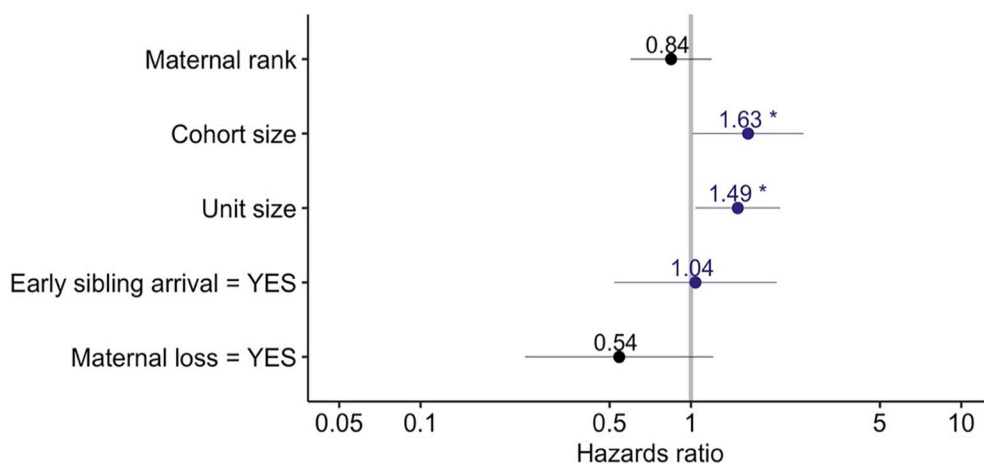
To inspect the effect of each category of predictor on dispersal age, we generated individual Kaplan-Meier curves adding predictors related to maternal resources (Fig. S12) and peer resources separately (Fig. 6). Since cohort size and unit size significantly affected dispersal age, we generated Kaplan-Meier 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. 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. S13).

**5. Discussion**

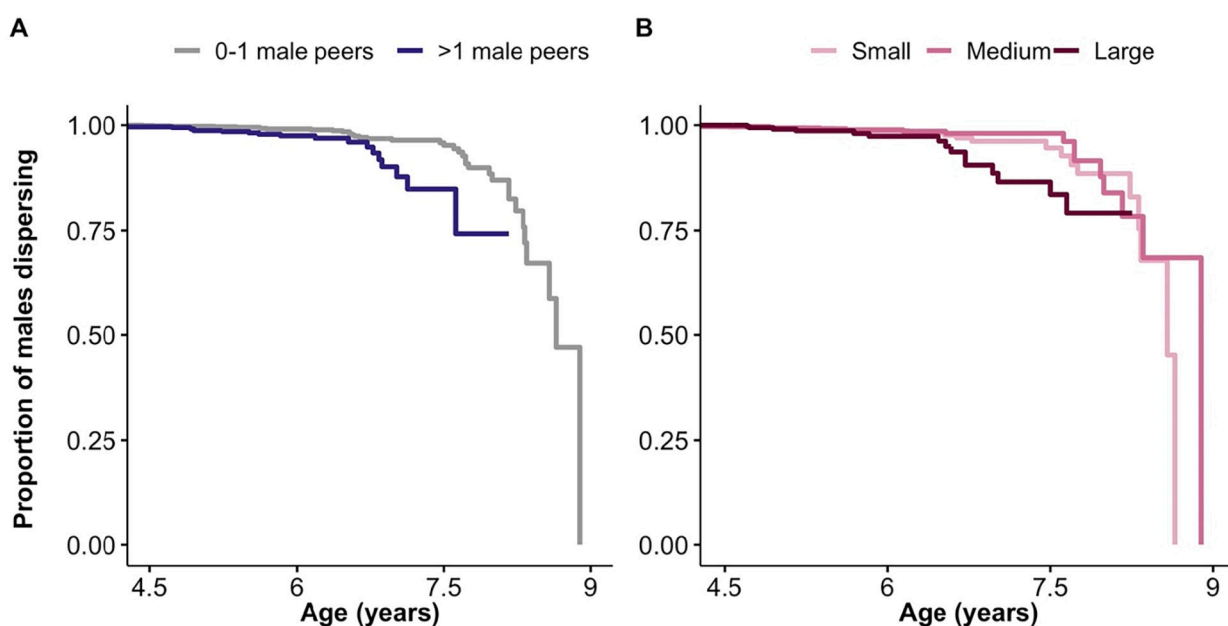
After validating an in-house epiandrosterone assay for measuring fecal androgen metabolites for use in geladas, we quantified the normative pattern of androgen production in males during development. Androgens were higher (at nearly adult levels) during the first year of life, and subsequently lower in the second and third year. From 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.

**5.1. 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., 2008; Bhattacharya et al., 2019; Willis et al., 2014). 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; Petruccio et al., 2019). The post-weaning period corresponds to the decline in fecal androgens as infants gain independence (Fig. 1). After age 3, androgen levels become higher each year, and we observe a marked rise in



**Fig. 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). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)



**Fig. 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.

androgens from ages 6 to 9, which coincides 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 juveniles to adults along with changes in dispersal status and mating behavior — hyenas: (Holekamp and Smale, 1998; Holekamp and 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 and Wickings, 2004); although we do not yet have systematic data on these measures for individual male geladas.

### 5.2. 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 males (aged 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 juvenile and adolescent males (4–9 years) — 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.

### 5.3. No observed surge in androgen levels around dispersal in geladas

We know that elevations in androgen levels often accompany dispersal in other species (Akinyi et al., 2017; Holekamp and 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 and Altmann, 1995a, b; Jack and Fedigan, 2004; Wolff, 1994) and, therefore, may not require the requisite androgen activation of secondary sexual 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, 2013). 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 and 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 we do not detect a surge in androgens because dispersal is not as risky for geladas as for other cercopithecines and maturation is not necessarily closely tied to dispersal. 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.

### 5.4. 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 and 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 and 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 and 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 results are 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.

### 5.5. 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 (*Equus ferus caballus*) that live in bands (Bond et al., 2021; Marjamäki et al., 2013). 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 closely monitoring 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 we add 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.

### Animal welfare

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).

### Funding

This study was supported by the National Science Foundation (grant numbers BCS-0715179, IOS-1255974, IOS-1854359, BCS-173228), multiple awards from the Leakey Foundation, and the University of Michigan. In addition, CBP received support from the National Science Foundation (BCS-1154314). SS received support from the Leakey Foundation Franklin Mosher Baldwin Fellowship and Research Grant (AWD007552, AWD012312, AWD011197) and from the National Science Foundation (BCS-2018489).

### ORCID iD authorship contribution statement

Sharmi Sen: Conceptualization, methodology, assay validation, investigation, data curation, formal analysis, funding acquisition, writing — original draft, writing — review & editing.

Sofia Carrera: Methodology, assay validation, writing — review & editing.

Michael Heistermann: Methodology, assay validation, writing — review & editing.

Caitlin Barale: Investigation, funding acquisition, writing — review & editing.

Alice Baniel: Investigation, data curation, writing — review & editing.

Lauren Petruccio: Assay validation, writing — review & editing.

Patricia DeLacey: Assay validation, writing — review & editing.

Amy Lu: Investigation, funding acquisition, project administration, writing — review & editing.

Jacinta Beehner: Conceptualization, methodology, investigation, funding acquisition, project administration, supervision, writing — original draft, review & editing.

### Data accessibility

Data and R code to conduct the analysis reported in this article can be found here: [https://github.com/GeladaResearchProject/Sen\\_et\\_al\\_Juv\\_male\\_MS\\_2022](https://github.com/GeladaResearchProject/Sen_et_al_Juv_male_MS_2022).

### Declaration of competing interest

None.

### Data availability

Data and code are available on the Gelada Project Github Page. Link: [https://github.com/GeladaResearchProject/Sen\\_et\\_al\\_Juv\\_male\\_MS\\_2022](https://github.com/GeladaResearchProject/Sen_et_al_Juv_male_MS_2022)

### Acknowledgements

This study would not have been possible without the continuing support of our Ethiopian collaborators, the former and current wildlife wardens (Berhanu Gebre, Maru Biadleggn, Abebaw Azanaw Haile) and wildlife experts at the Ethiopian Wildlife Conservation Authority (EWCA). We are grateful to our long-term research assistants (Esheti Jewaw, Ambaye Fanta, and Setey Girmay) who have been collecting demographic, behavioral, and hormonal data from our study population continuously since 2008 as well as all former camp managers and research assistants who assisted with data collection in the field. SS would also like to thank Andrea Heistermann and Teera Losch for their assistance in the laboratory and Andrew Marshall and Noah Snyder-Mackler for helpful feedback on the statistical analyses for this study. Finally, we would like to thank the two anonymous reviewers for their helpful feedback on an earlier draft.

## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.yhbeh.2022.105264>.

## References

- Akinyi, M.Y., Gesquiere, L.R., Franz, M., Onyango, P.O., Altmann, J., Alberts, S.C., 2017. Hormonal correlates of natal dispersal and rank attainment in wild male baboons. *Horm. Behav.* 94, 153–161. <https://doi.org/10.1016/j.yhbeh.2017.07.005>.
- Albers, P.C.H., de Vries, H., 2001. Elo-rating as a tool in the sequential estimation of dominance strengths. *Anim. Behav.* 61 (2), 489–495. <https://doi.org/10.1006/anbe.2000.1571>.
- Alberts, S.C., Altmann, J., 1995. Preparation and activation: determinants of age at reproductive maturity in male baboons. *Behav. Ecol. Sociobiol.* 36 (6), 397–406. <https://link.springer.com/article/10.1007/BF00177335>.
- Alberts, Susan C., Altmann, J., 1995. Balancing costs and opportunities: dispersal in male baboons. *Am. Nat.* 145 (2), 279–306. <http://www.jstor.org/stable/2463127>.
- Alexander, G.M., 2014. Postnatal testosterone concentrations and male social development. *Front. Endocrinol.* 5, 15. <https://doi.org/10.3389/fendo.2014.00015>.
- Andres, D., Clutton-Brock, T.H., Kruuk, L.E.B., Pemberton, J.M., Støper, K.V., Ruckstuhl, K.E., 2013. Sex differences in the consequences of maternal loss in a long-lived mammal, the red deer (*Cervus elaphus*). *Behav. Ecol. Sociobiol.* 67 (8), 1249–1258. <https://doi.org/10.1007/s00265-013-1552-3>.
- Archie, E.A., Tung, J., Clark, M., Altmann, J., Alberts, S.C., 2014. Social affiliation matters: both same-sex and opposite-sex relationships predict survival in wild female baboons. *Proc. R. Soc. B Biol. Sci.* 281 (1793) <https://doi.org/10.1098/rspb.2014.1261>.
- Barale, Caitlin L., Rubenstein, D.I., Beehner, J.C., 2015. Juvenile social relationships reflect adult patterns of behavior in wild geladas. *Am. J. Primatol.* <https://doi.org/10.1002/ajp.22443>.
- 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.
- Barton, K., Barton, M.K., 2015. In: Package ‘mumin.’ Version, 1(18), p. 439 <ftp://xyz.csail.mit.edu/pub/CRAN/web/packages/MuMIn/MuMIn.pdf>.
- Bates, D., Mächler, M., Bolker, B., Walker, S., 2014. Fitting linear mixed-effects models using lme4. *arXiv [stat.CO]*. <https://arxiv.org/abs/1406.5823>.
- Beehner, J.C., Bergman, T.J., Cheney, D.L., Seyfarth, R.M., Whitten, P.L., 2006. Testosterone predicts future dominance rank and mating activity among male chacma baboons. *Behav. Ecol. Sociobiol.* 59 (4), 469–479. <https://doi.org/10.1007/s00265-005-0071-2>.
- Beehner, Jacinta C., Gesquiere, L., Seyfarth, R.M., Cheney, D.L., Alberts, S.C., Altmann, J., 2009. Testosterone related to age and life-history stages in male baboons and geladas. *Horm. Behav.* 56 (4), 472–480. <https://doi.org/10.1016/j.yhbeh.2009.08.005>.
- Beehner, Jacinta C., Gesquiere, L., Seyfarth, R.M., Cheney, D.L., Alberts, S.C., Altmann, J., 2016. Corrigendum to “Testosterone related to age and life-history stages in male baboons and geladas” [*Horm. Behav.* 56/4 (2009) 472–480]. *Horm. Behav.* 80, 149. <https://doi.org/10.1016/j.yhbeh.2015.08.004>.
- Beehner, Jacinta C., McCann, C., 2008. Seasonal and altitudinal effects on glucocorticoid metabolites in a wild primate (*Theropithecus gelada*). *Physiol. Behav.* 95 (3), 508–514. <https://doi.org/10.1016/j.physbeh.2008.07.022>.
- Bekoff, M., 1977. Mammalian dispersal and the ontogeny of individual behavioral phenotypes. *Am. Nat.* 111 (980), 715–732. <https://doi.org/10.1086/283201>.
- Berger, J., 1987. Reproductive fates of dispersers in a harem-dwelling ungulate: the wild horse. *Mammalian Dispersal Patterns* 41–54.
- Berghänel, A., Heistermann, M., Schülke, O., Ostner, J., 2017. Prenatal stress accelerates offspring growth to compensate for reduced maternal investment across mammals. *Proc. Natl. Acad. Sci. U. S. A.* 114 (50), E10658–E10666. <https://doi.org/10.1073/pnas.1707152114>.
- Bernstein, R.M., Leigh, S.R., Donovan, S.M., Monaco, M.H., 2008. Hormonal correlates of ontogeny in baboons (*Papio hamadryas anubis*) and mangabeys (*Cercocebus atys*). *Am. J. Phys. Anthropol.* 136 (2), 156–168. <https://doi.org/10.1002/ajpa.20791>.
- Bernstein, R.M., Satchell, J.M., Verrier, D., Knapp, L.A., 2012a. Maternal effects and the endocrine regulation of mandrill growth. *Am. J. Primatol.* 74 (10), 890–900. <https://doi.org/10.1002/ajp.22038>.
- Bernstein, R.M., Sterner, K.N., Wildman, D.E., 2012b. Adrenal androgen production in catarrhine primates and the evolution of adrenarche. *Am. J. Phys. Anthropol.* 147 (3), 389–400. <https://doi.org/10.1002/ajpa.22001>.
- Bhattacharya, I., Sen Sharma, S., Majumdar, S.S., 2019. Pubertal orchestration of hormones and testis in primates. *Mol. Reprod. Dev.* 86 (11), 1505–1530. <https://doi.org/10.1002/mrd.23246>.
- Bolker, B.M., Brooks, M.E., Clark, C.J., Geange, S.W., Poulsen, J.R., Stevens, M.H.H., White, J.-S.S., 2009. Generalized linear mixed models: a practical guide for ecology and evolution. *Trends Ecol. Evol.* 24 (3), 127–135. <https://doi.org/10.1016/j.tree.2008.10.008>.
- Bond, M.L., Lee, D.E., Ozgul, A., Farine, D.R., König, B., 2021. Leaving by staying: social dispersal in giraffes. *J. Anim. Ecol.* <https://doi.org/10.1111/1365-2656.13582>.
- Burnham, K.P., Anderson, D.R., 1998. Practical use of the information-theoretic approach. In: Burnham, K.P., Anderson, D.R. (Eds.), *Model Selection and Inference: A Practical Information-Theoretic Approach*. Springer, New York, pp. 75–117. [https://doi.org/10.1007/978-1-4757-2917-7\\_3](https://doi.org/10.1007/978-1-4757-2917-7_3).
- Carrera, S.C., Sen, S., Heistermann, M., Lu, A., Beehner, J.C., 2020. Low rank and primiparity increase fecal glucocorticoid metabolites across gestation in wild geladas. *Gen. Comp. Endocrinol.* 293, 113494. <https://doi.org/10.1016/j.ygcen.2020.113494>.
- Cheney, D.L., Seyfarth, R.M., 1983. Nonrandom dispersal in free-ranging vervet monkeys: social and genetic consequences. *Am. Nat.* 122 (3), 392–412. <https://www.journals.uchicago.edu/doi/abs/10.1086/284142>.
- Clutton-Brock, T.H., 1991. *The evolution of parental care*. Princeton University Press. <https://play.google.com/store/books/details?id=uRS2WusqW8kC>.
- Collevatti, R.G., Souza-Neto, A.C., Silva Jr., N.J., Telles, M.P.C., 2013. Kin structure and parallel dispersal in the black-and-gold howler monkey *Alouatta caraya* (Platyrrhini, Atelidae). *Genet. Mol. Res.* 12 (4), 6018–6031. <https://doi.org/10.4238/2013.november.27.1>.
- Conley, A.J., Plant, T.M., Abbott, D.H., Moeller, B.C., Stanley, S.D., 2011. Adrenal androgen concentrations increase during infancy in male rhesus macaques (*Macaca mulatta*). *Am. J. Physiol. Endocrinol. Metab.* 301 (6), E1229–E1235. <https://doi.org/10.1152/ajpendo.00200.2011>.
- Dantzer, B., Newman, A.E.M., Boonstra, R., Palme, R., Boutin, S., Humphries, M.M., McAdam, A.G., 2013. Density triggers maternal hormones that increase adaptive offspring growth in a wild mammal. *Science* 340 (6137), 1215–1217. <https://doi.org/10.1126/science.1235765>.
- De Moor, D., Roos, C., Ostner, J., Schülke, O., 2020. Bonds of bros and brothers: kinship and social bonding in postdispersal male macaques. *Mol. Ecol.* 29 (17), 3346–3360. <https://doi.org/10.1111/mec.15560>.
- Dixon, A.F., Anderson, M.J., 2004. Sexual behavior, reproductive physiology and sperm competition in male mammals. *Physiol. Behav.* 83 (2), 361–371. <https://doi.org/10.1016/j.physbeh.2004.08.022>.
- Dloniak, S.M., French, J.A., Holekamp, K.E., 2006. Rank-related maternal effects of androgens on behaviour in wild spotted hyaenas. *Nature* 440 (7088), 1190–1193. <https://doi.org/10.1038/nature04540>.
- Enigk, D.K., Thompson, M.E., Machanda, Z.P., Wrangham, R.W., Muller, M.N., 2020. Competitive ability determines coalition participation and partner selection during maturation in wild male chimpanzees (*Pan troglodytes schweinfurthii*). *Behav. Ecol. Sociobiol.* 74 (7) <https://doi.org/10.1007/s00265-020-02872-7>.
- Feder, J.A., Beehner, J.C., Baniell, A., Bergman, T.J., Snyder-Mackler, N., Lu, A., 2022. Social drivers of maturation age in female geladas. *Behav. Ecol.* 33 (3), 654–664. <https://doi.org/10.1093/beheco/arc028>.
- Fedigan, L.M., 1983. Dominance and reproductive success in primates. *Am. J. Phys. Anthropol.* 26 (S1), 91–129. <https://doi.org/10.1002/ajpa.1330260506>.
- Fouquet, J.P., Meusy-Dessolle, N., Dang, D.C., 1983. Morphometry of fetal Leydig cells in the monkey (*Macaca fascicularis*), correlation with plasma testosterone. *Biol. Cell.* 49 (3), 267–272. <https://doi.org/10.1111/j.1768-322x.1984.tb00246.x>.
- Fox, J., Weisberg, S., Adler, D., Bates, D., Baud-Bovy, G., Ellison, S., Firth, D., Friendly, M., Gorjanc, G., Graves, S., 2012. In: Package ‘car’. R Foundation for Statistical Computing, Vienna, p. 16 <ftp://mirrors.ucr.ac.cr/CRAN/web/packages/car/car.pdf>.
- Fürtbauer, I., Heistermann, M., Schülke, O., Ostner, J., 2013. Brief communication: female fecal androgens prior to the mating season reflect readiness to conceive in reproductively quiescent wild macaques. *Am. J. Phys. Anthropol.* 151 (2), 311–315. <https://doi.org/10.1002/ajpa.22273>.
- Fuxjager, M.J., Miles, M.C., Schlinger, B.A., 2018. Evolution of the androgen-induced male phenotype. *J. Comp. Physiol. A Neuroethol. Sens. Neural Behav. Physiol.* 204 (1), 81–92. <https://doi.org/10.1007/s00359-017-1215-3>.
- Galbany, J., Tung, J., Altmann, J., Alberts, S.C., 2015. Canine length in wild male baboons: maturation, aging and social dominance rank. *PLoS One.* <https://doi.org/10.1371/journal.pone.0126415>.
- Ganswindt, A., Palme, R., Heistermann, M., Borragan, S., Hodges, J.K., 2003. Non-invasive assessment of adrenocortical function in the male African elephant (*Loxodonta africana*) and its relation to musth. *Gen. Comp. Endocrinol.* 134 (2), 156–166. [https://doi.org/10.1016/S0016-6480\(03\)00251-x](https://doi.org/10.1016/S0016-6480(03)00251-x).
- Gelman, A., 2008. Scaling regression inputs by dividing by two standard deviations. *Stat. Med.* 27 (15), 2865–2873. <https://doi.org/10.1002/sim.3107>.
- Gesquiere, L.R., Altmann, J., Khan, M.Z., Couret, J., Yu, J.C., Endres, C.S., Lynch, J.W., Ogola, P., Fox, E.A., Alberts, S.C., Wango, E.O., 2005. Coming of age: steroid hormones of wild immature baboons (*Papio cynocephalus*). *Am. J. Primatol.* 67 (1), 83–100. <https://doi.org/10.1002/ajp.20171>.
- Girard-Buttoz, C., Heistermann, M., Rahmi, E., Agil, M., Ahmad Fauzan, P., Engelhardt, A., 2015. Androgen correlates of male reproductive effort in wild male long-tailed macaques (*Macaca fascicularis*): a multi-level test of the challenge hypothesis. *Physiol. Behav.* 141, 143–153. <https://doi.org/10.1016/j.physbeh.2015.01.015>.
- Goldenberg, S.Z., Wittemyer, G., 2018. Orphaning and natal group dispersal are associated with social costs in female elephants. *Anim. Behav.* 143, 1–8. <https://doi.org/10.1016/j.anbehav.2018.07.002>.
- Gordon, I., Pratt, M., Bergunde, K., Zagoory-Sharon, O., Feldman, R., 2017. Testosterone, oxytocin, and the development of human parental care. *Horm. Behav.* 93, 184–192. <https://doi.org/10.1016/j.yhbeh.2017.05.016>.
- Greenwood, P.J., 1980. Mating systems, philopatry and dispersal in birds and mammals. *Anim. Behav.* [https://doi.org/10.1016/S0003-3472\(80\)80103-5](https://doi.org/10.1016/S0003-3472(80)80103-5).
- Hall, C.L., Fedigan, L.M., 1997. Spatial benefits afforded by high rank in white-faced capuchins. *Anim. Behav.* 53 (5), 1069–1082. <https://doi.org/10.1006/anbe.1996.0392>.
- Harrison, N.D., Maag, N., Haverkamp, P.J., Ganswindt, A., Manser, M.B., Clutton-Brock, T.H., Ozgul, A., Cozzi, G., 2021. Behavioural change during dispersal and its relationship to survival and reproduction in a cooperative breeder. *J. Anim. Ecol.* <https://doi.org/10.1111/1365-2656.13569>.

- Hau, M., 2007. Regulation of male traits by testosterone: implications for the evolution of vertebrate life histories. *Bioessays* 29 (2), 133–144. <https://doi.org/10.1002/bies.20524>.
- Higham, J.P., Heistermann, M., Maestriperi, D., 2013. The endocrinology of male rhesus macaque social and reproductive status: a test of the challenge and social stress hypotheses. *Behav. Ecol. Sociobiol.* 67 (1), 19–30. <https://doi.org/10.1007/s00265-012-1420-6>.
- Hirschenhauser, K., Oliveira, R.F., 2006. Social modulation of androgens in male vertebrates: meta-analyses of the challenge hypothesis. *Anim. Behav.* 71 (2), 265–277. <https://doi.org/10.1016/j.anbehav.2005.04.014>.
- Holekamp, K.E., Smale, L., 1998. Dispersal status influences hormones and behavior in the male spotted hyena. *Horm. Behav.* 33 (3), 205–216. <https://doi.org/10.1006/hbeh.1998.1450>.
- Holekamp, K.E., Smale, L., Simpson, H.B., Holekamp, N.A., 1984. Hormonal influences on natal dispersal in free-living Belding's ground squirrels (*Spermophilus beldingi*). *Horm. Behav.* 18 (4), 465–483. [https://doi.org/10.1016/0018-506x\(84\)90031-x](https://doi.org/10.1016/0018-506x(84)90031-x).
- Holekamp, K.E., Smale, L., Szykman, M., 1996. Rank and reproduction in the female spotted hyena. *J. Reprod. Fertil.* 108 (2), 229–237. <https://doi.org/10.1530/jrf.0.1080229>.
- Holekamp, Kay E., Sisk, C.L., 2003. Effects of dispersal status on pituitary and gonadal function in the male spotted hyena. *Horm. Behav.* 44 (5), 385–394. <https://doi.org/10.1016/j.yhbeh.2003.06.003>.
- Höner, O.P., Wachter, B., Hofer, H., Wilhelm, K., Thierer, D., Trillmich, F., Burke, T., East, M.L., 2010. The fitness of dispersing spotted hyena sons is influenced by maternal social status. *Nat. Commun.* 1, 60. <https://doi.org/10.1038/ncomms1059>.
- Jack, K.M., Fedigan, L., 2004. Male dispersal patterns in white-faced capuchins, *Cebus capucinus*: part 2: patterns and causes of secondary dispersal. *Anim. Behav.* 67 (4), 771–782. <https://doi.org/10.1016/j.anbehav.2003.06.015>.
- Jack, K.M., Sheller, C., Fedigan, L.M., 2012. Social factors influencing natal dispersal in male white-faced capuchins (*Cebus capucinus*). *Am. J. Primatol.* 74 (4), 359–365.
- Jack, K., Schoof, V., Isbell, L., 2009. What traits promote male parallel dispersal in primates? *Behaviour* 146 (4–5), 701–726. <https://doi.org/10.1163/156853908X399086>.
- Jarvey, J.C., Low, B.S., Pappano, D.J., Bergman, T.J., Beehner, J.C., 2018. Graminivory and fallback foods: annual diet profile of geladas (*Theropithecus gelada*) living in the Simien Mountains National Park, Ethiopia. *Int. J. Primatol.* 39 (1), 105–126. <https://doi.org/10.1007/s10764-018-0018-x>.
- Kalbitzer, U., Bergstrom, M.L., Carnegie, S.D., Wikberg, E.C., Kawamura, S., Campos, F. A., Jack, K.M., Fedigan, L.M., 2017. Female sociality and sexual conflict shape offspring survival in a neotropical primate. *Proc. Natl. Acad. Sci. U. S. A.* 114 (8), 1892–1897. <https://doi.org/10.1073/pnas.1608625114>.
- Koenig, A., 2002. Competition for resources and its behavioral consequences among female primates. *Int. J. Primatol.* 23 (4), 759–783. <https://doi.org/10.1023/A:1015524931226>.
- le Roux, A., Beehner, J.C., Bergman, T.J., 2011. Female philopatry and dominance patterns in wild geladas. *Am. J. Primatol.* 73 (5), 422–430. <https://doi.org/10.1002/ajp.20916>.
- Leigh, S.R., Setchell, J.M., Charpentier, M., Knapp, L.A., Wickings, E.J., 2008. Canine tooth size and fitness in male mandrills (*Mandrillus sphinx*). *J. Hum. Evol.* 55 (1), 75–85. <https://doi.org/10.1016/j.jhevol.2008.01.001>.
- Lu, A., Reitsema, L.J., Beehner, J.C., Bergman, T.J., Snyder-Mackler, N., 2017. Triangulating weaning in wild geladas (*Theropithecus gelada*) using observational, isotopic, and gut microbial evidence. *PLoS One* 12, 111 RIVER ST, HOBOKEN 07030-5774, NJ USA: WILEY.
- Lu, Amy, Feder, J.A., Snyder-Mackler, N., Bergman, T.J., Beehner, J.C., 2021. Male-mediated maturation in wild geladas. *Curr. Biol.* 31 (1), 214–219. <https://doi.org/10.1016/j.cub.2020.10.003> e2.
- Maestriperi, D., 2009. Maternal influences on offspring growth, reproduction, and behavior in primates. In: *Maternal Effects in Mammals*, 12. University of Chicago Press, pp. 256–291.
- Marjamäki, P.H., Contasti, A.L., Coulson, T.N., McLoughlin, P.D., 2013. Local density and group size interacts with age and sex to determine direction and rate of social dispersal in a polygynous mammal. *Ecol. Evol.* 3 (9), 3073–3082. <https://doi.org/10.1002/ece3.694>.
- Möhle, U., Heistermann, M., Palme, R., Hodges, J.K., 2002. Characterization of urinary and fecal metabolites of testosterone and their measurement for assessing gonadal endocrine function in male nonhuman primates. *Gen. Comp. Endocrinol.* 129 (3), 135–145. [https://doi.org/10.1016/S0016-6480\(02\)00525-7](https://doi.org/10.1016/S0016-6480(02)00525-7).
- Muehlenbein, M.P., Bribiescas, R.G., 2005. Testosterone-mediated immune functions and male life histories. *Am. J. Hum. Biol.* 17 (5), 527–558. <https://doi.org/10.1002/ajhb.20419>.
- Neumann, C., Duboscq, J., Dubuc, C., Ginting, A., Irwan, A.M., Agil, M., Widdig, A., Engelhardt, A., 2011. Assessing dominance hierarchies: validation and advantages of progressive evaluation with elo-rating. *Anim. Behav.* 82 (4), 911–921. <https://doi.org/10.1016/j.anbehav.2011.07.016>.
- Neumann, C., Kulik, L., 2014. EloRating: Animal dominance hierarchies by Elo rating. *R package version*, 43, 1–26., 43. <https://cran.microsoft.com/snapshot/2014-09-09/web/packages/EloRating/EloRating.pdf>.
- Oliveira, R.F., 2004. Social modulation of androgens in vertebrates: mechanisms and function. *Adv. Study Behav.* 34 (503), 165–239. [https://doi.org/10.1016/S0065-3454\(04\)34005-2](https://doi.org/10.1016/S0065-3454(04)34005-2), 34.
- Onyango, Patrick O., Gesquiere, L.R., Altmann, J., Alberts, S.C., 2013. Puberty and dispersal in a wild primate population. In: *Hormones and Behavior*. <https://doi.org/10.1016/j.yhbeh.2013.02.014>.
- Onyango, Patrick Ogola, Gesquiere, L.R., Altmann, J., Alberts, S.C., 2013. Testosterone positively associated with both male mating effort and paternal behavior in savanna baboons (*Papio cynocephalus*). *Horm. Behav.* 63 (3), 430–436. <https://doi.org/10.1016/j.yhbeh.2012.11.014>.
- Onyango, Patrick Ogola, Gesquiere, L.R., Wango, E.O., Alberts, S.C., Altmann, J., 2008. Persistence of maternal effects in baboons: mother's dominance rank at son's conception predicts stress hormone levels in subadult males. *Horm. Behav.* 54 (2), 319–324. <https://doi.org/10.1016/j.yhbeh.2008.03.002>.
- Ostner, J., Heistermann, M., Schülke, O., 2011. Male competition and its hormonal correlates in assamese macaques (*Macaca assamensis*). *Horm. Behav.* 59 (1), 105–113. <https://doi.org/10.1016/j.yhbeh.2010.10.017>.
- Palagi, E., 2018. Not just for fun! Social play as a springboard for adult social competence in human and non-human primates. *Behav. Ecol. Sociobiol.* 72 (6) <https://doi.org/10.1007/s00265-018-2506-6>.
- Palme, R., Möstl, E., 1994. Biotin–streptavidin enzyme immunoassay for the determination of oestrogen and androgens in boar faeces. Retrieved January 13, 2022, from: Görög, S. (Ed.), *Advances of Steroid Analysis*, pp. 111–117.
- Pappano, D.J., 2013. *The Reproductive Trajectories of Bachelor Geladas*. University of Michigan [PhD].
- Pappano, D.J., Beehner, J.C., 2014. Harem-holding males do not rise to the challenge: androgens respond to social but not to seasonal challenges in wild geladas. *R. Soc. Open Sci.* 1 (1), 140081 <https://doi.org/10.1098/rsos.140081>.
- Pappano, D.J., Roberts, E.K., Beehner, J.C., 2010. Testing extraction and storage parameters for a fecal hormone method. *Am. J. Primatol.* <https://doi.org/10.1002/ajp.20859>.
- Pereira, M.E., Fairbanks, L.A., 2002. Juvenile primates: life history, development and behavior, with a new foreword. University of Chicago Press. <https://play.google.com/store/books/details?id=1-HWKKKhBQC>.
- Perfito, N., Bentley, G.E., 2009. Opportunism, photoperiodism, and puberty: different mechanisms or variations on a theme? *Integr. Comp. Biol.* 49 (5), 538–549. <https://doi.org/10.1093/icb/052>.
- Petrullo, L., Hinde, K., Lu, A., 2019. Steroid hormone concentrations in milk predict sex-specific offspring growth in a nonhuman primate. *Am. J. Hum. Biol.* 31 (6), e23315 <https://doi.org/10.1002/ajhb.23315>.
- Prudom, S.L., Broz, C.A., Schultz-Darken, N., Ferris, C.T., Snowdon, C., Ziegler, T.E., 2008. Exposure to infant scent lowers serum testosterone in father common marmosets (*Callithrix jacchus*). *Biol. Lett.* 4 (6), 603–605. <https://doi.org/10.1098/rsbl.2008.0358>.
- R Core Team, 2020. R Foundation for Statistical Computing, Vienna, Austria, 4.0.3. <https://www.R-project.org/>. (Accessed October 2020).
- Rangel-Negrín, A., Dias, P.A.D., Chavira, R., Canales-Espinosa, D., 2011. Social modulation of testosterone levels in male black howlers (*Alouatta pigra*). *Horm. Behav.* 59 (1), 159–166. <https://doi.org/10.1016/j.yhbeh.2010.11.005>.
- Rincon, A.V., Maréchal, L., Semple, S., Majolo, B., MacLarnon, A., 2017. Correlates of androgens in wild male barbary macaques: testing the challenge hypothesis. *Am. J. Primatol.* 79 (10) <https://doi.org/10.1002/ajp.22689>.
- Robbins, M.M., Akantorana, M., Arinaitwe, J., Kabano, P., Kayijamahe, C., Gray, M., Guschanski, K., Richardson, J., Roy, J., Tindimwebwa, V., Vigilant, L., Robbins, A. M., 2019. Dispersal and reproductive careers of male mountain gorillas in bwindi impenetrable National Park, Uganda. *Primates* 60 (2), 133–142. <https://doi.org/10.1007/s10329-019-00718-z>.
- Roberts, E.K., Lu, A., Bergman, T.J., Beehner, J.C., 2017. Female reproductive parameters in wild geladas (*Theropithecus gelada*). *Int. J. Primatol.* 38 (1), 1–20. <https://doi.org/10.1007/s10764-016-9939-4>.
- Rutberg, A.T., Keiper, R.R., 1993. Proximate causes of natal dispersal in feral ponies: some sex differences. *Anim. Behav.* 46 (5), 969–975. <https://doi.org/10.1006/anbe.1993.1278>.
- Sapolsky, R.M., Romero, L.M., Munck, A.U., 2000. How do glucocorticoids influence stress responses? Integrating permissive, suppressive, stimulatory, and preparative actions. *Endocr. Rev.* 21 (1), 55–89. <https://doi.org/10.1210/edrv.21.1.0389>.
- Schneider-Crease, I., Chiou, K.L., Snyder-Mackler, N., Bergman, T.J., Beehner, J.C., Lu, A., 2020. Beyond infant death: the hidden costs of male immigration in geladas. *Anim. Behav.* 159, 89–95. <https://doi.org/10.1016/j.anbehav.2019.11.010>.
- Schoof, V.A.M., Jack, K.M., Isbell, L.A., 2009. What traits promote male parallel dispersal in primates? *Behaviour* 146 (4/5), 701–726. <http://www.jstor.org/stable/40296002>.
- Sen, S., Lu, A., Snyder-Mackler, N., Bergman, T.J., Beehner, J.C., 2022. Presence of former leader males improves infant survival in geladas. *Am. J. Biol. Anthropol.* 177, 166–166.
- Setchell, J.M., Wickings, E.J., 2004. Sequences and timing of dental eruption in semi-free-ranging mandrills (*Mandrillus sphinx*). *Folia primatologica. Int. J. Primatol.* 75 (3), 121–132. <https://doi.org/10.1159/000078302>.
- Setchell, Joanna M., Smith, T., Wickings, E.J., Knapp, L.A., 2008. Social correlates of testosterone and ornamentation in male mandrills. *Horm. Behav.* 54 (3), 365–372. <https://doi.org/10.1016/j.yhbeh.2008.05.004>.
- Setchell, Joanna M., Wickings, E.J., Knapp, L.A., 2006. Life history in male mandrills (*Mandrillus sphinx*): physical development, dominance rank, and group association. *Am. J. Phys. Anthropol.* 131 (4), 498–510. <https://doi.org/10.1002/ajpa.20478>.
- Sloan, E.T., Beehner, J.C., Bergman, T.J., Lu, A., Snyder-Mackler, N., Jacquemyn, H., 2022. Effects of climate variability on the demography of wild geladas. *Ecol. Evol.* 12 (3), e8759 <https://doi.org/10.1002/ece3.8759>.
- Snyder-Mackler, N., Alberts, S.C., Bergman, T.J., 2014. The socio-genetics of a complex society: female gelada relatedness patterns mirror association patterns in a multilevel society. *Mol. Ecol.* <https://doi.org/10.1111/mec.12987>.
- Snyder-Mackler, N., Beehner, J.C., Bergman, T.J., 2012. Defining higher levels in the multilevel societies of geladas (*Theropithecus gelada*). *Int. J. Primatol.* 33 (5), 1054–1068. <https://doi.org/10.1007/s10764-012-9584-5>.

- Stanton, M.A., Lonsdorf, E.V., Murray, C.M., Pusey, A.E., 2020. Consequences of maternal loss before and after weaning in male and female wild chimpanzees. *Behav. Ecol. Sociobiol.* 74 (2), 22. <https://doi.org/10.1007/s00265-020-2804-7>.
- Therneau, T.M., Grambsch, P.M., 2013. Modeling survival data: extending the cox model. Springer Science & Business Media. <https://play.google.com/store/books/details?id=oj0mBQAAQBAJ>.
- Therneau, T.M., Lumley, T., 2015. Package 'survival'. R Core Team, 2.38. <https://github.com/therneau/survival>.
- Tinsley Johnson, E., Feder, J.A., Bergman, T.J., Lu, A., Snyder-Mackler, N., Beehner, J.C., 2021. The goldilocks effect: female geladas in mid-sized groups have higher fitness. *Proc. Biol. Sci. R. Soc.* 288 (1952), 20210820 <https://doi.org/10.1098/rspb.2021.0820>.
- Tinsley Johnson, E., Snyder-Mackler, N., Beehner, J.C., Bergman, T.J., 2014. Kinship and dominance rank influence the strength of social bonds in female geladas (*Theropithecus gelada*). *Int. J. Primatol.* <https://doi.org/10.1007/s10764-013-9733-5>.
- Tinsley Johnson, E., Snyder-Mackler, N., Lu, A., Bergman, T.J., Beehner, J.C., 2018. Social and ecological drivers of reproductive seasonality in geladas. *Behavioral ecology: official journal of the international society for. Behav. Ecol.* <https://doi.org/10.1093/beheco/ary008>.
- Tung, J., Archie, E.A., Altmann, J., Alberts, S.C., 2016. Cumulative early life adversity predicts longevity in wild baboons. *Nat. Commun.* 7, 11181. <https://doi.org/10.1038/ncomms11181>.
- Van Loo, P.L., Mol, J.A., Koolhaas, J.M., Van Zutphen, B.F., Baumans, V., 2001. Modulation of aggression in male mice: influence of group size and cage size. *Physiol. Behav.* 72 (5), 675–683. [https://doi.org/10.1016/s0031-9384\(01\)00425-5](https://doi.org/10.1016/s0031-9384(01)00425-5).
- Walker, K.K., Pusey, A.E., 2020. Inbreeding risk and maternal support have opposite effects on female chimpanzee dispersal. *Curr. Biol.* 30 (2), R62–R63. <https://doi.org/10.1016/j.cub.2019.11.081>.
- Weiß, B.M., Kulik, L., Ruiz-Lambides, A.V., Widdig, A., 2016. Individual dispersal decisions affect fitness via maternal rank effects in male rhesus macaques. *Sci. Rep.* 6, 32212. <https://doi.org/10.1038/srep32212>.
- Whitlock, K.E., Illing, N., Brideau, N.J., Smith, K.M., Twomey, S., 2006. Development of GnRH cells: setting the stage for puberty. *Mol. Cell. Endocrinol.* 254–255, 39–50. <https://doi.org/10.1016/j.mce.2006.04.038>.
- Wikberg, E.C., Jack, K.M., Campos, F.A., Fedigan, L.M., Sato, A., Bergstrom, M.L., Hiwatashi, T., Kawamura, S., 2014. The effect of male parallel dispersal on the kin composition of groups in white-faced capuchins. *Anim. Behav.* <https://doi.org/10.1016/j.anbehav.2014.07.016>.
- Wikberg, E.C., Jack, K.M., Fedigan, L.M., Kawamura, S., 2018. The effects of dispersal and reproductive patterns on the evolution of male sociality in white-faced capuchins. In: Kalbitzer, U., Jack, K.M. (Eds.), *Primate Life Histories, Sex Roles, and Adaptability: Essays in Honour of Linda M. Fedigan*. Springer International Publishing, pp. 117–132. [https://doi.org/10.1007/978-3-319-98285-4\\_7](https://doi.org/10.1007/978-3-319-98285-4_7).
- Willis, E.L., Wolf, R.F., White, G.L., McFarlane, D., 2014. Age- and gender-associated changes in the concentrations of serum TGF-1 $\beta$ , DHEA-S and IGF-1 in healthy captive baboons (*Papio hamadryas anubis*). *Gen. Comp. Endocrinol.* 195, 21–27. <https://doi.org/10.1016/j.yggen.2013.10.004>.
- Wolf, T.E., Schaebs, F.S., Bennett, N.C., Burroughs, R., Ganswindt, A., 2018. Age and socially related changes in fecal androgen metabolite concentrations in free-ranging male giraffes. *Gen. Comp. Endocrinol.* 255, 19–25. <https://doi.org/10.1016/j.yggen.2017.09.028>.
- Wolff, J.O., 1994. More on juvenile dispersal in mammals. *Oikos* 71 (2), 349–352. <https://doi.org/10.2307/3546284>.
- Wooddell, L.J., Kaburu, S.S.K., Dettmer, A.M., 2020. Dominance rank predicts social network position across developmental stages in rhesus monkeys. *Am. J. Primatol.* 82 (11), e23024 <https://doi.org/10.1002/ajp.23024>.
- Zipple, M.N., Altmann, J., Campos, F.A., Cords, M., Fedigan, L.M., Lawler, R.R., Lonsdorf, E.V., Perry, S., Pusey, A.E., Stoinski, T.S., Strier, K.B., Alberts, S.C., 2021. Maternal death and offspring fitness in multiple wild primates. *Proc. Natl. Acad. Sci. U. S. A.* 118 (1) <https://doi.org/10.1073/pnas.2015317118>.
- Zipple, M.N., Archie, E.A., Tung, J., Altmann, J., Alberts, S.C., 2019. Intergenerational effects of early adversity on survival in wild baboons. *elife* 8. <https://doi.org/10.7554/eLife.47433>.