Hormonal correlates of natal dispersal and rank attainment in wild male baboons

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ABSTRACT

In many mammals, maturational milestones such as dispersal and the attainment of adult dominance rank mark stages in the onset of reproductive activity and depend on a coordinated set of hormonal and socio-behavioral changes. Studies that focus on the link between hormones and maturational milestones are uncommon in wild mammals because of the challenges of obtaining adequate sample sizes of maturing animals and of tracking the movements of dispersing animals. We examined two maturational milestones in wild male baboons—adult dominance rank attainment and natal dispersal—and measured their association with variation in glucocorticoids (fGC) and fecal testosterone (fT). We found that rank attainment is associated with an increase in fGC levels but not fT levels: males that have achieved any adult rank have higher fGC than males that have not yet attained an adult rank. This indicates that once males have attained an adult rank they experience greater energetic and/or psychosocial demands than they did prior to attaining this milestone, most likely because of the resulting participation in both agonistic and sexual behaviors that accompany rank attainment. In contrast, natal dispersal does not produce sustained increases in either fGC or fT levels, suggesting that individuals are either well adapted to face the challenges associated with dispersal or that the effects of dispersal on hormone levels are ephemeral for male baboons.

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1. Introduction

In mammals, maturational milestones such as puberty, adult dominance rank attainment and natal dispersal mark important transitions associated with the onset of reproductive activity (Adkins-Regan, 2005; Jack et al., 2014; Pusey, 1987). These transitions critically depend on a set of coordinated hormonal and socio-behavioral changes (Finch and Rose, 1995). Further, they require the mobilization of resources from individuals' energy stores, and physiological preparation for reproduction (see discussion in Belthoff and Dufty, 1995, 1998; Nunes et al., 1999; Ronce and Clobert, 2012). Steroid hormones, specifically glucocorticoids (GC) and testosterone (T) are presumed to play key roles in these processes because of their involvement in energy mobilization and reproduction (Dixson, 2012; Nelson, 2011; Sapolsky et al., 2000).

Adult dominance rank attainment—the stage at which a maturing male consistently begins to outrank at least one adult male in agonistic encounters—represents an important maturational milestone in many primate species, because individuals (especially males) are often unable to acquire mating opportunities prior to adult rank attainment (Alberts et al., 2006; Alberts and Altmann, 1995b; Beehner et al., 2009; Charpentier et al., 2008; Hamilton and Bulger, 1990; Van Noordwijk and Van Schaik, 2001). In some primates, males are unable to reproduce until they attain a high dominance rank, but in other species, the attainment of an adult rank per se is sufficient (reviewed in Alberts et al., 2003; Bulger, 1993; Cowlishaw and Dunbar, 1991).

Dispersal is nearly ubiquitous across the animal kingdom, enhancing gene flow between populations, limiting inbreeding, and allowing individuals to distribute themselves over available resources (Clutton-Brock, 1989; Greenwood, 1980; Johnson and Gaines, 1990; Lawson Handley and Perrin, 2007; Paradis et al., 1998). Dispersal represents a major maturational milestone for many mammals, because individuals often do not reproduce prior to dispersal (Greenwood, 1980; Pusey and Packer, 1987; Pusey, 1987). Many mammals – including baboons (*Papio cynocephalus*), the subjects of this study – exhibit male-biased dispersal, so that social groups consist of families of female kin,

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with immigrant males who tend to be unrelated to other group members other than their own offspring (Greenwood, 1980; Pusey, 1987; Clutton-Brock, 1989).

Adult rank attainment and natal dispersal both represent a potent combination of social, reproductive, and energetic challenges, possibly among the greatest challenges that an animal will experience in its lifetime. For instance, dispersing primates may face increased mortality risk as a result of predation, partly because they may often be alone (Alberts and Altmann, 1995a; Cuarón, 1997; Fernandez-Duque, 2009; Isbell and Jack, 2009). Dispersing individuals may also experience nutritional stress resulting from lack of familiarity with existing resources in new areas (Pusey and Packer, 1987). Some dispersing individuals travel long distances before they encounter a new group, potentially depleting energy stores during dispersal (see discussions in Dufty and Belthoff, 2001). Successful dispersal and rank attainment may also involve fighting with conspecifics, resulting in injuries or occasionally death (see discussion in Isbell and Jack, 2009; Van Noordwijk and Van Schaik, 2001). In the aggregate, the challenges and changes associated with these maturational events are likely to be reflected in hormonal changes.

Hormones and socio-sexual behavior operate in a feedback loop, each responding to and contributing to the regulation of the other (Bercovitch and Ziegler, 2002; Nelson, 2011). For instance, a stressful event—an event that has the potential to perturb physiological homeostasis (Sapolsky, 2004)—leads to activation of the hypothalamic-pituitary-adrenal axis and the adrenomedullary system, which in turn leads to downstream secretion of catecholamines (epinephrine and norepinephrine) and glucocorticoids (GC) (e.g., cortisol and corticosterone) (Elenkov and Chrousos, 2002; Sapolsky et al., 2000). Secretion of these hormones in turn stimulates or suppresses various cardiovascular, metabolic, and immune system processes (e.g., heart rate, blood pressure, gluconeogenesis, lipolysis, inflammation), all of which may have immediate or downstream consequences for behavior. A short-term release of GC during acutely stressful events is adaptive and aids in survival. On the other hand, chronic release of GC is thought to be immunosuppressive and consequently leads to increased susceptibility to disease and infection (Sapolsky et al., 2000; Sapolsky, 2004; Selva et al., 2011).

Testosterone (T) is produced in the testes and regulated by the hypothalamic-pituitary-gonadal axis (Hirschenhauser and Oliveira, 2006). Testosterone regulates the production of gametes, enhances anabolism, and maintains musculoskeletal performance (Adkins-Regan, 2005; Bardin, 1996; Bribiescas, 2001). Testosterone has previously been associated with behaviors such as territoriality, mate guarding/consortship, aggression, and mating display (Beehner et al., 2006; Onyango et al., 2013a; Wickings and Dixson, 1992; Wingfield et al., 1990). The 'challenge hypothesis,' designed to explain the link between T and competitive behavior in seasonal breeders, predicts that T levels rise in response to social challenges, particularly those associated with competition for mates, and specifically that T levels can be rapidly elevated when critically needed to promote aggressive competition in a reproductive context (Wingfield et al., 1990). Research in seasonally breeding birds has supported this hypothesis by showing that T is low in the absence of mating behavior or mate competition and elevated during aggressive episodes and mating (Wingfield et al., 2000). Studies in both seasonally and non-seasonally breeding nonhuman primate species have also broadly supported the challenge hypothesis (e.g., chacma baboons (*Papio hamadryas ursinus*): Beehner et al., 2006; howler monkeys (*Alouatta palliata*): Cristóbal-Azkarate et al., 2006; ring-tailed lemurs (*Lemur catta*): Gould and Ziegler, 2007; moustached tamarin monkeys (*Saguinus mystax*): Huck et al., 2005; tufted capuchin monkeys (*Cebus apella nigritus*): Lynch et al., 2002; bonobos (*Pan paniscus*): Marshall and Hohmann, 2005; chimpanzees (*Pan troglodytes*): Muller and Wrangham, 2004; red-fronted lemurs (*Eulemur fulvus rufus*): Ostner et al., 2002; reviewed in Muller, 2016). Testosterone is energetically costly to maintain at high levels because of its anabolic effects (e.g. muscle mass building). These energetic costs will lead to decreased investment in immune function and increased susceptibility to disease (Muehlenbein and Bribiescas, 2005; Zuk and McKean, 1996).

Studies that focus on the link between hormones and maturational milestones are uncommon in wild mammals because of the challenges of obtaining adequate sample sizes of maturing animals and of tracking the movements of dispersing animals. Only a few studies have looked at the endocrine correlates of dispersal in mammals (yellow baboons: Alberts et al., 1992; chacma baboons: Beehner et al., 2006, Bergman et al., 2005; spotted hyenas (*Crocuta crocuta*): Holekamp and Smale, 1998; white-faced capuchin monkeys (*Cebus capucinus*): Jack et al., 2014; chimpanzees: Kahlenberg et al., 2008; Belding's ground squirrels (*Spermophilus beldingi*): Nunes et al., 1999; Muriqui monkeys (*Brachyteles arachnoides*): Strier and Ziegler, 2000 and crested macaques (*Macaca nigra*): Marty et al., 2017). Some studies of GC or T in relation to dispersal have compared hormone levels in immigrant males with those in resident males, whereas others have compared hormone levels in the same individuals before and after dispersal, or at different stages after immigration. For example, in spotted hyenas, immigrant males – those that have immigrated within the previous 7 days – have higher circulating T than natal males even after controlling for the effects of age (Holekamp and Smale, 1998). Alberts et al. (1992) found unusually high GC and T levels in a particularly aggressive male baboon immediately after he immigrated into a new group. In chacma baboons, T levels appear to rise in anticipation of future mating opportunities and rank rises (Beehner et al., 2006; Bergman et al., 2005). Fecal GC levels are higher in immigrant male chacma baboons in the month following immigration than they are in subsequent months of residency (Bergman et al., 2005), and the same is qualitatively true in gray-cheeked mangabeys (*Lophocebus albigena*) (Arlet et al., 2009). Among chimpanzees, recent immigrants to a community have higher GC levels than natal residents (Kahlenberg et al., 2008). Fecal GC levels are higher in immigrant male crested macaques in the first few days after immigration and return to baseline levels quickly (Marty et al., 2017). However, a longitudinal study in black howler monkeys (*Alouatta pigra*) showed that immigrant males did not differ in their GC and T levels 2 weeks before and after immigration (Van Belle et al., 2009). In Muriqui monkeys, cortisol levels did not differ between natal emigrant females and recent immigrant females (Strier and Ziegler, 2000). Notably, only one study to our knowledge has looked at T variation around the time of adult rank attainment, in three primate species (chacma baboons, yellow baboons, and geladas (*Theropithecus gelada*): (Beehner et al., 2009). In that study, the acquisition of adult ranks in males occurs at the onset of adult T levels but before peak T levels (Beehner et al., 2009).

1.1. Maturation and reproduction in male baboons

To provide context and background for the goals of this analysis, we review here the general sequences of maturational events that male baboons experience, and their functional consequences for males' physical and social lives. Among the wild baboons in the Amboseli basin of southern Kenya, the subjects of this study, males experience testicular enlargement (puberty) at a median age of 5.41 years (Fig. S1; Onyango et al., 2013b). Testicular enlargement signals physiological maturity and the ability to produce viable sperm (Bercovitch and Goy, 1990; Plant, 1994). However, unlike females, who conceive their first offspring about 1 year after puberty (menarche), males experience a 2 year period of reproductive quiescence after testicular enlargement—an adolescent phase that is generally termed subadulthood. Adolescence involves a growth spurt that, by the age of 7–8 years, results in male body size approximately double that of adult females (Altmann and Alberts, 2005).

Once males attain this large body size, they are able to agonistically challenge adult males and take a place in the adult male dominance hierarchy; this milestone, the attainment of adult rank, occurs at a median age of 7.45 years in Amboseli and signals the transition from

subadulthood to adulthood (Fig. S1). Natal dispersal, the second milestone of interest in this analysis, often occurs immediately after adult rank attainment, but may occur well before or well after it (Fig. S1). In addition, some males in Amboseli engage in reproductive activity via mate guarding and copulation (generally referred to as consorting in primates) before dispersing, although most do not (Alberts and Altmann, 1995a).

In Amboseli, males never mate guard before they attain an adult rank, and usually begin mate guarding very soon afterwards (Alberts and Altmann, 1995b; also Fig. S2). As in some other baboon populations, this effect is not dependent upon males attaining a rank in the top three positions (defined as high-ranking) of the adult male dominance hierarchy. Both high and low-ranking male baboons can and do engage in mate-guarding episodes and father offspring, but low-ranking males are not as successful in obtaining mate-guarding opportunities as high-ranking males, on average. In our data set, approximately half of the males attained a high rank in the 6-month period after adult rank attainment, and approximately half did not (Fig. S3; (Alberts et al., 2006, 2003, see also Bercovitch, 1988, 1986; Bulger, 1993). Specifically, the extent of reproductive skew is density-dependent. In small groups, high-ranking males have a large advantage; in large groups, high-ranking males have only a small advantage. On average in this population, the highest ranking male attains 20% of available mate guarding opportunities (Alberts et al., 2003).

1.2. Goals, hypotheses, and predictions

In the present study, we examined two maturational milestones in wild male baboons that are associated with the transition from subadulthood to adulthood: adult dominance rank attainment and natal dispersal. We measured the association between the timing of these milestones and variation in fecal glucocorticoids (fGC) and testosterone (fT) (see Gesquiere et al., 2005; Onyango et al., 2013b for similar analyses for age at puberty). Our study focused on the developmental period after puberty and into early adulthood (6–10 years) to eliminate pubescent males and also to eliminate males that were long past maturational process. Specifically, we modeled fecal steroid concentrations as a function of maturational status (which of the two milestones of interest had been attained) and other variables known to affect hormone concentrations. We tested the hypothesis that psychosocial and energetic demands on male baboons will be substantially higher after dispersal and/or rank attainment than before them. Animals may experience increased nutritional stress and other energetic and social demands as they adjust to their new environment after dispersal, and males are likely to experience substantially increased reproductive activity following rank attainment. This hypothesis yielded two predictions that we tested. 1) We predicted that individuals that had attained one or both of these milestones would have higher levels of fGC than those that had not. 2) We predicted that individuals that had attained one or both of these milestones would have higher levels of fT than those that had not as a consequence of greater mating and agonistic activity after milestone attainment.

2. Methods

2.1. Study population

Our study focused on members of a well-studied wild baboon population in the Amboseli region of Kenya. This baboon population is composed of yellow baboons, *Papio cynocephalus*, that experience some admixture with neighboring populations of olive baboons, *Papio anubis* (Alberts and Altmann, 2001; Charpentier et al., 2012; Tung et al., 2008). The Amboseli baboon population has been studied for the last four decades; this research has produced longitudinal, individual-based behavioral and demographic data, as well as fecal samples used for the measurement of hormone metabolites. Demographic, behavioral, and

life-history data (births, emigration, immigration and maturation events) are collected on a near-daily basis on known individuals in the study population (Alberts and Altmann, 2012) and are stored in Babase, the Amboseli baboon project database (Pinc et al., 2016). During the study period (January 2000 to November 2013), the number of study groups varied, as groups occasionally fissioned, and some groups were dropped from continuous observations. Number of study groups at any given time varied from 4 to 6 (Table 1).

2.2. Study subjects and maturational milestones

The subjects of this study were all males that were (i) born into Amboseli study groups and known from birth (hence their ages were known to within a few days), and (ii) males for whom hormone data are available for the period before and after they attained adult rank and/or dispersed. The resulting sample includes 114 males born between October 1990 and July 2007, attained adult dominance rank and/or dispersed between January 2000 and November 2013.

As described above, we consider the attainment of adult rank to signal the transition for males from subadulthood—a period of rapid growth but reproductive quiescence after puberty—to adulthood (Alberts and Altmann, 1995b; Altmann and Alberts, 2005). Adult rank attainment occurs at a median age of 7.45 years (range 6.2 to 8.7 years; Onyango et al., 2013b; Fig. S1). The attainment of a dominance rank among adult males, even if it is not a high rank, is a pre-requisite for obtaining reproductive opportunities in this population (Fig. S2). The other maturational milestone we considered here, natal dispersal, is usually attained after testicular enlargement (maturational milestone of puberty), but 5% of males disperse before testicular enlargement. Natal dispersal occurs at a median age of 7.67 years (age range of post-pubertal natal dispersal is 6.81–13.42 years; Onyango et al., 2013b). Our study focused on the two post-pubertal maturational milestones: the attainment of adult dominance rank and dispersal from the natal group to a non-natal group. Rank attainment and natal dispersal are frequently, but not always, attained within a few weeks or months of each other in our study population, making them highly associated ($X^2 = 1809.6$, $p < 0.001$, Cramer's V = 0.781; Fig. S1; Alberts and Altmann, 1995b; Onyango et al., 2013b).

Table 1
Description of predictors for hormone levels.

Predictor variable	Description
a) Random effects	
Male ID	Male identity.
Social group	The social group the individual was in at the time of fecal sample collection. We observed between 4 and 6 social groups at any given time during the course of the study (see Study population, Methods).
Year	Year of sample collection.
b) Fixed effects	
Maturation status	The maturation status of the individual at the time the fecal sample was collected (categorical). Statuses included: dispersed (he had dispersed but not attained rank), ranked (he had attained rank but had not dispersed), neither (he had neither dispersed nor attained rank) and both (he had dispersed and attained rank).
Age	Age in years at fecal sample collection (continuous). Age at sample collection ranged from 6.0 to 10 years.
Season	Whether the fecal sample was collected during a wet or dry season (wet, dry); binary.
Number of adult males	Number of adult males in the individual's social group at the time of fecal sample collection. Number of adult males in a group: 9.71 ± 4.36 (mean ± SD), range 1–21.
Dominance rank	Ordinal dominance rank of the individual at the time of fecal sample collection. This varied considerably, including as it did both subadults and adult males. Range: 1–29.

Male dominance ranks were determined by assigning wins and losses in dyadic agonistic encounters between males. Males are considered to win agonistic encounters in which their opponent gives only submissive gestures while they give only aggressive or neutral (nonsubmissive) gestures (Alberts et al., 2003; Hausfater, 1975). This procedure of assigning wins and losses allows the construction of a square matrix of interactions in which entries below the diagonal (which would represent wins by the lower-ranking animal) are few or zero; males are assigned ordinal dominance ranks based on their position in this matrix. Ordinal dominance ranks based on these interactions were assigned monthly to each male in each study group, with the highest rank status as 1. Males were assigned an ordinal dominance rank whether or not they had attained a dominance rank among adult males. For instance, in a group with 7 fully adult males, the highest-ranked subadult male (i.e., a male who had never successfully challenged an adult male in an agonistic encounter but won encounters with all other subadults) held an ordinal rank of 8, with lower-ranking subadult males assigned successively higher ordinal rank numbers. In other words, the male's maturational status (whether or not he had attained a rank among adult males) and his ordinal rank (the rank number that he was assigned) were two separate pieces of information about the male's rank, both of which we considered in our analyses.

2.3. Fecal sample collection, hormone extraction, validation and analyses

Fresh fecal samples for hormone analysis were opportunistically collected from individually known males, labeled with the individual male's ID and the date of sample collection, and stored in 95% ethanol. Protocols for extraction and measurement of fGC and fT metabolites are well-established and have been previously validated in research on this population (Beehner et al., 2006; Gesquiere et al., 2005; Khan et al., 2002). These samples were freeze dried, sifted, and weighed; they underwent methanol and solid phase extraction using Waters Oasis HLB cartridges. fGC and fT metabolites in the samples were measured in ng/g of dried feces using radioimmunoassays (RIA). RIA specific to fGC and fT metabolites have previously been validated for our population (Beehner et al., 2009; Gesquiere et al., 2011; Khan et al., 2002; Lynch et al., 2003). For fT assays, we have used different kits over the years, all of which produce highly correlated results. These kits have included the kit from Equate (SolidPhase, Portland, ME; See Lynch et al., 2003 for validation), the kit from Diagnostic Systems Laboratories (Beckman Coulter, Webster TX; Beehner et al., 2009; Gesquiere et al., 2011), and the kit from Pantex (Santa Monica, CA; Gesquiere et al., 2014). To render the fT concentrations directly comparable across kits, a correction factor was applied to the fT from the different kits (details in Gesquiere et al., 2011).

2.4. Data analysis

2.4.1. Mixed model analysis of variation in fGC and fT metabolites associated with adult rank attainment and natal dispersal

2.4.1.1. Response variables and modeling approach. Our data set included measures of hormone levels from 2955 fecal samples collected from the 114 unique subadult and adult males (aged 6–10 years) described above; most of these individuals were represented in our data set by multiple fecal samples (mean number of fecal samples per individual = 26, range 1 to 97). To test our predictions, we ran two general linear mixed models with Gaussian error distribution, one for each hormone. The response variables for the models were log-transformed fGC levels or log-transformed fT levels. Predictor variables are described below and in Table 1. To generate our mixed effect models, we used the 'glmmadmb' and 'lme4' package (Fournier et al., 2012) in the R Statistical software, version 3.2.3 (R Foundation for Statistical Computing, 2014). Visual inspection of the data for all models indicated no violations of the assumptions regarding the normality of residuals and

homogeneity of error variances. The variance inflation factors for the predictors were measured using the 'car' package in R statistical software and were all ≤5.7 and Cook's distance measured by the 'influence.ME' package in R did not indicate influential cases.

2.4.1.2. Predictor variables. Our fixed effect of interest was the maturation status of the individual at the time the fecal sample was collected. Individuals were assigned to one of the following categories for maturation status: dispersed (he had dispersed but not attained rank, $N = 114$ fecal samples, 13 males), ranked (he had attained rank but had not dispersed, $N = 209$ fecal samples, 35 males), neither (he had neither dispersed nor attained rank, $N = 1419$ fecal samples, 101 males), and both (he had dispersed and attained rank, $N = 1213$ fecal samples, 50 males). Our models included three random variables; 1) the identity of the individual, to account for multiple samples from most individuals, 2) year of sample collection, to account for samples collected across multiple years and 3) the social group the individual was in at the time of sample collection, to account for multiple samples from each social group.

Age, season, and the male's ordinal dominance rank were included in all analyses as covariates because they are known to predict fGC and fT hormone levels in male baboons. Specifically, fT levels in Amboseli males are stable prior to puberty between 2 and 5 years of age, increase through early adulthood to a peak at 9.5 years, and then gradually decline with age throughout adulthood (Altmann et al., 2010; Beehner et al., 2009; Onyango et al., 2013b). In addition, fGC levels are higher during the dry season (June–October) than the wet season (November–May), while fT levels show the reverse pattern with higher levels during the wet season (Alberts et al., 2005; Altmann et al., 2002; Gesquiere et al., 2011). Following previous studies, we categorized each month of our study period as a dry month (June through October) or a wet month (November through May). With respect to dominance rank, high-ranking adult males have lower fGC and higher fT levels than lower ranking males, with the exception of the alpha male, who exhibits high levels of both fGC and fT (Gesquiere et al., 2011). We also included the number of adult males in the social group at the time of sample collection as a predictor of hormone levels because it acts as a proxy for male-male competition (a potential stressor). For example, (Marty et al., 2017) have shown that male crested macaques have higher fGC levels when they immigrate into groups with larger numbers of adult males.

2.4.2. Categorical analysis of variation in fGC and fT metabolites associated with adult rank attainment and natal dispersal

Finally, following Bergman et al. (2005), we tested the possibility that hormone levels would be elevated in the month immediately following the attainment of a maturational milestone (adult dominance rank or natal dispersal) but not during later months. We ran independent analyses for each maturational milestone. Specifically, we grouped fecal samples into two classes, those that were collected within one month of maturational milestone attainment, and those that were collected more than one month after attaining either milestone (i.e., between 2 and 6 months post-milestone attainment). Then we identified subjects for whom we had fecal samples in both categories. Restricting the analysis to these males, we calculated the mean hormone concentration for each male in each category. For each milestone, we used the Wilcoxon test (a non-parametric equivalent of paired t-test) to examine whether mean log hormone levels (fGC and fT) differed between the two categories. This differed slightly from the approach taken by Bergman et al. (2005) because in their analysis, post-dispersal fGC levels did not vary across individuals, allowing them to disregard individual identity and perform an ANOVA. In our case, we had significant heterogeneity among individuals in post-milestone hormone levels: for post-dispersal fGC levels ($F_{38,184} = 3.473$, $p < 0.0001$, range = 1.4–2.2) and fT ($F_{38,184} = 5.344$, $p < 0.001$, range = 1.5–2.5). Reported ranges for fGC and fT levels are log

transformed values. Rank attainment analysis showed similar trends; post-rank attainment fGC levels ($F_{33,34} = 1.568$, $p < 0.09$, range = 1.0–2.2) and fT levels ($F_{33,34} = 1.943$, $p < 0.029$, range = 1.3–2.9). Thus, we opted for the paired Wilcoxon sign ranked test to control for these individual differences.

3. Results

3.1. Mixed model analysis of variation in fGC and fT metabolites associated with adult rank attainment and natal dispersal

Fecal glucocorticoid (fGC) levels were significantly higher in males with a status of 'ranked' or 'both' than in males with a status of 'neither'. Fecal GC levels were 15% higher in individuals in the 'ranked' category compared to neither ($p = 0.005$, CI = 5–25%) and 11% higher in individuals in the 'both' category compared to neither ($p = 0.059$, CI = 2–20%). In our fGC model, the random effects (i.e. individual identity, social group and year) accounted for 0.4%, 0.2%, and 0.2% of variance in fGC respectively. In contrast, males with a status of 'dispersed' (i.e. dispersed but not ranked) did not have higher fGC levels than males with a status of 'neither' (Table 2). Further, the effect estimate for 'dispersed' males was negative, indicating that the non-significance of this predictor was unlikely to be simply the result of limited statistical power. In combination these results suggest that the significant estimate for males in the 'both' category is driven by males that had attained rank (whether or not they had dispersed), and that rank attainment but not dispersal was associated with elevated fGC. In support of this inference, a visual comparison of fGC levels shows that individuals that had attained rank (i.e., those in the 'both' category plus those in the 'ranked' category) had higher fGC levels than those that had not (i.e., those in the 'neither' category plus those in the 'dispersed' category; Fig. 1A). However, a parallel visual comparison for the dispersal case showed no effect of dispersal: those that had dispersed (i.e., those in the 'both' category plus the 'dispersed' category) had fGC levels that were indistinguishable from those that had not dispersed (Fig. 1B). These comparisons support our conclusion that rank attainment status has a robust association with fGC, while dispersal status does not, and that the significant estimate for males in the 'both' category is driven by males that have attained rank (with or without dispersing).

Consistent with previous analyses, fGC levels were higher in the dry season; 5% lower in the wet season compared to the dry season ($p = 0.009$, CI = 1–10%). We did not find any effect of age on fGC levels in the age range we examined (Table 2). Individuals in groups with a large number of males were more likely to have high fGC levels; our models indicate a 2% increase in a male's fGC for every additional male in his social group, ($p < 0.001$, CI = 1–3%). In agreement with previous results from this population, high-ranking individuals generally had lower fGC concentrations than low-ranking males; our models indicate a 2% decrease in a male's fGC for every increase in rank ($p = 0.001$, CI = 1–3%).

Fecal T levels (fT) showed somewhat different patterns than fGC levels. Fecal T levels were statistically indistinguishable among the four categories of maturation status for males (Table 3). In other words, neither attaining an adult dominance rank nor dispersing left any lasting detectable effect on fT levels in male baboons (Fig. 1C, D).

Consistent with previous analyses, fT levels were 12% higher in the wet season compared to the dry season ($p < 0.001$, CI = 7–17%). In addition, we found that fT levels had a curvilinear relationship with age, such that fT increased with age then declined slightly in the later age classes we considered. The rest of our covariates – number of adult males and dominance rank – did not predict fT levels.

3.2. Categorical analysis of variation in fGC and fT metabolites associated with adult rank attainment and natal dispersal

The paired Wilcoxon signed ranked tests revealed no statistically significant differences in either fGC levels ($W = 248$, $p = 0.41$, $N = 34$) or fT levels ($W = 208$, $p = 0.13$, $N = 34$) in the two post-rank attainment categories (one month post-rank attainment, versus 2–6 months post-rank attainment). Parallel analysis on the post-dispersal period revealed similar trends, i.e. no statistically significant differences in fGC levels in the post-dispersal categories ($W = 73$, $p = 0.2166$, $N = 14$) or in fT levels ($W = 65$, $p = 0.4631$, $N = 14$). These results indicate that individuals do not appear to experience elevated fGC or fT levels in the month following either milestone relative to later time periods.

4. Discussion

We asked whether two important maturational milestones in male baboons (natal dispersal and rank attainment) predict hormone levels in post-pubescent males between 6 and 10 years of age. Our well-supported result is that male rank attainment was associated with an increase in fGC concentrations; males that had attained an adult rank had higher fGC than males that had not yet attained an adult rank, when we controlled for the season, their age, their ordinal rank, and the number of males in the group. In male baboons, adult rank attainment is an important event, because males do not acquire reproductive opportunities until they achieve adult rank, but do so almost immediately afterwards, with a median lag time between these two events of 2.5 months (Alberts and Altmann, 1995b; Figs. S1 and S2). Males in this species need not attain one of the highest ranks in order to achieve mate guarding (consortship) opportunities (Alberts et al., 2006; Bercovitch, 1986; Bercovitch, 1988; Bulger, 1993), although adult rank attainment may signal the onset of a rapid rise to high dominance rank (Hamilton and Bulger, 1990). Because dominance rank is a major predictor of male mating and paternity success in baboons, as in many other primate species, attainment of adult dominance rank has important fitness consequences (Alberts, 2012; Alberts et al., 2006, 2003; Bulger, 1993; Cowlishaw and Dunbar, 1991). Our results suggest that once males have attained an adult rank they experience greater energetic demands and/or psychosocial stress than they did prior to attaining this milestone. This result is somewhat puzzling in light of the fact that males prior to rank attainment are presumably emerging from a prolonged growth spurt, but it is consistent with data on behavioral differences associated with rank attainment. Specifically, after rank attainment but not before, males engage in mate guarding episodes, which are known to be energy limiting and time consuming (Alberts et al., 1996; Packer, 1979).

Contrary to our expectations, natal dispersal did not predict fGC levels. We predicted that natal dispersal, like rank attainment, would involve psychosocial stress and energetic demands that are substantially higher than before dispersal, hence that fGC levels would be higher after dispersal. We posit that the apparent lack of an effect of natal dispersal on fGC levels reflects the fact that individuals are well adapted to face the long-term challenges associated with dispersal, and that the short-term stress associated with dispersal is relatively ephemeral and thus difficult to detect unless hormone levels are sampled within hours or a few days of dispersal (see Alberts et al., 1992; Arlet et al., 2009; Bergman et al., 2005; Marty et al., 2017). In addition, in this study most individuals dispersed to adjacent social groups that share the home ranges of their natal group. This may have removed key

Table 2
GLMM for fGC levels (fecal samples = 2955, males = 114).

Variables	Estimate	SE	Z value	p value	Direction
Intercept	1.71	0.05	31.04	<0.001	
Maturation status					
Dispersed	−0.03	0.02	−1.17	0.242	
Ranked	0.06	0.02	2.8	0.005	High fGC - ranked
Both	0.04	0.02	1.89	0.059	High fGC - both
Season (wet)	−0.02	0.01	−2.59	0.009	High fGC - dry
Age	0.00	0.01	0.22	0.826	
# of Adult males	0.01	0.00	4.21	<0.001	High fGC - more males
Dominance rank	−0.01	0.00	−3.19	0.001	High fGC - low rank
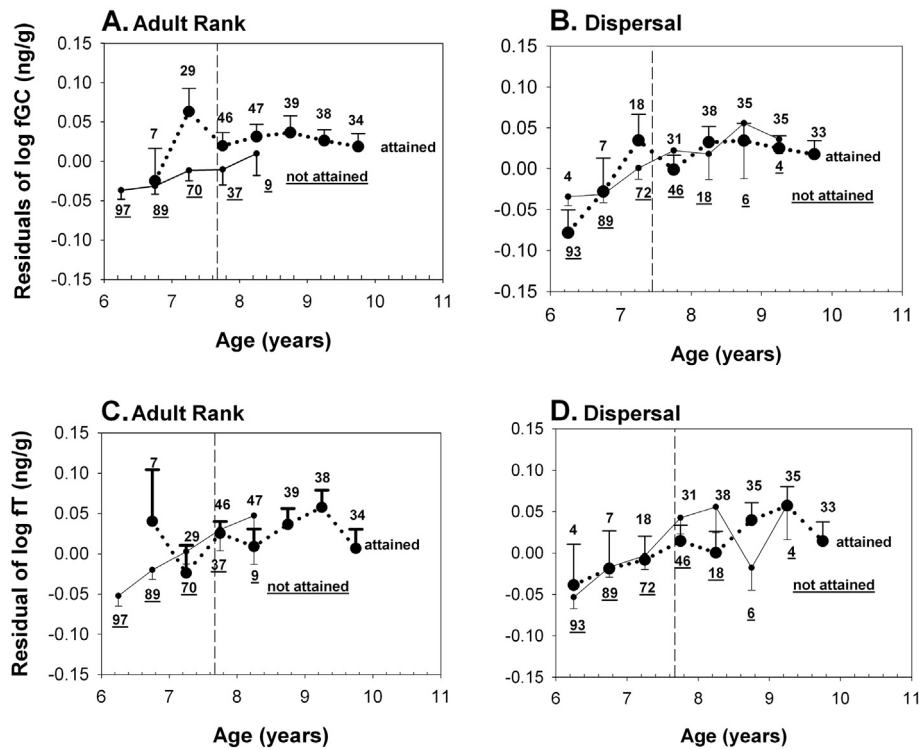
Fig. 1. Average residual values of hormone concentrations as a function of age in male baboons. Residuals were calculated from a model containing season and number of adult males as predictors and male identity, social group, and year as random variables; thus, the pictured trends include the effects of both the maturational milestone in question, and the dominance rank that a male had attained. Each value represents the mean + SE or mean − SE across males of the residuals of log transformed hormone concentrations for a 6-month period. Numbers above the data points represent the numbers of males sampled for each age period. A) Comparison of residual fGC levels for males who had attained rank (i.e., males in the 'ranked' plus the 'both' category) and males who had not attained rank (males in the 'neither' plus the 'dispersed' category). B) Comparison of residual fGC levels for males who had attained dispersal (males in the 'dispersed' plus the 'both' category) and males who had not attained dispersal (males in the 'neither' plus the 'ranked' category). C) Comparison of residual fT levels for males who had and had not attained rank (categories as in panel A). D) Comparison of residual fT levels for males who had and had not attained dispersal (categories as in panel B). The dashed lines in A and C represent median age at rank attainment (7.45 years). The dashed lines in B and D represent median age at dispersal (7.67 years).

costs of dispersal, such as the lack of familiarity with resources and the long travel distances that characterize some dispersal events (see discussions in Pusey and Packer, 1987; Dufty and Belthoff, 2001). Importantly, this tendency to disperse into neighboring groups is a common pattern in primates, and has been reported in olive baboons, vervet monkeys (*Chlorocebus aethiops*), rhesus macaques (*Macaca mulatta*), ring-tailed lemurs and gorillas (*Gorilla gorilla* and *Gorilla beringei*) (see review in Pusey and Packer, 1987).

The lack of a persistent effect of natal dispersal on fGC levels may also reflect the fact that males' experiences of dispersal are quite heterogeneous. For instance, some males may attain adult rank very soon after dispersal, so that an increase in fGC occurs in association with high levels of aggression. Thus, the high GC and T levels reported by Alberts et al. (1992) in a single immigrant male were associated with unusually high levels of aggression directed by that male to other group members (see also Bergman et al., 2005). Other males, in contrast, may spend many months avoiding direct challenges to resident males. In support

of the idea that males' experiences upon immigration may be quite heterogeneous, Van Noordwijk and Van Schaik (1985) report two different types of immigrant males in long-tailed macaques: "unobtrusive immigrants" enter a new group low in the dominance hierarchy and form associations with females over a period of months before challenging high-ranking males, while "bluff immigrants" attempt to take over the highest dominance rank immediately upon entry. Demographic factors in the new group, such as the relative numbers of adult males and adult females, may also be variable, and this variability will in turn influence aggressive and reproductive encounters. Thus, the variable nature of the dispersal experience – how far males travel, what demographic conditions they encounter in the new group, and how much they engage in aggression and reproduction after dispersal – may explain the absence of a clear, sustained pattern of change in hormone levels in post-dispersers compared to pre-dispersers. We were able to control for at least one of these variables—the number of adult males in a group—which acted as a proxy for male-male competition. Despite controlling for this variable, the effect of dispersal was still insignificant.

Fecal testosterone (fT) levels did not change systematically with either rank attainment or natal dispersal. Instead, our results show that fT levels between the ages of 6 and 10 years were relatively simply described by a quadratic function of age, and were higher in the wet season than in the dry season (Table 2). Pappano and Beehner (2014) also report seasonal effects on fT such that male geladas have higher T during the wet season compared to the dry season. Although we cannot rule out the possibility that our data set lacked the power to detect a subtle change in fT in response to these maturational milestones, we can say with confidence that the effects of attaining these milestones were certainly weaker than the effects of age or season. In addition, we found that the dominance rank position a male held at the time of fecal sampling did not predict his fT concentrations. This result contrasts

Table 3
GLMM for fT levels (fecal samples = 2955, males = 114).

Variables	Estimate	SE	Z value	p value	Direction
Intercept	0.82	0.25	3.296	0.001	
Maturation status					
Dispersed	0.02	0.03	0.6	0.550	
Ranked	−0.01	0.24	−0.28	0.777	
Both	0.03	0.02	1.23	0.217	
Season (wet)	0.05	0.01	5.57	<0.001	High fT - wet
Age	0.26	0.06	4.26	<0.001	High fT - older
Age^2	−0.01	0.00	−3.7	0.002	Low fT - older
# of adult males	0.004	0.00	1.45	0.147	
Dominance rank	−0.001	0.00	−0.45	0.651	

with previous research that demonstrates a link between high dominance rank and high fT levels in adult male baboons (Gesquiere et al., 2011). However, this contrast certainly stems from the fact that our study subjects here were not all adults; instead, subjects were experiencing a maturational process whose effects predominated over any effect of the rank that the male actually held. Male baboons experience a post-pubertal growth spurt between 6 and 8 years of age, during which they nearly double in body mass (Alberts and Altmann, 1995b; Altmann et al., 2010); this growth spurt is likely to be associated with the anabolic functions of T (Nelson, 2011). Testosterone is an important predictor of growth during and after puberty in several primate species (chacma baboons and mangabeys: Bernstein et al., 2008; chimpanzees: Copeland et al., 1985; white-faced capuchins: Jack et al., 2014). In our population as in other primates, fT is upregulated at the onset of reproductive maturity, and begins to decline with age starting at around 9.5 years of age (Altmann et al., 2010; Beehner et al., 2009). Beehner et al. (2009) examined overall fT patterns and maturational milestones in both chacma and yellow baboons and found that male baboons generally attain adult rank after they achieve fT levels in the adult range, but before they achieve peak fT levels. This means that fT levels are already increasing in male baboons before they attain adult rank. Our results build on the study by Beehner et al. (2009) by demonstrating that after controlling for other predictors of fT levels, we did not find any effect of either maturational milestone on fT.

In conclusion, our results indicate that male baboons experience marked increases in fGC levels after rank attainment but not after dispersal, and that they experience no marked or persistent changes in fT levels associated with either adult rank attainment or natal dispersal. Our data combined with previous results in this population reveal that males experience a steady increase in fT beginning between 4 and 5 years of age, coincident with the onset of testicular enlargement, which continues throughout the subadult and early adult period, peaks around 9.5 years of age, and then begins to decline with age (Altmann et al., 2010; Beehner et al., 2009; Gesquiere et al., 2005; Onyango et al., 2013b). Fecal GC levels, too, increase with age across the age range studied here, but the attainment of adult dominance rank signals a marked change in these steroid hormones. Increased mate guarding (consorting) will generally produce increased energetic demands. Thus, our results suggest that the elevation in fGC after adult rank attainment results from increased energetic demands on newly adult males rather than increased psychosocial stress.

Additional research will be needed to elucidate more fine-grained or short-lived effects of dispersal and adult rank attainment on steroid hormones in this as well as in other group-living species. For instance, fine-grained sampling has shown that male baboons that engage in more frequent mating exhibit higher T levels than those that engage in less mating (Onyango et al., 2013a). Similarly, fine-grained analyses of behavior with densely sampled hormone concentrations (i.e. daily or near-daily fecal samples) could potentially identify variation in fGC or fT associated with inter-individual differences in the attainment of maturation milestones. For example, individuals that travel longer distances should experience more energetic and psychosocial stress (and have higher GC levels) than those who disperse to neighboring areas, and individuals that experience more mating after rank attainment should experience higher GC levels than those who experience less. Near-daily repeated sampling of individuals during and immediately after the dispersal phase will be needed to reveal such inter-individual differences.

Acknowledgments

Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx. doi.org/10.1016/j.yhbeh.2017.07.005.

References

Adkins-Regan, E., 2005. Hormones and Animal Social Behavior. Princeton University Press, Princeton.

Alberts, S.C., 2012. Magnitude and sources of variation in male reproductive performance. In: Mitani, J., Call, J., Kappeler, P., Palombit, R., Silk, J.B. (Eds.), Evolution of Primate Societies. University of Chicago Press, Chicago.

Alberts, S.C., Altmann, J., 1995a. Balancing costs and opportunities: dispersal in male baboons. Am. Nat. 145, 279–306.

Alberts, S.C., Altmann, J., 1995b. Maturity of age at reproductive determinants and activation: preparation in male baboons. Behav. Ecol. Sociobiol. 36, 397–406.

Alberts, S.C., Altmann, J., 2001. Immigration and hybridization patterns of yellow and Anubis baboons in and around Amboseli, Kenya. Am. J. Primatol. 154, 139–154.

Alberts, S., Altmann, J., 2012. The Amboseli Baboon Research Project: themes of continuity and change. In: Kappeler, P.M., Watts, D.P. (Eds.), Long-Term Field Studies of Primates. Springer Science and Business Media, New York, pp. 261–288.

Alberts, S.C., Sapolsky, R.M., Altmann, J., 1992. Behavioral, endocrine, and immunological correlates of immigration by an aggressive male into a natural primate group. Horm. Behav. 26:167–178. http://dx.doi.org/10.1016/0018-506X(92)90040-3.

Alberts, S.C., Altmann, J., Wilson, M.L., 1996. Mate guarding constrains foraging activity of male baboons. Anim. Behav. 51 (6), 1269–1277.

Alberts, S.C., Watts, H.E., Altmann, J., 2003. Queuing and queue-jumping: long-term patterns of reproductive skew in male savannah baboons, Papio cynocephalus. Anim. Behav. 65:821–840. http://dx.doi.org/10.1006/anbe.2003.2106.

Alberts, S.C., Hollister-Smith, J.A., Mututua, R., Sayialel, S.N., Muruthi, P.M., Warutere, J.K., Altmann, J., 2005. Seasonality and long term change in a wild primate population. In: Brockman, D.K., Van Schaik, C.P. (Eds.), Seasonality in Primates: Studies of Living and Extint Human and Non-Human Primates. Cambridge University Press, Cambridge, p. 571.

Alberts, S.C., Buchan, J.C., Altmann, J., 2006. Sexual selection in wild baboons: from mating opportunities to paternity success. Anim. Behav. 72:1177–1196. http://dx.doi.org/10.1016/j.anbehav.2006.05.001.

Altmann, J., Alberts, S.C., 2005. Growth rates in a wild primate population: ecological influences and maternal effects. Behav. Ecol. Sociobiol. 57:490–501. http://dx.doi.org/10.1007/s00265-004-0870-x.

Altmann, J., Alberts, S.C., Altmann, S.A., Roy, S.B., 2002. Dramatic change in local climate patterns in the Amboseli basin, Kenya. Afr. J. Ecol. 40, 248–251.

Altmann, J., Gesquiere, L., Galbany, J., Onyango, P.O., Alberts, S.C., 2010. Life history context of reproductive aging in a wild primate model. Ann. N. Y. Acad. Sci. 1204:127–138. http://dx.doi.org/10.1111/j.1749-6632.2010.05531.x.

Arlet, M.E., Grote, M.N., Molleman, F., Isbell, L.A., Carey, J.R., 2009. Reproductive tactics influence cortisol levels in individual male gray-cheeked mangabeys (Lophocebus albigena). Horm. Behav. 55:210–216. http://dx.doi.org/10.1016/j.yhbeh.2008.10.004.

Bardin, C.W., 1996. The anabolic action of testosterone. N. Engl. J. Med. 266, 52–53.

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. 59:469–479. http://dx.doi.org/10.1007/s00265-005-0071-2.

Beehner, J.C., Gesquiere, L., Seyfarth, R.M., Cheney, D.L., Alberts, S.C., Altmann, J., 2009. Testosterone related to age and life-history stages in male baboons and geladas. Horm. Behav. 56:472–480. http://dx.doi.org/10.1016/j.yhbeh.2009.08.005.

Belthoff, J.R., Dufty Jr., A.M., 1995. Locomotor activity levels and the dispersal of western screech-owls, Otus kennicottii. Anim. Behav. 50:558–561. http://dx.doi.org/10.1006/anbe.1995.0272.

Belthoff, J.R., Dufty Jr., A.M., 1998. Corticosterone, body condition and locomotor activity: a model for\natal dispersal in birds. Anim. Behav. 55:405. http://dx.doi.org/10.1006/anbe.1997.0625.

Bercovitch, F.B., 1986. Male rank and reproductive activity in savanna baboons. Int. J. Primatol. 7, 533–550.

Bercovitch, F.B., 1988. Coalitions, cooperation and reproductive tactics among adult male baboons. Anim. Behav. 36:1198–1209. http://dx.doi.org/10.1016/S0003-3472(88)80079-4.

Bercovitch, F.B., Goy, R.W., 1990. The socioendocrinology of reproductive development and reproductive success in macaques. In: Ziegler, T., Bercovitch, F.B. (Eds.), Socioendocrinology of Primate Reproduction. Wiley-Liss, New York, pp. 59–93.

Bercovitch, F.B., Ziegler, T.E., 2002. Current topics in primate socioendocrinology. Annu. Rev. Anthropol. 31:45–67. http://dx.doi.org/10.1146/annurev.anthro.31.040202.105553.

Bergman, T.J., Beehner, J.C., Cheney, D.L., Seyfarth, R.M., Whitten, P.L., 2005. Correlates of stress in free-ranging male chacma baboons, *Papio hamadryas ursinus*. Anim. Behav. 70:703–713. http://dx.doi.org/10.1016/j.anbehav.2004.12.017.

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. 136:156–168. http://dx.doi.org/10.1002/ajpa.20791.

Bribiescas, R.G., 2001. Reproductive ecology and life history of the human male. Am. J. Phys. Anthropol. 44:148–176. http://dx.doi.org/10.1002/ajpa.10025.

Bulger, J.B., 1993. Dominance rank and access to estrous females in male savanna baboons. Behaviour 127, 67–103.

Charpentier, M.J.E., Tung, J., Altmann, J., Alberts, S.C., 2008. Age at maturity in wild baboons: genetic, environmental and demographic influences. Mol. Ecol. 17: 2026–2040. http://dx.doi.org/10.1111/j.1365-294X.2008.03724.x.

Charpentier, M.J.E., Fontaine, M.C., Cherel, E., Renoult, J.P., Jenkins, T., Benoit, L., Barthes, N., Alberts, S.C., Tung, J., 2012. Genetic structure in a dynamic baboon hybrid zone corroborates behavioural observations in a hybrid population. Mol. Ecol. 715–731. http://dx.doi.org/10.1111/j.1365-294X.2011.05302.x.

Clutton-Brock, T.H., 1989. Female transfer and inbreeding avoidance in social mammals. Nature http://dx.doi.org/10.1038/337070a0.

Copeland, K.C., Eichberg, J.W., Parker, R.C., Bartke, A., 1985. Puberty in the chimpanzee: somatomedin-C and its relationship to somatic growth and steroid hormone concentrations. J. Clin. Endocrinol. Metab. 60, 1154–1160.

Cowlishaw, G., Dunbar, R.I.M., 1991. Dominance rank and mating success in male primates. Anim. Behav. 41:1045–1056. http://dx.doi.org/10.1016/S0003-3472(05)80642-6.

Cristóbal-Azkarate, J., Chavira, R., Boeck, L., Rodríguez-Luna, E., Veàl, J.J., 2006. Testosterone levels of free-ranging resident mantled howler monkey males in relation to the number and density of solitary males: a test of the challenge hypothesis. Horm. Behav. 49:261–267. http://dx.doi.org/10.1016/j.yhbeh.2005.07.015.

Cuarón, A.D., 1997. Conspecific aggression and predation: costs for a solitary mantled howler monkey. Folia Primatol. 68, 100–105.

Dixson, A.F., 2012. Primate Sexuality: Comparative Studies of the Prosimians, Monkeys, Apes, and Humans. Second ed. Oxford University Press, Oxford.

Dufty, A.M., Belthoff, J.R., 2001. Proximate mechanisms of natal dispersal: the role of body condition and hormones. In: Clobert, J., Danchin, E., Dhondt, A.A., Nicholas, D.J. (Eds.), Dispersal. Oxford University Press, New York, pp. 217–229.

Elenkov, I.J., Chrousos, G.P., 2002. Stress hormones, proinflammatory and antiinflammatory cytokines, and autoimmunity. Ann. N. Y. Acad. Sci. 966:290–303. http://dx.doi.org/10.1111/j.1749-6632.2002.tb04229.x.

Fernandez-Duque, 2009. Natal dispersal in monogamous owl monkeys (*Aotus azarai*) of the Argentinean Chaco. Behaviour 146:583–606. http://dx.doi.org/10.1163/156853908X397925.

Finch, C.E., Rose, M., 1995. The Quarterly of Life History Evolution. 70 pp. 1–52.

Fournier, D.A., Skaug, H.J., Ancheta, J., Ianelli, J., Magnusson, A., Maunder, M., Nielsen, A., Sibert, J., 2012. AD model builder: using automatic differentiation for statistical inference of highly parameterized complex nonlinear models. Optim. Methods Softw. 27, 233–249.

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. 67:83–100. http://dx.doi.org/10.1002/ajp.20171.

Gesquiere, L.R., Onyango, P.O., Alberts, S.C., Altmann, J., 2011. Endocrinology of year-round reproduction in a highly seasonal habitat: environmental variability in testosterone and glucocorticoids in baboon males. Am. J. Phys. Anthropol. 144:169–176. http://dx.doi.org/10.1002/ajpa.21374.

Gesquiere, L.R., Ziegler, T.E., Chen, P.A., Epstein, K.A., Alberts, S.C., Altmann, J., 2014. General and comparative endocrinology measuring fecal testosterone in females and fecal estrogens in males: comparison of RIA and LC/MS/MS methods for wild baboons (*Papio cynocephalus*). Gen. Comp. Endocrinol. 204, 141–149.

Gould, L., Ziegler, T.E., 2007. Variation in fecal testosterone levels, inter-male aggression, dominance rank and age during mating and post-mating periods in wild adult male ring-tailed lemurs (*Lemur catta*). Am. J. Primatol. 69, 1325–1339.

Greenwood, B.Y.P.J., 1980. Mating Systems, Philopatry and Dispersal in Birds and Mammals. pp. 1140–1162.

Hamilton, W.J., Bulger, J.B., 1990. Natal male baboon rank rises and successful challenges to resident alpha males. Behav. Ecol. Sociobiol. 26:357–362. http://dx.doi.org/10.1007/BF00171102.

Hausfater, G., 1975. Dominance and reproduction in baboons (*Papio cynocephalus*). A quantitative analysis. Contrib. Primatol. 7, 1–150.

Hirschenhauser, K., Oliveira, R.F., 2006. Social modulation of androgens in male vertebrates: meta-analyses of the challenge hypothesis. Anim. Behav. 71:265–277. http://dx.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. 33:205–216. http://dx.doi.org/10.1006/hbeh.1998.1450.

Huck, M., Petra, L., Heymann, E.W., Heistermann, M., 2005. Characterization and social correlates of fecal testosterone and cortisol excretion in wild male *Saguinus mystax*. Int. J. Primatol. 26. http://dx.doi.org/10.1007/s10764-005-0728-8.

Isbell, L.A., Jack, K.M., 2009. Dispersal in primates: advancing an individualized approach. Behaviour 146:429–436. http://dx.doi.org/10.1163/156853909X410612.

Jack, K.M., Schoof, V.A.M., Sheller, C.R., Rich, C.I., Klingelhofer, P.P., Ziegler, T.E., Fedigan, L.M., 2014. Hormonal correlates of male life history stages in wild white-faced capuchin monkeys (*Cebus capucinus*). Gen. Comp. Endocrinol. 195:58–67. http://dx.doi.org/10.1016/j.surg.2006.10.010.

Johnson, M.L., Gaines, M.S., 1990. Evolution of dispersal - theoretical models and empirical tests using birds and mammals. Annu. Rev. Ecol. Evol. Syst. 21, 449–480.

Kahlenberg, S.M., Thompson, M.E., Muller, M.N., Wrangham, R.W., 2008. Immigration costs for female chimpanzees and male protection as an immigrant counterstrategy to intrasexual aggression. Anim. Behav. 76:1497–1509. http://dx.doi.org/10.1016/j.anbehav.2008.05.029.

Khan, M.Z., Altmann, J., Isani, S.S., Yu, J., 2002. A matter of time: evaluating the storage of fecal samples for steroid analysis. Gen. Comp. Endocrinol. 128, 57–64.

Lawson Handley, L.J., Perrin, N., 2007. Advances in our understanding of mammalian sex-biased dispersal. Mol. Ecol. 16:1559–1578. http://dx.doi.org/10.1111/j.1365-294X.2006.03152.x.

Lynch, J.W., Ziegler, T.E., Strier, K.B., 2002. Individual and seasonal variation in fecal testosterone and cortisol levels of wild male tufted capuchin monkeys, *Cebus apella nigritus*. Horm. Behav. 41:275–287. http://dx.doi.org/10.1006/hbeh.2002.1772.

Lynch, J.W., Khan, M.Z., Altmann, J., Njahira, M.N., Rubenstein, N., 2003. Concentrations of four fecal steroids in wild baboons: short-term storage conditions and consequences for data interpretation. Gen. Comp. Endocrinol. 132:264–271. http://dx.doi.org/10.1016/S0016-6480(03)00093-5.

Marshall, A.J., Hohmann, G., 2005. Urinary testosterone levels of wild male bonobos (*Pan paniscus*) in the Lomako Forest, Democratic Republic of Congo. Am. J. Primatol. 92: 87–92. http://dx.doi.org/10.1002/ajp.20099.

Marty, P.R., Hodges, K., Heistermann, M., Agil, M., Engelhardt, A., 2017. Is social dispersal stressful? A study in male crested macaques (*Macaca nigra*). Horm. Behav. 87:62–68. http://dx.doi.org/10.1016/j.yhbeh.2016.10.018.

Muehlenbein, M.P., Bribiescas, R.G., 2005. Testosterone-mediated immune functions and male life histories. Am. J. Hum. Biol. 17:527–558. http://dx.doi.org/10.1002/ajhb.20419.

Muller, M.N., 2016. Hormones and behavior testosterone and reproductive effort in male primates. Horm. Behav. http://dx.doi.org/10.1016/j.yhbeh.2016.09.001.

Muller, M.N., Wrangham, R.W., 2004. Dominance, aggression and testosterone in wild chimpanzees: a test of the "challenge hypothesis". Anim. Behav. 67:113–123. http://dx.doi.org/10.1016/j.anbehav.2003.03.013.

Nelson, R., 2011. An Introduction to Behavioral Endocrinology. Fourth ed. Sinauer Associates, Inc., Sunderland.

Nunes, S., Muecke, E., Anthony, J.A., Batterbee, A.S., 1999. Endocrine and energetic mediation of play behavior in free-living Belding's ground squirrels. Horm. Behav. 165, 153–165.

Onyango, P.O., Gesquiere, L.R., Altmann, J., Alberts, S.C., 2013a. Testosterone positively associated with both male mating effort and paternal behavior in savannah baboons (*Papio cynocephalus*). Horm. Behav. 63:430–436. http://dx.doi.org/10.1016/j.yhbeh.2012.11.014.Testosterone.

Onyango, P.O., Gesquiere, L.R., Altmann, J., Alberts, S.C., 2013b. Puberty and dispersal in a wild primate population. Horm. Behav. 64:240–249. http://dx.doi.org/10.1016/j.yhbeh.2013.02.014.

Ostner, J., Kappeler, P.M., Heistermann, M., 2002. Seasonal Variation and Social Correlates of Androgen Excretion in Male Redfronted Lemurs (*Eulemur fulvus rufus*). : pp. 485–495. http://dx.doi.org/10.1007/s00265-002-0532-9.

Packer, C., 1979. Male dominance and reproductive activity in Papio anubis. Anim. Behav. 27, 37–45.

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. 1:140081. http://dx.doi.org/10.1098/rsos.140081.

Paradis, E., Baillie, S.R., Sutherland, W.J., Gregory, R.D., 1998. Patterns of natal and breeding dispersal in birds. J. Anim. Ecol. 67:518–536. http://dx.doi.org/10.1046/j.1365-2656.1998.00215.x.

Pinc, K.O., Altmann, J., Alberts, S.C., Gorgon, J.B., 2016. Technical Specifications for the Amboseli Baboon Project Data Management System. WWW Document. URL. http://papio.biology.duke.edu/babase_system.html.

Plant, T., 1994. Puberty in primates. In: Knobil, E., Neill, J.D. (Eds.), The Physiology of Reproduction. Raven Press, New York.

Pusey, A., 1987. Sex-biased dispersal and inbreeding avoidance in birds and mammals. Trends Ecol. Evol. 2:295–299. http://dx.doi.org/10.1016/0169-5347(87)90081-4.

Pusey, A.E., Packer, C., 1987. The evolution of sex-biased dispersal in lions. Behaviour 101: 275–310. http://dx.doi.org/10.1163/156853987X00026.

R Core Team, 2014. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria URL https://www.R-project.org/.

Ronce, O., Clobert, J., 2012. In: Clobert, J., Baguette, M., Benton, T., Bullock, J. (Eds.), Dispersal Ecology and Evolution. Oxford University Press, Oxford, pp. 119–138.

Sapolsky, R.M., 2004. Social status and health in humans and other animals. Annu. Rev. Anthropol. 33:393–418. http://dx.doi.org/10.1146/annurev.anthro.33.070203.144000.

Sapolsky, R.M., Romero, L.M., Munck, A.U., 2000. How do glucocorticoids influence stress responses? Preparative actions*. Endocr. Rev. 21:55–89. http://dx.doi.org/10.1210/er.21.1.55.

Selva, N., Cortés-Avizanda, A., Lemus, J.A., Blanco, G., Mueller, T., Heinrich, B., Donázar, J.A., 2011. Stress associated with group living in a long-lived bird. Biol. Lett. 7:608–610. http://dx.doi.org/10.1098/rsbl.2010.1204.

Strier, K., Ziegler, T., 2000. Lack of pubertal influences on female dispersal in muriqui monkeys, *Brachyteles arachnoides*. Anim. Behav. 59:849–860. http://dx.doi.org/10.1006/anbe.1999.1387.

Tung, J., Charpentier, M.J.E., Garfield, D.A., Altmann, J., Alberts, S.C., 2008. Genetic evidence reveals temporal change in hybridization patterns in a wild baboon population. Mol. Ecol. 17:1998–2011. http://dx.doi.org/10.1111/j.1365-294X.2008.03723.x.

Van Belle, S., Estrada, A., Ziegler, T.E., Strier, K.B., 2009. Social and hormonal mechanisms underlying male reproductive strategies in black howler monkeys (*Alouatta pigra*). Horm. Behav. 56:355–363. http://dx.doi.org/10.1016/j.yhbeh.2009.08.006.

Van Noordwijk, M.A., Van Schaik, C.P., 1985. Male migration and rank acquisition in wild long-tailed macaques (*Macaca fascicularis*). Anim. Behav. 33:849–861. http://dx.doi.org/10.1016/S0003-3472(85)80019-1.

Van Noordwijk, M.A., Van Schaik, C.P., 2001. Career Moves: Transfer and Rank Challenge Decisions by Male Long-Tailed Macaques. Behaviour 138. BRILL Stable:pp. 359–395 URL: http://www.jstor.org/stable/4535827. Career Moves: Transfer and Rank Chall.

Wickings, E.J., Dixson, A.F., 1992. Testicular function, secondary sexual development, and social status in male mandrills (*Mandrillus sphinx*). Physiol. Behav. 52:909–916. http://dx.doi.org/10.1016/0031-9384(92)90370-H.

Wingfield, J.C., Hegner, R.E., Dufty Jr., A.M., Ball, G.F., 1990. The "challenge hypothesis": theoretical implications for patterns of testosterone secretion, mating systems, and breeding strategies. Am. Nat. 136:829. http://dx.doi.org/10.1086/285134.

Wingfield, J.C., Jacobs, J.D., Tramontin, A.D., Perfito, N., Meddle, S., Maney, D.L., Soma, K., 2000. Toward an ecological basis of hormone behavior interactions in reproduction of birds. In: Wallen, K., Schneider, J.E. (Eds.), Reproduction in Context: Social and Environmental Influences on Reproduction. MIT Press, Cambridge, Massachusetts, pp. 85–128.

Zuk, M., McKean, K.A., 1996. Sex differences in parasitic infections: patterns and processes. Int. J. Parasitol. 26, 1009–1024.