



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



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ARTICLE INFO

Article history:

Received 26 September 2016

Revised 14 July 2017

Accepted 14 July 2017

Available online 8 August 2017

Keywords:

Baboons

Dispersal

Rank attainment

Glucocorticoids

Testosterone

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 (Dixon, 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; Cowlshaw 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 nigrinus*): 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, 2017). 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

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