# BALANCE OF INVESTMENT BETWEEN PARENTAL CARE AND MATING EFFORT IN MALE BABOONS

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#### ABSTRACT

Non-monogamous males that provide care to their offspring face a potential conflict in investment between paternal care and mating effort. This conflict arises either because of resource or temporal constraints. I investigated potential conflict between paternal care and mating effort among adult male baboons that are part of a wild population in the Amboseli basin, southern Kenya. Specifically, I determined whether the number of a male's immature offspring 1) is correlated with the male's intensity of paternal care, 2) constrains the male's mating effort, 3) constrains the male's intensity of mate guarding, 4) is correlated with the male's concentrations of testosterone, and 5) influences the male's dispersal decisions.

I used demographic, behavioral, and ecological data, records of genetic paternity assignments, and non-invasively derived concentrations of the male reproductive hormone, testosterone (T). First, I demonstrate that the number of immature offspring a male has in the group is indicative of the male's opportunity for paternal care. In addition, I show that mating effort was higher among high-ranking males than in lowranking males, and higher during the wet than during the dry season. However, I did not find evidence that opportunities for paternal care constrain mating effort presumably due to differences in male body condition. Second, I show that season and female reproductive quality predict male mating effort within episodes of mate guarding. These results suggest that energetic constraints shape the evolution of reproductive behaviors in male baboons.

Third, I show that males experiencing high mating success had high concentrations of T, which is consistent with the stimulatory role of T on male mating

behavior and sexual activity. I also found that older males had low concentrations of T than younger adults. This gerontological pattern of T has been reported for other species of primates including humans. In addition, I show that concentrations of T during the wet season were higher than those during the dry season. The positive correlation between mating effort and T together with the absence of a significant correlation between opportunities for paternal care and T suggest a potential decoupling between mechanisms for the secretion of T and those for the expression of care behavior. Lastly, I show that high-ranking males, old males, and males experiencing high mating success are less likely to disperse. In contrast, I did not find evidence that opportunity for paternal care influence male dispersal decisions. Overall, I have demonstrated that investment in mating effort and investment in offspring care are influenced by opportunities for each, and are under extrinsic energetic constraints.

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#### **GENERAL INTRODUCTION**

When males in non-monogamous species provide care to their offspring, they face trade-offs between paternal care and mating effort (Magrath & Komdeur, 2003). Tradeoffs between paternal care and mating effort arise from energy and time constraints. Research on male reproductive success, particularly for mammalian males, has primarily focused on offspring production (Bateman 1948). As a result, how mammalian males in non-monogamous species balance investment between offspring care and production is largely unknown.

For males with immature offspring, investment in offspring care potentially conflicts with investment in production of additional offspring. This conflict can arise in two ways. First, individuals have a limited pool of resources such that investment in one component of fitness constrains investment others (Zahavi 1975; Anderson 1994). During a male's reproductive career, if we compartmentalize his investment into mating effort, paternal care, and somatic maintenance (Magrath & Komdeur 2003), investment in mating effort, for instance, will constrain how much resources are allocated to paternal care and somatic maintenance. Second, the conflict can simply arise from the fact behaviors that enhance paternal care are generally incompatible with those that enhance offspring production (reviewed in Magrath & Komdeur 2003; Stiver & Alonzo 2009). At any given time, non-monogamous that provide care to their offspring are thus faced with a tradeoff between investment in mating effort and care of offspring. Tradeoffs between mating effort and paternal care are presumably amplified in species that reproduce throughout year and those in which offspring undergo a prolonged period of development and thus dependence on parents.

I investigated the potential conflict of investment between offspring production and offspring care among male baboons in a wild population in Amboseli, southern Kenya. Specifically, I asked the question To what extent does a male's opportunities for paternal care constrain the male's investment in offspring production? A question of this nature is best answered in the broader context of variation in availability of ecological resources and variability in environmental factors as well as from the perspective of social milieu that each individual must navigate. Consequently, I integrated seasonal differences in rainfall between the dry and wet season, variability in temperature, and differences in individual traits such as age and dominance rank in my investigation of tradeoffs between mating effort and paternal care.

The savanna baboon is an excellent system for studies of reproductive tradeoffs for several reasons. First, the species exhibits a high intensity of sexual selection revealed in dimorphism between the sexes such that males fight to gain access reproductive mates. Second, it has recently been demonstrated that male baboons provided care to their offspring and that they improve their fitness in doing so (Buchan et al. 2003; Charpentier et al. 2008). Third, the occurrence of mating within specific context of mate-guarding episodes, called consortships, also makes it an excellent system for studying reproductive tradeoffs at a fine scale. The episodes of mate guarding are known to be expensive to males in both time and energy as males attempt to monopolize mating with the female consort. Fourth, reproduction in the study population is year-round (Altmann 1980), which together with the long period of immaturity in this species (Altmann 1980)

suggests that males are potentially faced with simultaneous opportunities for paternal care and offspring production.

Another key feature of savanna baboons that is pertinent to the goal of this study is the phenomenon of dispersal. Male baboons disperse, transfer from, their group of birth after attaining age of reproductive maturity, and may transfer from group to another thereafter (Alberts & Altmann 1995). In contrast, females live in their birth group throughout their life. Dispersal makes it possible to examine the circumstances under which males may transfer from one group to another.

Furthermore, the study population has been the focus of a longterm study spanning nearly four decades, which has made it possible to track individuals throughout the lifespan and thus to monitor their life histories. Knowledge of a population at the individual level is important in studies such as mine that rely on fine details of demographic, behavioral, ecological, and physiological data that I collected as well as those collected by others.

In Chapter 1, I first determined whether a male's number of immature offspring predicted the male's investment in paternal care. I next determined whether a male's number of immature offspring constrained whether a male gained access to fertile females, which is a strong predictor of paternity success in the study population (Alberts et al. 2003, 2006). For males, that obtained a consortship, I determined whether the number of a male's immature offspring constrained how much consortship time he obtained. In Chapter 2, I focused on male sexual behavior and activity during a consortship so as to quantify his mating effort. Given variability in reproductive quality across cycles within and among females, I included female reproductive quality in my

investigation of tradeoffs between mating effort and paternal care. In Chapter 3, I evaluated testosterone correlates of investment between offspring production and care. In Chapter 1, 2, and 3, I integrated differences in ecological resource availability and differences in male traits in this investigation. Finally, in Chapter 4, I determined whether opportunities for paternal care influence male dispersal decisions. Specifically, I determined whether males with more immature offspring are less likely to disperse than those with few or no immature offspring in the group.

The work presented in this dissertation includes my own work as well as those conducted by or in collaboration with Jeanne Altmann (my advisor), Susan Alberts, and Laurence Gesquiere. My contribution to this dissertation includes conception and design of the study, choosing and performing all statistical tests, producing the first drafts of each chapter, producing all revised drafts in light of feedback, conducting all detailed behavioral fieldwork, and performing all wet-lab procedures for hormone purification and assays from all fecal samples collected during 8 months of fieldwork, designing and performing all database querying and analyses to calculate demographic, environmental, paternity assignments, age and dominance records, and of additional hormonal values. Dr. Altmann and Dr. Alberts designed and directed, and collected some of the data for the longterm project that I used. Dr. Alberts and members of her lab at Duke University produced genetic paternity data that were available for some offspring. Dr. Gesquiere developed and maintains overall quality control for hormonal assays in our lab including those samples used in this study.

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# **CHAPTER ONE:** Paternal care does not constrain mating effort in a wild population of savannah baboons

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#### ABSTRACT

Non-monogamous males that care for their offspring face potential tradeoffs in investment between care and mating effort because of time and resource constraints. This is especially true in species that reproduce throughout the year and that have young with long periods of immaturity. We examined factors influencing potential tradeoffs between mating effort and care in adult male baboons in Amboseli, Kenya. First, we determined whether the number of a male's immature offspring present in the group predicted paternal care behavior. Second, we determined the extent to which the number of a male's immature offspring constrained mating effort. We quantified mating effort as 1) whether a male entered into a consortship and 2) the amount of consortship time a male obtained in a given month if he entered into any consortships. We controlled for factors such as a male's age and his dominance rank and seasonal differences in food availability, which are known to influence the extent of tradeoffs between mating effort and paternal care. Males with more immature offspring present in the group invested more in paternal care behaviors than males with fewer immature offspring. High-ranking males had higher mating effort than low-ranking males. Mating effort was higher during the wet than during the dry season. Results of the present study suggest that a male's investment in offspring care and offspring production in the non-monogamous savanna baboon is influenced by opportunities for each and is contingent upon a male's prevailing status and extrinsic energetic constraints.

#### **INTRODUCTION**

An extensive body of theory and empirical research on diverse species has investigated male investment in offspring production (reviewed in Clutton-Brock 1988; Anderson 1994). Increasingly, research has begun to include the problem of how males in some taxa allocate effort between offspring production and offspring care, the two components of reproductive effort (reviewed in Magrath & Komdeur 2003; Stiver & Alonzo 2009). However, few empirical studies have investigated the question of conflict between mating effort and paternal care among mammalian species. As a result, how mammalian males whose behavior can affect the survival and quality of their offspring balance investment between offspring production and care is largely unknown. Conflict between offspring production and care is likely to be exacerbated in highly social species that are non-seasonal in their reproduction and those that have long periods of immaturity, because the opportunities for both mating and care occur simultaneously throughout the year and potentially over several years during each offspring's development. Both these exacerbating conditions apply to savanna-dwelling baboons, the species (*Papio cynocephalus*) that we investigated in the present study.

In many cercopitherine primates including savanna baboons, matings occur within specific contexts of mate-guarding episodes also called consortships, which are characterized by intense male-male competition as the males attempt to out-compete each other in order to monopolize matings with a receptive female (Carpenter 1942; Bercovitch 1983, 1995; Rasmussen 1985; Alberts et al. 1996; Manson 1997). Gaining access to a receptive female and maintaining the consortship over a longtime during the period of

likely ovulation reliably predicts paternity success (Altmann et al. 1996; Constable et al. 2001; Alberts et al. 2003, 2006). Consortships are associated with considerable costs for males in time and energy including increased risks of injury or even death to gain access to a receptive female and to maintain the consortship (Drews 1996; Kitchen et al. 2005).

Consequently, for males that provide care for their offspring, paternal care is expected to constrain a male's ability to enter into a consortship and his success in maintaining it. Paternal care in primates includes overt behaviors such as favorable interventions on behalf of infants or juveniles during social conflicts (Buchan et al. 2003), and infant carrying (Smuts 1985; Smuts & Gubernick 1992). In addition, and arguably as important, is less overt care in which mothers, their infants, and juveniles are provided with a 'safe zone' simply by maintenance of close proximity between them and an associated male (Altmann 1980; Bales 1980; Hamilton 1984; Stein 1984; Noë & Sluitjer 1990; Smuts & Gubernick 1992; Borries et al. 1999; Buchan et al. 2003; Nguyen et al. 2009). Females with dependent young often attract the interest of other group members resulting in interactions that may have deleterious physical or psychosocial consequences. For example, rough handling (Kleindorfer & Wasser 2004; Nguyen et al. 2009), kidnapping (Altmann 1980), and infanticide (Palombit et al. 1997) have been reported in various baboon populations. Consequently, safe zones provided by adult males often provide protection against conspecifics (Altmann 1980; Palombit et al. 1997; Nguyen et al. 2008) and enhanced feeding opportunities for the mothers, their infants as well as for juveniles. Although a male may sometimes provide care to young other than his own offspring perhaps as a potential means of enhancing future mating opportunities (Bales 1980; Smuts 1985; Smuts & Gubernick 1992), recent genetic and behavioral data

confirm that such care behavior is disproportionately directed toward offspring rather than non-offspring (Borries et al. 1999; Buchan et al. 2003; Moscovice et al. 2009; Nguyen et al. 2008). Paternal care presumably explains the association between a baboon father's presence in the group during his offspring's juvenile period and accelerated maturation of the offspring (Charpentier et al. 2008). Realizing fitness benefits of offspring care, however, will generally constrain the extent to which a male can successfully compete for mating opportunities.

The nature and extent of the tradeoffs between mating effort and paternal care may also depend on ecological resources such as food availability. In the Eastern African savannas, differences in food, water, and shade availability between the dry and wet season may create more need to balance conflicting investments. At the individual level, relative opportunities for gains through mating and gains through offspring care will differ among males depending on opportunities for each component of reproductive effort and on differences on life history traits including those that predict body condition such as age and male dominance rank. For example, a male with no immature young in a group could simply focus on mating, and a male with no mating opportunities but who has several immature young in his group, could simply focus on care of young. However, most males will usually be faced with some mix of opportunities. In species living in socially structured societies, dominance rank predicts access to ecological resources as well as reproductive opportunities across many taxa (reviewed in Ellis 1995) and specifically among cercopithecine males (e.g. Dewsbury 1982; Cowlishaw & Dunbar 1991; Bulger 1993; Weingrill et al. 2000; Alberts et al. 2003, 2006; Setchell et al. 2005; Engelhardt et al. 2006).

The present study was based on the premise that a male will adjust his investment between offspring production and care based on his immediate opportunities for each. To test this idea, we determined, first, whether the number of a male's immature offspring predicted intensity of care behavior. Second, we determined whether the number of a male's immature offspring constrained whether a male entered into any consortships, and for those that did, whether it constrained how much consortship time they obtained in each month. We predicted that if male baboons face a tradeoff between paternal care and mating effort, mating effort would be low among males with more immature offspring compared to those with few or no immature offspring.

#### **METHODS**

#### **Study Population**

We studied savanna baboons in the Amboseli/Longido basin, at the foot of Mt. Kilimanjaro. Baboons mate and give birth throughout the year; inter-birth intervals are approximately two years (Altmann 1980), and puberty occurs at about 4.5 years for females and a year later for males. After puberty, males experience a several year period of rapid adolescent growth resulting in body size double that of adult females (Altman & Alberts 1987, 2005; Strum 1991; Alberts & Altmann 1995b). The attainment of full size at about 8 years of age allows males to achieve full social maturation, and confers on them the competitive ability needed for obtaining reproductive mates (Alberts & Altmann 1995b). Baboons are highly social and live in relatively permanent groups comprised of males and females of all ages. Adult females residing in a group have lived there since birth, whereas males disperse from their natal group around early adulthood, and reside in non-natal study groups as adults (Packer 1979; Hamilton & Bulger 1990; Alberts & Altmann 1995a).

The Amboseli baboon population has been the focus of longterm research by the Amboseli Baboon Research Project. We conducted our investigations in two stages. In the first stage, we determined whether the number of immature offspring a male had in the group predicted the male's intensity of paternal care. Data for this stage were collected between September 2007 and April 2008, and involved 37 adult males distributed across 4 groups and consisted of 614 focal samples, see further details under 'Behavioral data collection and measurement'. In the second stage, we determined whether the number of a male's immature offspring constrained the male's mating effort. Data for this stage were obtained from the longterm database and covered a 13-year period, January 1996 to December 2008, included 151 adult males distributed in 6 groups, and involved 5406 male-months.

Ages of subjects that were born into any of the study groups were known to within a few days because of the near-daily records of group demographics, whereas ages of the other males, those that immigrated into the study groups from non-study groups of the population, were estimated by visually comparing their size and patterns of physical condition including coat condition, degree of scarring, body carriage, and condition of canines with those of males of known ages (Alberts & Altmann 1995b). Ages of the adult

male subjects ranged from 7.8 to 18.8 years for the 8-month dataset and from 6.2 to 21.8 years for the 12-year dataset.

We assigned dominance ranks monthly based on winner-loser outcomes of dyadic agonistic interactions during that month (Hausfater 1975). The highest-ranking male was assigned rank 1, the second rank 2, and so on. Dominance ranks for males included in this study ranged from 1 to 14 for the 8-month dataset and from 1 to 19 for the 12-year dataset.

#### Seasonality of rainfall in Amboseli

Rainfall occurs in variable amount from November to May whereas June to October remains predictably dry (Altmann et al. 2002; Alberts et al. 2005). During the dry season, when all water pools from rains as well as the seasonal Lake Amboseli dry up, groups travel long distances from their sleeping groves to the few permanent water sources. Although baboons are eclectic foragers, during the dry season they revert to fallback foods, which require more time to process (Alberts et al. 2005; Altmann 2009). Differences in food availability between the dry and wet season potentially influence how males partition energy among various fitness components, including between mating and care of offspring. We examined the effect of season on intensity of paternal care and on the tradeoffs between paternal care and mating effort. We hereafter refer to the period from June through October as the dry season, and that from November through May as the wet season.

#### **Reproductive effort**

#### 1) Paternal care

#### Behavioral data collection and measurement

In order to determine whether the number of immature offspring a male had in the group predicted intensity of paternal care, we focused data collection on a focal male's proximity to immature and to adult females with young. We restricted all care behaviors to immatures conceived when the focal male was in the group thereby increasing the probability that they were likely to be the fathers.

Behavioral data were collected during 40 min periods of focal sampling (Altmann 1974). Proximity was scored as nearest neighbor data, and involved recording the IDs of nearest 2 adults and the nearest immature within 5m of the focal male; these data were collected as instantaneous point samples and were recorded at the min every 2 min. All these records were logged into a hand-held computer, Psion Workabout, Psion Teklogix <sup>™</sup>, and were later parameterized as the proportion of the point samples when a focal male was near a an immature and a female with young. We hereafter refer to this proportion as intensity of paternal care. See 'Data analysis' for details on how this measure was later parametized before analysis. During the 8-month period, we observed males for over 395 hrs. Number of focal samples available for each male ranged from 8 to 19 totaling 314 min to 764 min.

We quantified investment in offspring care simply as the average proportion of time the focal male had a female with immature and an immature as his neighbor during each focal sample.

#### Number of immature offspring as opportunities for paternal care

We defined immature individuals as all females that had not reached menarche and males that had not undergone testicular enlargement; these transitions occur on average at 4.5 yrs (Altmann et al. 1981) for females and 6.5 yrs for males (Alberts & Altmann 1995b). We estimated each adult male's number of immature offspring, for 546 immature individuals during the present study, by using a hierarchy of information about paternity for each infant or juvenile. Genetic paternity assignment was available for 319 immature individuals; for the remaining 227 immatures, we took advantage of various data available from the long-term project to estimate probability of paternity. To do so, we assigned probability of paternity to each male present in the group for each offspring based on 1) proportion of consortship time a male obtained for a consortship if consortship observations were available during the 5-day period of likely conception, or 2) each male's dominance rank and the number of adult males in a group during the period of likely conception. As a result, we assigned multiple paternity to offspring for which behavioral data did not indicate a single clear father.

The proportion of consortship time that a male obtains during the period when ovulation is likely to occur, the 5-day window, has been shown to be a good predictor of paternity outcomes in our population (Altmann et al. 1996; Alberts et al. 2006). For each

immature, its 5-day conception window was identified in the longterm database from its mother's reproductive cycles, and we could identify all observed consortships during those days. Following Alberts et al. (2006), if at least 5hrs of consortship were observed during the 5-day conception window (n = 158 conceptions), paternity was apportioned to each adult male present in the group at the time according to the proportion of consortship time he obtained. For instance, if a male obtained all of the observed consortship time for a given conception, he was assigned as the sole father of the offspring. However, if one male obtained 80% of the consortship time and a second male obtained 20% of the consortship time for a given conception, they were each assigned a fraction of paternity for that offspring (0.8 and 0.2 respectively). We called these consortship-based estimates of paternity.

If no consortship observations were available for the 5-day conception window for a given conception (n= 47 conceptions), each male in the group was assigned a fraction of paternity for that conception based on the number of adult males in the group and the dominance rank of each male. In these cases, the fraction of paternity assigned to each male was based on the distribution of known paternity for 272 infants across males of different ranks in groups of different sizes (Alberts et al. 2006 and unpublished data). According to these data, which are largely consistent with the priority of access model (Altmann 1962), a rank 1 male in a group with a total of two adult males has 0.92 chance of obtaining paternity but this probability drops as the number of adult males in the group increases such that in a group of 4 adult males, a rank 1 male has a 0.73 chance, ranks 2 and 3 both have a 0.14 chance, and rank 4 has a zero chance. We called these paternity

assignments based on male rank and the number of adult males in the group demographic-dominance-based estimate of paternity.

Finally, if some consortship observations were available but fewer than 5 hrs were observed for a conception (n = 111 conceptions), rather than use only a consort-based estimate or only a demographic-dominance-based estimate, we used a combination of the two, and we gave more weight to the consortship-based estimate the closer the observed number of consort hours was to 5 hrs. Specifically, we modeled paternity estimates as an expected value by calculating a consortship-based estimate and a demographic-dominance-based estimate as above and then weighting the consortship proportion by the fraction that the observed consortship time was for that conception out of 5hrs. The demographic-dominance estimate was then weighted as 1 minus the consort proportion. Taken together, we modeled paternity estimates for all immatures for whom genetic paternity outcomes are not known as follows:

$$\{(pCt \times Ct \max 300 \div 300) + [(DemographicDominanceEstimate) \times (1 - (Ct \max 300 \div 300)]\}$$

#### where

pCt = proportion of observed consortship time a male obtained;

Ct = total observed consortship time that the female experienced during that conception Ctmax = maximum value of which is set at 300 min or 5hrs;

DemographicDominanceEstimate = proportion of paternity assigned to a male based on both his dominance rank and adult male group size at the time of conception of an infant in reference. The total number of offspring assigned to each male, was then the sum of offspring for whom he was assigned as the sole father (from genetic or behavioral, or demographic-dominance assignment) plus the fraction of each offspring that was assigned to him where single paternity could not be assigned. The number of immature offspring among males at date of behavioral data collection ranged from 0 to 13.99.

#### 2) Mating effort

We defined mating effort in two ways 1) whether a male gained any consortships, and 2) how much consortship time a male gained in a given month. In order to assess a male's mating effort, we collated data on consortship activity from the longterm database. In our study population, success in entering into a consortship and how long a male maintains it are strong predictors of how paternity is distributed among males in a group (Altmann et al. 1996).

Data on consortships are routinely collected as part of the longterm project. These data include identity of the male and of female and the duration of the consortship. These data enabled us to examine whether the number of a male's immature offspring constrained 1) whether a male entered into a consortship, and for those that did, 2) how much consortship time they obtained in a month. We used both measures to quantify mating effort. Inter-group differences in mating effort, as defined above, may derive from differences in how long each group is observed in each month. As a result, we used conditional statistical tests (see 'Data analysis' for further details) in order to control for differences in observation time across groups.

#### Data analysis

We performed data analysis in two steps. First, we evaluated whether the number of a male's immature offspring predicted the male's intensity of paternal care. For this analysis, we identified for each focal sample, the focal male's estimated number of immature offspring, his age and dominance rank as the predictor variables. We also examined the effect of season on the intensity of paternal care. The response variable, intensity of paternal care, was the average proportion of time the focal had an immature or a female with young as his neighbor during each focal sample. The variance-mean ratio of this outcome variable was less than 1 and so its was parametized as a binomial variable: samples where the focal had an immature or a female with young as a neighbor got a score of 1 and a score of 0 if otherwise; we thus determined the probability of care. In this first step, we used the focal sample as the unit of analysis and the data consisted of 614 focal samples.

Second, we evaluated whether the number of male's immature offspring constrained a male's mating effort, which we measured as the 1) probability to gain a consortship, and 2) amount of consortship time a male obtained per month if he did have any consortships. In other words, we had separate models for each measure of mating effort. For each model, we also examined whether the male's age and dominance rank, and season predicted variance in mating effort. Finally, we controlled for the effect of differences in observation time across study groups. In this second step, we used month as the unit of analysis and the data consisted of 5406 male-months.

We used mixed-effects models to determine the extent to which the number of a male's immature offspring predicted variance in paternal care behavior. Mixed-effects models are robust for correcting for pseudoreplication, for dealing with unequal samples among subjects, and for dealing with variable sampling intervals among subjects, and for increasing statistical power (Pinheiro & Bates 2000; West et al. 2007; Baayen et al. 2008). We entered group and male id as random effects. All statistical tests were performed in R version 2.9.2. Hypothesis tests were based on conditional statistics and the threshold statistical significance was set at 0.05.

#### RESULTS

# Does the estimated number of a male's immature offspring predict intensity of paternal care behavior?

The number of a male's immature offspring significantly predicted intensity of paternal care behavior (z = 3.381, p = 0.0007) Table 1. Males with more immature offspring in the group were more likely to spend more time in close proximity to immatures and to females with young than males with fewer immature offspring or those that had none, Figure 1. Intensity of paternal care increased as the number of immature offspring increased but it appears to decrease in focal samples from males with four or immature offspring. This apparent decline can be attributed to that fact that we considered both infants and juveniles as immatures in this study. It can be expected that males with more immature offspring may have stayed in their present group longer and so some of their

offspring are juveniles. Juveniles may not require close monitoring from their father as do infants. Male age and dominance rank did not explain significant differences in probability of paternal care. In addition, differences in intensity of paternal care between the dry and the wet season were not significant (Table 1).

#### Does paternal care constrain mating effort?

Opportunities for paternal care did not predict whether a male obtained a consortship during a month (z = -0.854, p = 0.3693), nor did it predict how much consortship time he obtained in the month (t = 1.414, p = 0.1574) if he obtained any consortships. In contrast, and as we expected, high-ranking males were more likely to obtain consortships (z = -16.754, p < 0.0001) and also spent significantly more time consortship than low-ranking males (t=-6.742, p < 0.0001); Table 2 and Figure 2. Similarly, males were more likely to consort (z = 4.064, p < 0.0001), and spent significantly more time consorting during the wet season than they did during the dry season (t=3.100, p = 0.0020). In contrast, male age did not predict the probability of obtaining a consort nor the amount of consortship time a male obtained in a given month, Table 2.

Table 1: The number of a male's immature offspring predicts probability of paternal care.

Estimate for covariates represents slope and that for categorical variable (i.e. season)

represents difference in means between the dry and the wet season.

Predictor variable	Estimate	Std error	z-value	P value
Number of immature offspring	0.300	0.089	3.381	0.0007
Age	-0.012	0.069	-0.179	0.8580
Dominance rank	-0.010	0.060	-0.160	0.8732
Season	-0.281	0.243	-1.159	0.2463

Figure 1. Intensity of paternal care increases as the number of a male's immature offspring increases. Intensity of paternal care expressed as proportion of time a male spent in proximity to immature and to female with young.



Number of immature offspring

Table 2: Dominance rank and season predict the probability of obtaining a consortship per month. Values in italics are derived from the model where mating effort in each malemonth is expressed as whether a male obtained a consortship or not; otherwise where mating effort is expressed as the amount of consortship time a male obtained in each male-month. In each case, significant predictors are shown in bold. Estimate for covariates represents slope and that for categorical variable (i.e. season) represents the difference in means between the dry and the wet season using the dry season as the reference level.

Predictor variable	Estimate	Std error	z-value	P value
Number of immature offspring	-0.016	0.018	-0.898	0.3694
	0.013	0.009	1.414	0.1574
Age	0.019	0.017	1.131	0.2581
	-0.010	0.010	-1.019	0.3083
Dominance rank	-0.220	0.013	-16.754	<0.0001
	-0.053	0.008	-6.742	<0.0001
Season	0.242	0.059	4.064	<0.0001
	0.108	0.035	3.100	0.0020
Observation period	0.007	0.002	3.133	0.0017
	0.017	0.001	13.181	<0.0001
Figure 2: High-ranking males spent more time in consorts than low-ranking males. Consort time expressed as the total minutes a male obtain per month divided by how long his group was observed that month. Residuals obtained after controlling for season and age as fixed effects and for differences among study groups and individuals.



#### Is conflict between mating effort and paternal care resolved in savanna baboons?

Up to this point, the results present a paradox. On one hand, probability to care increases with the number of immature offspring a male has in the group. On the other hand, high-ranking males have higher mating effort than low-ranking males. However, given that males produce more offspring when they are high-ranking, they may have more immature offspring in the than low-ranking males (Alberts et al. 2003, 2006). Consequently, the results suggest an apparent resolution of tradeoffs between mating effort and paternal care and raise the question: What enables high-ranking males to apparently invest in offspring care without constraining their investment in offspring production?

We hypothesized that young adult males may have the somatic capacity to successfully seek mating opportunities without constraining investment in offspring care. To test this hypothesis, we used an age cutoff of 15 years and designated males younger than 15 years as 'young' whereas those older as 'old'. We are aware that the 15-year cutoff is a coarse delineation and that individuals may show variability in gerontological patterns of their somatic capacity. However, previous findings from our population has shown that the number of offspring per male declines after this age (Alberts et al. 2006, figure 2a).

We determined the extent to which this categorical index of age, in addition to the number of immature offspring, dominance rank, season, and observation time, predicted the probability of entering into a consortship in a given month or the amount of consortship time if a male obtained any consortship during that month. Young males were more likely to enter into a consortship during a month than old males (z = 2.544, p

= 0.0110); however, once a male had entered into a consortship, there was no significant difference between young and old males in how much time the male spent in consortships that month (t = 1.247, p = 0.2124).

# DISCUSSION

Offspring protection and other aspects of care are predicted to evolve when they confer fitness benefits to males through increased offspring quality and survival (Maynard Smith 1977; Woodroffe & Vincent 1994). Results of the present study thus extend previous findings from our study population, which demonstrated that offspring care is an important component of reproductive effort in male baboons (Buchan et al. 2003; Charpentier et al. 2008). For example, Buchan et al. (2003) showed that fathers intervened favorably on behalf of their offspring during social interactions. In addition to such favorable interventions (Buchan et al. 2003), the safe zone provided to females and their immature offspring by baboon fathers previously demonstrated (Nguyen et al. 2009) and confirmed in the present study presumably explains enhanced fitness of offspring whose fathers were present during the offspring's juvenile period (Charpentier et al. 2008).

However, our results suggest that paternal care does not constrain mating effort in savanna baboons. One assumption we made is that all consortships have equal reproductive quality. Consortships vary in reproductive quality depending on the female as well as on the phase of estrous cycle. For example, parous females of several nonhuman primates species are more likely to conceive at any given cycle and their

offspring are more likely to survive than are nulliparous females (e.g. Mandrills: Setchell & Wickings 2006; baboons: Gesquiere et al. 2007). In addition, female baboons have a 5day window, the ovulatory phase, preceding the luteal phase of the estrous, during which ovulation is likely to occur (Wildt et al. 1977; Shaikh et al. 1982). Consortships during the 5-day window are therefore of higher reproductive quality than those that occur prior to the ovulatory phase. Furthermore, within-female differences in conceptive probabilities across cycles have been demonstrated in baboons and chimpanzees (Bulger 1993; Gesquiere et al. 2007; Emery Thompson & Wrangham 2008). Consequently, it is possible that paternal care may constrain the probability to enter into a high reproductive quality consort and how much time a male obtains in such consortships.

Behaviors that enhance a male's chances of securing mating opportunities are energetically costly (Rasmussen 1985; Alberts et al. 1996; Kitchen et al. 2005). It is expected that a male's capacity to access these opportunities will change during a male's reproductive career. It is, therefore, not surprising that high-ranking males, usually in prime body condition, show higher investment in such behaviors and activities than lowranking males. But dominance rank in baboons, including in our study population is also strongly correlated with age (e.g. Packer 1979; Alberts et al. 2003, 2006; Weingrill et al. 2003) such that opportunities for producing additional offspring are expected to decline with adult age. In other words, as a male advances in age, his ability to acquire and maintain high dominance rank also declines and so does his priority of access to resources including mates (e.g. baboons: Alberts et al. 2003, 2006; macaques: Bissonnette et al. 2009). This may explain why young adult males invested more in mating effort than older ones. Given that males produce more offspring when they are high-ranking than when they are not, high-ranking males may have more immature offspring present in the group than low-ranking males. To the extent that they are also typically in good body condition, young adults may be able to successfully invest in mating without substantially constraining their investment in paternal care (Griffith et al. 2002; Schradin et al. 2009). Body condition may thus explain the apparent absence of conflict between mating effort and paternal care in male baboons. Consequently, results of the present study suggest that male baboons attempt to maximize investment in offspring production and care during the phase of their adult life that favors doing so.

The strong seasonal effect on mating effort suggests a role for extrinsic energetic constraint in patterning male investment in offspring production. As income feeders, baboons constantly need resources both for their somatic maintenance and to allocate to other fitness enhancing activities including mating and paternal care. Males are therefore more likely to recuperate more readily from the time and energy-demands of consortships during the wet season than they are during the dry season. In addition, the seasonal effects may arise from differences in the probabilities of conception and successful pregnancies between the dry and the wet season. It has been shown that female baboons in our study population are more likely to cycle, conceive, and carry pregnancy to term during the wet season than they are during the dry season (Beehner et al. 2006a, b). The results suggest that extrinsic energetic constraints and how they influence schedules of reproduction among female baboons may also shape reproductive behaviors and activities among males.

In summary, we have demonstrated that male baboons with more immature offspring in the group are more likely to provide care than those with few or none. We have also demonstrated that high-ranking males show higher mating effort than their lowranking counterparts. In addition, we have documented that mating effort is higher during the wet than during the dry season. However, the extent of a male's investment in either offspring production or care depends both on opportunities for each and on energetic constraints. In addition, the apparent resolution of tradeoffs between mating effort and paternal care presumably derives from differences in male body condition among males.

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# **CHAPTER TWO:** Season and female reproductive quality but not opportunities for paternal care predict intensity of male mate guarding in a non-seasonally breeding primate

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# ABSTRACT

In many primates, mating occurs almost exclusively in the context of mate-guarding episodes. These episodes are characterized by a male persistently following an estrous female while he attempts to monopolize mating with her. Males incur high costs in time and energy when mate guarding. As a result of these costs, mate-guarding episodes provide excellent opportunities for investigating whether paternal care constrains mating effort. In the present study of adult male savanna baboons, we evaluated the potential conflict between opportunities for paternal care and mating effort using a predictive framework that incorporates seasonal differences in resource availability, female reproductive quality, male dominance rank, and the estimated number of a male's immature offspring as a measure of his opportunity for paternal care. Intensity of mate guarding was higher during the wet than during the dry season and when males guarded females of high reproductive quality than when they guarded females of low reproductive quality. In contrast, differences in male dominance rank or in the estimated number of immature offspring each male had in the group did not account for significant variance in intensity of mate guarding. These results suggest that any constraints of paternal care on mating effort in this species probably occur outside mate-guarding episodes. Our results, that mate guarding is compromised during periods of energetic stress and also when mate guarding is less likely to result in successful offspring production because of low partner quality, support a role of energetic constraints in shaping reproductive behavior of male baboons.

#### INTRODUCTION

Conflict between parental care and mating effort has been shown in many species but its extent remains largely unknown for mammalian males. Conflict or trade-offs between parental care and mating effort in males arises primarily from energetic and temporal constraints (Magrath and Komdeur 2003; Stiver and Alonzo 2009). Energetic constraints occur because individuals have limited resources (Sterns 1992); energetic investment in mating may be constrained by energetic investment in offspring care (Zahavi 1975; Folstad and Karter 1992; Andersson 1994). Temporal constraints, on the other hand, occur because paternal care is generally incompatible with mating effort such that both cannot occur simultaneously (e.g. Mulvihill et al. 2009; for reviews see Magrath and Komdeur 2003; Stiver and Alonzo 2009). Here we investigate the extent to which opportunities for paternal care constrain mating effort in a wild population of savanna baboons, *Papio cynocephalus*.

In many cercopithecines and other primates, mating occurs almost exclusively in the context of mate-guarding episodes, also called consortships (Carpenter 1942; Manson 1997). During mate guarding in baboons, for example, a male persistently follows an estrous female, keeps other males away from her, and may forego feeding in order to monopolize mating (Bercovitch 1983; Rasmussen 1985; Alberts et al. 1996). As a result, males incur high costs in energy, time, and risks of injury during these mate-guarding episodes especially when they last for several hours or days (Bercovitch 1983; Rasmussen 1985; Alberts et al. 1996; Drews 1996; Kitchen et al. 2005). Because of these costs, mate-guarding episodes provide an excellent opportunity for investigating the

extent to which a male's investment in other activities such as offspring care reduces his mating effort.

Mating effort can be thought of as having two components for male primates such as baboons. One is the set of decisions a male makes about how to distribute mating across females: this includes the effort involved in gaining access to a female in the first place, and the male's decisions about which females to pursue. The second is the intensity with which a male guards the female consort partner; this is the focus of the current study. Males in many nonhuman primate species that engage in mate guarding offset costs of mate guarding by discriminating among females based on female reproductive quality. As a result, males are likely to consort 1) with parous rather than nulliparous females (mandrills: Setchell and Wickings 2006; baboons: Gesquiere et al. 2007); 2) with females at the time when ovulation is most likely to occur (baboons: Bulger 1993; Tonkean macaques: Aujard et al. 1998; chimpanzees: Emery Thompson and Wrangham 2008); and 3) with females experiencing a conceptive cycle rather than those experiencing a non-conceptive one (baboons: Bulger 1993; Gesquiere et al. 2007; chimpanzees: Emery Thompson and Wrangham 2008). Despite these biases, female consort partners will vary in their probability of successfully producing offspring. Consequently, female reproductive quality is expected to influence the intensity with which a male guards his partner so as to monopolize matings with her (his mating effort as defined for this manuscript).

In non-seasonal species that live in semi-arid ecosystems, such as the East African savannas, a major source of variability in energetic costs of mate guarding derives from seasonal differences in resource availability based on rainfall. During the dry season

when food and water availability is low resulting in increased travel distance between resources as well as time to process foods (Bronikowski and Altmann 1996; Altmann et al. 2002; Alberts et al. 2005; Altmann, 2009), males are expected to invest less in mating effort. Even within a season, individuals in group-living species differ in the quantity and quality of resources that they obtain. This variability is predicted by an individual's fighting ability, which is often indexed as dominance rank such that high-ranking males, often in prime body condition, are expected to be able to invest more in mating and paternal care than low-ranking males (Ellison 2003; Magrath and Komdeur 2003)

Paternal care increases a male's fitness through increased quality and survival prospects of his offspring (e.g. Wolf et al. 1988; Clutton-Brock 1989, 1991; Ketterson and Nolan 1994; Charpentier et al. 2008). In primates, paternal care includes activities such as protecting offspring during social conflicts (Borries et al. 1999; Buchan et al. 2003), infant carrying (Smuts 1985), and perhaps, most importantly, providing a 'safe zone' by maintaining close proximity to his immature offspring (Altmann 1980; Bales 1980; Hamilton 1984; Palombit et al. 1997; Borries et al. 1999; Buchan et al. 2003; Lemasson et al. 2008; Nguyen et al. 2009). These behaviors take time and as a result, they might reduce a male's intensity of mate guarding.

Consequently, males are likely to face a tradeoff between paternal care and mating effort due to both time and energy constraints. In this study we specifically focus on male behavior during mate-guarding episodes to investigate whether opportunities for paternal care constrain a male's intensity of mate guarding. We recognize that a conflict between paternal care and mating effort might be manifested in whether a male engages in mate guarding at all, and not only through the intensity of mate guarding when it

occurs; in the current study we have focused on the second of these two potential contexts for tradeoffs and will address the first in a another paper. We do so within a predictive framework that integrates variability in energetic constraints as indexed by season, variability in cues of female quality, and individual differences among males in both dominance rank and the number of immature offspring each male had in the group.

#### **METHODS**

# Study population and subjects

Study subjects (Appendix 1) were 39 individually known adult male savanna baboons distributed across 5 baboon social groups that ranged in size from 30 to 100 individuals, members of a well-studied wild population in the Amboseli basin, southern Kenya (Alberts et al. 2005; Altmann et al. 2010). All subjects had attained adult dominance rank, a developmental milestone that marks the beginning of adulthood and reproduction in the study population (Alberts and Altmann 1995). The number of adult males ranged from 4 to 17 among the groups. The ages of fourteen subjects who were born into study groups were known to within a few days, which was possible because of the near-daily visits to each study group that occur as part of regular research on this population. Ages of males that were not born into study groups were estimated when the male first joined a study group by visually comparing him with males of known age using several physical features including coat condition, body carriage, degree of scarring, and condition of canines (Alberts and Altmann 1995). At the time of data collection subjects ranged in age from 7.75 to 18.81 years. We conducted the fieldwork for the study between September 2007 and April 2008.

#### Environmental variability in energetic constraints: dry vs wet season

In Amboseli, a predictable long five-month dry season, during which rainfall is negligible, occurs from June through October (Altmann et al. 2002; Alberts et al. 2005). The remaining seven months, November through May, experience variable amounts of rainfall and are termed the wet season (e.g. Alberts et al. 2005); total annual rainfall averages 346.5 mm, range 132.0-553.4mm, (Altmann et al. 2002; and unpublished data). During the dry season, baboons in our study population increase their feeding time presumably to compensate for a decline in food availability and increased distance traveled between resources as well as increased time and energy to process foods (Alberts et al., 2005). The resulting energetic stress due to differences in food availability between the dry and the wet season is indeed reflected in higher levels of stress hormones during the dry season (Gesquiere et al. 2008; Gesquiere et al. 2010). Consequently, males that guard females during the dry season are expected to be more energetically constrained than those that guard in the wet season and, therefore, to show lower intensity of mate guarding.

# Indicators of female reproductive quality: parity and stage of menstrual cycle

Whether a female has had prior reproductive experience and what stage of her menstrual cycle she is in affect her quality as a potential mate. Parity predicts various measures of female reproductive quality including probability of conception and infant survival (e.g. Williams 1966; Sterns 1992; Förslund and Pärt 1995). In our study population, for example, parous females are more likely to conceive at any given cycle than their nulliparous counterparts (Altmann 1980; Gesquiere et al. 2007), and parous females produce offspring that are larger-for-age and more likely to survive (Altmann et al. 1988, Altmann and Alberts 2005). We grouped females into two categories: 1) nulliparous (females that had never conceived), and 2) parous (females that had previously conceived) using information in our long-term project database.

Stage of the menstrual cycle also predicts female quality as a mate because fertility varies across cycle days. The follicular phase of the menstrual cycle in baboons begins with the onset of menstruation. Within a few days, female baboons develop a highly visible and turgid 'sex skin' swelling, which is under the influence of estrogen (e.g. Gesquiere et al. 2007) and increases in size over approximately a two-week period. The first day of the luteal phase of the cycle then begins on the first day of sex-skin deturgescence, termed D day; the day prior to D day (day D-1) is considered the last day of the follicular phase. Mate-guarding episodes generally occur solely during the follicular phase of the cycle, during turgescence, but are seen both early and late during that phase. Ovulation in baboons primarily occurs during the last 5 days of the follicular phase (Wildt et al. 1977; Shaikh et al. 1982).

We determined whether a male's consort partner was nulliparous or parous and whether she was in the early or late (ovulatory) phase of her cycle using field data coded into our long-term database. Reproductive information, including that needed to determine pregnancies and births for all females in the population, is collected on a near daily basis. We used these records to classify a female retrospectively as either nulliparous or parous. Also recorded is information on menstrual signs (indicated by blood stains on the perineum) and sex skin swelling size scored by a visual estimation on a scale of 0 to 10. These data enable us to subsequently delineate the follicular phase into two periods based on differences in fertility: the ovulatory phase as the last 5 days of the follicular phase, and the pre-ovulatory phase as the rest of the follicular phase.

We produced a composite index of female reproductive quality during each focal sample by combining the female partner's parity and her probability of ovulation on that day. That is, females in each focal sample belonged to one of four categories corresponding to increasing reproductive quality: nulliparous – pre-ovulatory, nulliparous – ovulatory, parous – pre-ovulatory, and parous – ovulatory.

# Male life history traits

# Male dominance rank

Male dominance rank has a strong impact on male reproduction and life history (Alberts and Altmann 1995), so we examined it as a potential source of variance in male intensity of mate guarding. We assigned monthly dominance ranks by constructing a matrix of win-loss outcomes of dyadic agonistic interactions (Hausfater 1975). The highest-ranking male in each group was assigned rank 1, the second rank 2, and so on. Dominance ranks for the study subjects ranged from 1 to 13, Appendix 1.

#### Number of a male's living immature offspring

We defined an immature as a female that had not reached menarche, which occurs at about age 4.5 yrs (Altmann et al. 1977) or as a male that had not undergone testicular enlargement, which occurs at about age 5.7 yrs (Alberts and Altmann 1995). We included in our calculations all individuals within this immature period because previous findings in our study population show that fathers intervene preferentially on behalf of their offspring throughout the immature period (Buchan et al. 2003) and the longer fathers are present throughout this period, the greater the fitness consequences for their offspring (Charpentier et al. 2008).

We estimated each adult male's number of immature offspring by using a hierarchy of information about paternity for each infant or juvenile. Genetic paternity assignment was available and used for 17 immatures alive in the study groups during the study, leaving 160 immatures for whom paternity was estimated. In the absence of genetic paternity assignments, we took advantage of various data available from the long-term project to assign paternity based on relationships that were previously validated in the population. Specifically, for each immature we assigned a probability of paternity to each adult male present in the group, based on 1) the proportion of consortship time a male obtained if consortship observations were available during the ovulatory phase of the menstrual cycle; or 2) each male's dominance rank and the number of adult males in a

group during the ovulatory period. These estimation procedures (described below) resulted in either a single, clear, high-probability father, or two or more males that might be fathers. In the latter case, we assigned partial paternity to immatures.

*Paternity estimation procedure 1 – consortship-based estimates of paternity.* The proportion of consortship time that a male obtains during the 'ovulatory period' has been shown to be a good predictor of paternity outcomes in our population (Altmann et al. 1996; Alberts et al 2006). For each immature, its 5-day conception window was identified in the long-term database from its mother's reproductive cycles all observed consortships during those days were used in the estimation. Following Alberts et al (2006), if at least 5hrs of consortship were observed during the 5-day conception window paternity was apportioned to each adult male present in the group at the time according to the proportion of consortship time he obtained. This applied to 84 offspring. For instance, if a male obtained all of the observed consortship time for a given conception, he was assigned as the sole father of the offspring. However, if one male obtained 80% of the consortship time and a second male obtained 20% of the consortship time for a given conception, they were each assigned a fraction of paternity for that offspring (0.8 and 0.2 respectively).

Paternity estimation procedure 2 – male rank and density-based estimates of paternity. If no consortship observations were available for the 5-day conception window (this applied to 16 offspring), each male in the group was assigned a fraction of paternity for that conception based on the number of adult males in the group and the dominance rank of each male. In these cases, the fraction of paternity assigned to each male was based on the distribution of genetically determined paternity for 272 infants across males

of different ranks in groups of different sizes (Alberts et al. 2006 and unpublished data). According to these data, a male ranked 1 in a group with a total of two adult males has a 0.92 chance of obtaining paternity; but this probability drops as the number of adult males in the group increases such that in a group of 4 adult males, a male ranked 1 has a 0.73 chance, ranks 2 and 3 both have a 0.13 chance, and rank 4 has a zero chance; and in a group of 8 adult males, rank 1 has a 0.21, rank 2 a 0.19, and ranks 6 onwards each have a 0.03 chance, and so on. We called these paternity assignments "demographic-dominance-based estimates of paternity," because they were based on male rank and the number of adult males in the group.

Paternity estimation procedure 3 – a combination of consortship-based and demographic-dominance–based paternity assignment. If some consortship observations were available but fewer than 5 hrs were observed for a conception (this applied to 60 offspring), rather than use only a consort-based estimate or only a demographicdominance-based estimate, we used a combination of the two. We gave more weight to the consortship-based estimate the closer the observed number of consort hours was to 5 hrs. Specifically, we modeled paternity estimates as an expected value by calculating a consortship-based estimate and a demographic-dominance-based estimate as above and then weighting the consortship proportion by the fraction of consortship time observed for that conception out of 5hrs. The demographic-dominance estimate was then weighted as 1 minus the consort proportion.

*Overview of paternity assignments.* Taken together, we modeled paternity estimates for all immatures for whom genetic paternity outcomes are not known as follows:

{ $(pCt \times Ct \max 300 \div 300) + [(DemographicDominanceEstimate) \times (1 - (Ct \max 300 \div 300)]}$ 

where

pCt = proportion of observed consortship time a male obtained;

Ct = total observed consortship time that the female experienced during that conception; Ctmax = maximum consort duration set at 300 min;

DemographicDominanceEstimate = proportion of paternity assigned to a male based on both his dominance rank and adult male group size at the time of conception of an infant in reference.

The total number of offspring assigned to each male at the time of sample collection was then the sum of offspring for whom he was assigned as the sole father (from genetic, behavioral, or demographic-dominance assignment) plus the fraction of each offspring that was assigned to him where single paternity could not be assigned. The estimated number of immature offspring across males ranged from 0 to 9.93, Appendix 1.

Although these estimates of paternity are necessarily less accurate than genetic assignments, they rely heavily on information about the distribution of paternity that we obtained from past genetic assignments. Consequently, although they may not accurately identify the particular offspring that a male has sired, we are confident that they represent a good estimate of the number of offspring he has in the group, which is the most relevant parameter for this study.

# Measuring intensity of mate-guarding within mate-guarding episodes

In order to quantify intensity of mate guarding, we collected data on three specific behavioral events (frequency data on grooming, sexual mounts, and approaches) and two behavioral states (proximity to the consort partner and time spent feeding) that are important for maintaining a consortship and in monopolizing matings therein (Fedigan 1982; Bercovitch, 1995; Alberts, et al., 1996; Aujard et al. 1998). Proximity and feeding were collected as point samples at the minute every two minutes, whereas data on grooming, sexual mounts, and approaches were collected as events throughout the focal sample (Altmann 1974). Data were collected on a Workabout hand-held computer by Psion Teklogix<sup>TM</sup> and downloaded into a computer at the end of each field day. Focal samples were 40 min, or shorter if the consort dyad moved out of sight or if the consortship ended. In total we collected 131 focal samples, which involved 39 different males and 46 different females. The samples comprised 54 and 77 samples for females in the pre-ovulatory and ovulatory phases of the sexual cycle, respectively, and 31 and 100 samples involving nulliparous and parous females, respectively. The number of samples among subjects ranged from 1 to 9; the number of times each of the 46 females was consorted ranged from 1 to 9; there were a total of 85 different mate-guarding dyads and the sample frequency ranged from 1 to 8 across dyads. See Appendix 1 for further details on the nature of the mate-guarding samples.

We parameterized the 5 behavioral measures as follows. We quantified proximity data as the proportion of point samples during which a focal male was observed within 5m of the female consort partner, and feeding data as the proportion of point samples

when a male was observed 'not-feeding'. We parameterized the remaining behavioral measures (grooming, mounting, and approaches) as rates (number of events per minute). Next, we used Principal Component Analysis to obtain linear combinations, principal components (PCs), of the measures of mate-guarding intensity that explained the most variance. Because the 5 measures were in different units, rates and proportions, we scaled them to achieve unit variance before obtaining the PCs. The 5 behavioral measures loaded with nearly similar weights on PC1, which also accounted for the highest variance across samples and was used in subsequent tests as the intensity of mate guarding.

#### Effect of female behavior on male intensity of mate guarding

The dyadic nature of mate-guarding episodes may result in reciprocal behaviors between the male and female partners. To explicitly address the potential for reciprocal behaviors between members of the consorting pair, and thus the extent to which female behavior might influence the intensity with which a male guards the female, we also collected data on the behavior of the female consort partner within each mate-guarding sample. Specifically, we collected data on the frequency with which the female groomed and approached the male consort partner, the two major female social behaviors within consortships. Data on these behavioral events were collected alongside those of the focal male, within the 40-min sample.

#### Data analysis

#### *Evaluating potential confounding factors*

First, to evaluate the effect of a female consort partner's behavior on the intensity of male mate guarding, we first obtained a simple average of the two female behaviors, [(rate of grooming + rate of approaches)/2], which we refer to hereafter as the 'female effort'. We then included female effort as a predictor variable in our initial model, see *Statistical analysis*, for predicting intensity of mate guarding.

Second, we took into consideration the fact that consort samples were collected at different times of the day, which might result in differences in some of the measures of intensity of mate guarding, such as feeding behavior. Therefore, we determined the effect of time of sampling on intensity of mate guarding by including it as a fixed effect in the mixed-effects model; see *Statistical analysis* below.

Third, a male might in theory consort a female who has an immature offspring that was sired by him, thereby potentially reducing the extent to which caring for the offspring constrained the male's intensity of guarding the offspring's mother. We examined how often this occurred and whether it had an impact on the intensity of mate guarding. In fact this occurred in only 7 out of the 131 consort samples, which limited our ability to evaluate its impact on the intensity of mate guarding. Nonetheless, we initially included it in our model as a potential confounding variable termed 'paternity' by parameterizing it as 1 or 0, where 1 indicated samples where the focal male guarded a female whose immature offspring had a non-zero paternity estimate for that male.

# Statistical analysis

We constructed a general linear mixed model predicting male intensity of mate guarding using the 4 main predictor variables of interest – male dominance rank, number of immature offspring, female reproductive quality, and season – plus the 3 potential confounding variables – female effort, time of sample collection, and paternity. The unit of analysis for male intensity of mate guarding was the individual focal sample, that is, we did not take means or pooled values across males or across females. Because of the uneven number of samples among male subjects, we modeled intensity of mate guarding using a mixed-effects model that is robust to both heterogeneity and pseudo-replication (Pinheiro and Bates 2000; West et al. 2007). We entered focal id nested within group as random effect.

For hypothesis testing, we used conditional tests (Pinheiro and Bates 2000; West et al. 2007). All statistical tests were performed in R 2.9.1 and in SPSS ver. 15; statistical significance level was set at 0.05.

#### RESULTS

Intensity of mate guarding was higher during the wet season than during the dry season (t = 2.402, p = 0.022), Table 1, Figure 1. Similarly, the index of female reproductive quality was also a strong predictor of mate-guarding intensity (t = 3.723, p < 0.001); males invested more when guarding females of high reproductive quality than when guarding those of low reproductive quality, Table 1. Using a simple analysis of variance, we found significant differences in intensity of mate guarding (after controlling for seasonality, male dominance rank, the estimated number of a male's immature

offspring, and the random effect of focal id nested within group) among the four categories of female reproductive quality (Welch test, p = 0.003). Post-hoc analysis (LSD) showed that intensity of mate guarding for nulliparous – pre-ovulatory was significantly lower than that for each of the other three categories (vs nulliparous – ovulatory: p = 0.008; vs parous – pre-ovulatory: p = 0.004; vs parous – ovulatory: p < 0.0001; Figure 2). Differences between other categories were in the directions predicted, but were not statistically significant (nulliparous – ovulatory vs parous – pre-ovulatory: mean difference (low quality minus high quality)= -0.001, p = 0.973; nulliparous – ovulatory vs parous – ovulatory: p = 0.180, mean difference = -0.321; parous – preovulatory vs parous – ovulatory: p = 0.102, mean difference = -0.321; Figure 2).

In contrast to the effects of seasonality and female reproductive quality on intensity of mate guarding, neither male dominance rank nor the estimated number of a male's immature offspring, significantly predicted intensity of mate guarding, Table 1. In addition, female effort, time of sampling, and paternity failed to predict significant variance in the intensity of mate guarding (time of sampling: t = 0.089, p = 0.930; paternity: t = 0.074, p = 0.941; female effort: t = 0.366, p = 0.717).

**Table 1.** Season and female reproductive quality significantly predicted mating effort within mate-guarding episodes; fixed effects (predictor variables) that explained significant variance in mating effort are in bold. Estimate for covariates represents slope and that for categorical variable (i.e. season and female reproductive quality) represents difference in means between the dry and the wet season such that, for season for example, the wet season mean is referenced on the dry season mean.

Fixed effect	Estimate	Std. error	df	t-value	p-value
Season	0.639	0.266	37	2.402	0.022
Female reproductive quality	0.428	0.115	37	3.723	<0.001
Male rank	0.028	0.035	37	0.795	0.432
Number of immature offspring	0.003	0.044	37	0.063	0.950

Figure 1: Intensity of mate guarding was higher during the wet than during the dry season. Intensity of mate guarding was adjusted for male rank, number of a male's immature offspring, and female reproductive quality as fixed effects and focal id nested with group id as a random effect. Number above each bar represents the number of samples in each season



Figure 2: Intensity of mate guarding increased with increasing female reproductive quality. Intensity of mate-guarding presented as residuals obtained after controlling for male rank, number of immature offspring a male had in the group, and seasonality as well as focal id nested within group id differences as the random effect. Number above each bar represents the number of samples in each category of female reproductive quality. See Results for details



# DISCUSSION

Conflict between parental care and mating effort is of particular importance partly because of its role in shaping life history strategies within and between the sexes (Magrath and Komdeur 2003; Stiver and Alonzo 2009). However, a paucity of empirical studies on the extent of trade-offs between parental care and mating effort has addressed this topic for mammalian males. In the present study, we addressed this topic using a predictive model that accounted for energetic constraints deriving from seasonal differences in the amount of rainfall between the dry and wet season, female reproductive quality, male dominance rank, and opportunities for paternal care in a wild population of savanna baboons. Results of the present study demonstrate that season and female reproductive quality predict mating effort within mate-guarding episodes. In contrast, we did not find evidence for the role of male dominance rank or for opportunities for paternal care in explaining variability in mating effort during mate-guarding episodes. Moreover, we ruled out the effects of three potential confounding factors: the behavior of the female consort, time of sampling, and the presence of an immature offspring the focal male may have sired by the female consort partner which might have reduced conflict between caring for that offspring and guarding its mother.

# Seasonality

A defining characteristic of the savanna ecosystem is the pronounced seasonal changes in resource availability (Alberts et al. 2005 and references therein). During the dry season, which is predictable and long in Amboseli, time to process food is long and so is travel distance to food and water (Bronikowski and Altmann 1996; Altmann et al. 2002; Alberts et al. 2005). The resulting energetic stress associated with these seasonal differences may explain the low intensity of mate guarding during the dry season that we have identified in the present study. That is, as food availability declines, the amount of energy that a male can obtain and allocate to both somatic maintenance and to reproduction is also constrained.

In some species food availability also affects the extent of offspring care by both parents such that the relative energetic cost of care to parents declines with increasing food abundance, which in turn relieves pressure on males as well as females and allows them to seek additional mating opportunities (e.g. Dunn and Robertson 1992; Hoi-Leitner et al. 1999). The converse, that low food availability during the dry season may lead to increased investment in offspring care by males, may be a feasible explanation for the seasonal differences in intensity of mate guarding, *ceteris paribus*. We propose to test this hypothesis in a separate study.

Energetic stress can also influence male mating effort indirectly by influencing female body condition (Brockman and van Schaik 2005), which in turn can impact the strength of cues of female reproductive quality such as sex skin swelling size (Nunn 1999). The extent to which our findings could be explained by energetic constraints during the dry season that affected female body condition was beyond the scope of the present study.

# *Female reproductive quality*

Energetic costs associated with mate guarding, and the seasonal differences in food availability that mediate these costs, shape male investment decisions within mateguarding episodes. The results of the present study are thus consistent with the expectation that males should respond to cues of female reproductive quality so as to invest maximally when the probability of successful reproduction is high. In this study, males invested less in guarding nulliparous females, which is not surprising because nulliparity is associated not only with lower conception probability (Dierschke et al. 1974; Altmann 1980; Bulger 1993; Weingrill et al. 2000; Domb and Pagel 2001; Setchell et al. 2002; Gesquiere et al. 2007; Higham et al. 2009), but also with lower survival of the first offspring (Altmann et al. 1988; Cheney et al. 2004; Parga and Lessnau 2005).

#### Male dominance rank and opportunities for parental care

Variability in traits, such as age and body condition, among individuals is central to the study of conflict between paternal care and mating effort (e.g. Ellison, 2003; Magrath and Komdeur 2003; Alonzo 2009). However, in the present study, differences in male competitive ability as measured by dominance rank (Bulger 1993; Weingrill et al. 2000; Alberts et al. 2003, 2006) did not translate into differences in intensity during mate-guarding episodes.

Similarly, opportunity for paternal care as measured by the estimated number of a male's immature offspring did not constrain intensity of mate guarding. These findings suggest that investment in offspring production by male baboons may be a 2-step process. Males compete, first, to access mate-guarding opportunities. Their effort and success in

that competition is based on their fighting ability (Alberts et al. 2003), and the probability that they will engage in that competition in the first place is presumably adjusted for constraints due to other sources of energetic demands such as paternal care. Once a male has gained access to a receptive female, however, and has entered into a consortship, the magnitude of his investment in mating is predicted by energetic constraints and the female's reproductive quality, and not by his fighting ability or the potential demands of paternal care.

Taken together, the results of our study suggest that the energetic constraints typical of semi arid environments shape reproductive behavior of male baboons within mate-guarding episodes in ways that may impact male socio-sexual behavior both within and outside these specific contexts of mating.
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	Number samples per season		Observation	Male age		Male rank		Number immature offspring		
			time							
focal	dry	wet	total	minutes	min	max	min	max	min	max
APO	0	3	3	116	18.51	18.81	10	11	3.05	3.08
ARS	0	1	1	36	11.69	11.69	4	4	0.10	0.10
AYU	2	7	9	336	10.97	11.56	5	6	4.27	4.30
AZI	0	1	1	40	13.74	13.74	6	6	0.23	0.23
BAG	0	3	3	114	14.41	14.72	8	9	1.07	1.08
DAG	1	0	1	40	7.75	7.75	1	1	0.00	0.00
DUB	0	2	2	68	10.49	10.54	6	6	6.26	6.29
EDU	0	1	1	40	14.54	14.54	10	10	0.08	0.08
ELV	1	0	1	40	9.72	9.72	4	4	4.84	4.84
GAB	0	4	4	134	9.32	9.55	5	5	0.00	0.00
GAN	2	5	7	280	12.74	13.37	1	2	7.95	9.93
GYP	1	0	1	40	16.87	16.87	5	5	2.69	2.69
IDI	0	2	2	80	17.57	17.69	8	8	1.34	1.34
JOB	0	7	7	256	9.46	9.89	2	3	0.70	0.91
KAG	0	5	5	194	10.18	10.34	7	7	1.64	1.64
LAX	0	2	2	80	9.82	10.03	2	2	1.09	1.09
LEB	0	2	2	66	10.48	10.88	2	3	1.22	1.24
LOB	0	4	4	160	8.94	9.17	2	2	0.98	1.36
LOG	1	3	4	158	8.45	9.03	3	3	0.38	1.38
LUI	0	1	1	40	11.01	11.01	3	3	0.32	0.32
NIN	1	2	3	102	10.13	10.49	1	1	1.05	1.26
NJU	1	0	1	38	9.93	9.93	9	9	0.00	0.00
OBR	0	3	3	116	13.15	13.44	6	7	0.17	0.20
ОЈU	0	9	9	360	11.47	11.90	2	4	1.77	2.72
ORN	1	0	1	34	14.31	14.31	13	13	0.00	0.00
OTI	0	6	6	230	16.45	16.82	9	11	0.24	0.27
QUA	0	1	1	40	11.46	11.46	7	7	1.12	1.12
RAJ	0	4	4	160	11.23	11.47	4	4	2.11	2.11
TAP	3	3	6	212	9.05	9.63	1	2	0.00	0.27
THR	0	4	4	156	7.85	8.06	1	1	0.00	0.00
TOG	1	7	8	310	10.38	10.89	3	3	2.06	2.06
VEI	0	1	1	26	12.18	12.18	9	9	4.13	4.13
VIB	1	0	1	40	9.10	9.10	6	6	0.01	0.01
VOY	2	0	2	76	10.60	10.61	4	4	8.03	8.03
WRI	0	3	3	96	8.11	8.28	1	3	0.00	0.00
YOB	2	5	7	246	10.07	10.65	3	6	1.16	1.26
ZAN	2	2	4	158	9.20	9.52	11	12	1.03	1.03
ZIB	0	2	2	70	13.48	13.65	4	5	4.80	5.36
ZOR	1	3	4	148	12.43	12.86	4	5	0.39	0.39

**Appendix 1.** List of focal males, number of samples, and distributions of variables across males.

# CHAPTER THREE: Testosterone correlates of paternal care and mating effort in savanna baboons (*Papio cynocephalus*)

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#### ABSTRACT

Testosterone (T) is widely used as a biomarker of reproductive tradeoffs primarily because it is positively associated with sexual behavior and physiology on the one hand and negatively associated with paternal care on the other. However, previous studies on the association between T and the two components of reproductive effort, mating effort and paternal care, have mostly focused on monogamous species or on seasonal breeders. Consequently, there are major gaps in our knowledge of whether T mediates tradeoffs between mating effort and paternal care among non-monogamous males in species that breed throughout the year. In the present study of adult males in a wild population of savannah baboons, we determined whether mating activity and opportunities for paternal care predicted fecal concentrations of T (fT). Mating activity was estimated from the amount of consortship time a male obtained in a given month. Opportunities for paternal care were estimated using the number of immature offspring a male had in the group. Males that had consortships showed higher levels of fT than those that did not, ft increased with the amount of consortship time, decreased with age, and was higher during the wet than during the dry season. In contrast, the number of immature offspring a male had in a group was not significantly correlated with fT. Our findings are consistent with the predicted stimulatory effect of T on mating effort but not with its inhibitory role on paternal care. High fT among high-ranking and young adults, and higher concentrations during the wet than during the dry season suggest that the secretion of T in the polygynandrous male baboon responds to energetic constraints from both a life history and environmental perspective.

#### INTRODUCTION

The antagonism in the reproductive functions of testosterone (T) has led to its wide use as a biomarker in studies of reproductive tradeoffs across many species. On the one hand, T enhances reproductive function including sexual behavior (Wingfield et al. 1990; Dixon 1998; Holekamp & Smale 1998) and spermatogenesis (e.g. Nelson, 2005), yet on the other hand, it inhibits parental investment (Wingfield et al. 1990; Brown et al. 1995; Ketterson & Nolan 1999; Reburn & Wynne-Edwards 1999). As a result, and particularly for monogamous species and or species with seasonal breeding schedules, variation in levels of T has been demonstrated to mediate differential investment between mating effort and parental care (reviewed in Hau 2007). However, major gaps persist in our knowledge of the association between T and reproductive effort and tradeoffs therein among non-monogamous males in species that reproduce throughout the year.

Among primates, studies on humans have taken the lead in the investigation of the role of T in mediating tradeoffs between mating effort and paternal care (e.g. Burnham et al. 2003; van Anders & Watson 2007; Gray et al. 2006; Alvergne et al. 2009). Key findings from these studies are that 1) pair-bonding in the form of co-habitation or marriage, and 2) transition to fatherhood, which among other things presumably signals a shift in the balance of resource allocation between mating and paternal care, are associated with a decline in levels of T. Among cultivation agriculturalists in Senegal, for example, fathers have lower T than non-fathers (Alvergne et al. 2009).

A few studies on non-human primates, predominantly on biparental neotropical species, have also reported results that are largely consistent with the prediction of the role of T in mediating tradeoffs between mating effort and paternal care (e.g. Nunes et al. 2001; Ziegler et al. 2009).

Male savannah baboons (*Papio cynocephalus*), the subjects of the present study, compete for mating opportunities either individually or by forming coalitions with others (Noë & Sluijter 1990). Fights for access to reproductive mates are associated with risks of injuries and sometimes death (Drews 1996; Kitchen et al. 2005). The intensity of male-male competition within each group of baboons and across time may thus depend on the degree of skew in the distribution of mating opportunities among males. Dominance rank in baboons, as is typical of many cercopithecines, strongly predicts the distribution of mating opportunities among males such that high-ranking male savannah baboons have access to disproportionately more mating opportunities (e.g. Bercovitch, 1987; Bulger 1993; Weingrill et al. 2000; Alberts et al. 2003, 2006).

For males that derive fitness benefits from offspring care, paternal care represents a potential constraint on prospects of access to reproductive mates and investment in offspring production. Paternal care among male primates typically involves males intervening favorably on behalf of their offspring during social conflicts (Buchan et al. 2003), carrying their infants (e.g. Itani, 1959), and providing a "safe zone" for immature offspring as well as their mothers (Altmann, 1980; Bales 1980; Smuts 1985; Noë & Sluitjer 1990; Smuts & Gubernick 1992; Borries et al. 1999; Buchan et al. 2003; Nguyen et al. 2009). Proximity and other associative behaviors between particular adult males and females protect both the mother and the infant from stressful interactions such as rough

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handling, kidnapping, and infanticide (Altmann, 1980; Palombit et al. 1997; Kleindorfer & Wasser 2004; Nguyen et al. 2009). Paternal care may account for accelerated maturation in offspring whose fathers are present in the social group during the offspring's juvenile period (Charpentier et al. 2008).

The goal of the present study was to determine whether T is correlated with mating effort and opportunity for paternal care in the polygynous male savannah baboon in a wild population. Specifically, we investigated the extent to which a male's mating activity, and the estimated number of immature offspring a male has in the group predict concentrations of T in adult male baboons. The relationship between hormones and behavior is inherently bidirectional (Almond et al. 2008; Schradin & Anzenberger 2002). In this study, we focus on examining the nature of the relationship between T and mating effort and paternal care in the non-monogamous male savanna baboon.

### **METHODS**

## Study population

Savanna baboons, *Papio cynocephalus*, live in multi-male multi-female societies (Altmann 1980). Males leave their group of birth after reaching reproductive maturity whereas females are philopatric, that is, spend the rest of their life in their natal group (Alberts & Altmann 1995). In baboons, as is characteristic of many cercopithecines, mating occurs mostly in the context of mate-guarding episodes also called consortships. Consortships are characterized by an increase in sexual behavior and activity between an adult male and a female in estrus (Alberts et al. 1996). Consequently, gaining access to a

consortship and maintaining it are strong predictors of mating and ultimately paternity success in baboons (Alberts et al. 2003, 2006). Males thus incur high costs in time and energy during consortships.

The present study was based on data collected over an 8-year period, January 2000 to December 2008. The data included records of demographic, behavioral, ecological, and hormonal concentrations. Because of other data collection constraints and due to the nature of our non-invasive collection of samples for hormonal analysis from fecal samples, hormonal data were not always available for each male during each month for which the male was studied. We averaged a male's hormonal values in each month when a male had multiple hormonal samples. Consequently, we also obtained monthly averages for all the variables used in this study; details of the other variables are provided below.

We studied 127 adult male savanna baboons that are a part of a wild population. Our subjects were distributed among 5 study groups in a population that has been the focus of a longterm study, the Amboseli Baboon Research Project (ABRP). All baboons in the 5 study groups are individually identifiable, and are habituated to human observers.

## Male life history traits: age and dominance rank

We examined the effect of age on the concentration of T among our subjects because T is known to decline with age (e.g. Dabbs 1990; Altmann et al. 2010; Gesquiere et al. 2011). We were able to determine the ages of our study subjects because birth dates of males that were born into study groups were known due to a near-daily visitation of each of the 5 study groups. We estimated ages of immigrant males (those not born into study groups) by comparing their developmental markers to those of individuals with known birth dates (Alberts & Altmann, 1995).

In addition, we examined the extent to which male dominance rank predicted variance in concentrations of T. Dominance rank explains significant variance in the distribution of mating opportunities and ultimately of paternity success among males in our study population (Alberts et al., 2003, 2006). We estimated dominance ranks from within-group dyadic agonistic interactions and assigned rank 1 to the highest-ranking male, rank 2 to the next in rank and so on. Dominance rank for our study subjects ranged from 1 to 18 and were assigned monthly such that each subject had only one rank score during any given month.

## Components of reproductive effort

# Mating effort: consortship activity

Variability in the concentrations of T is associated with mating activity such that T increases at peak mating activity (e.g. Muller & Wrangham 2004) presumably due to sexual activity or to intense male-male competition (Wingfield et al. 1990) during mateguarding episodes. In baboons and other cercopithecine primates, matings occur within the context of mate-guarding episodes called consortships, which are characterized by sexual activity between the pair and intense male-male competition as the consorting male attempts to out-compete rival males for exclusive access to the female partner (reviewed in Manson 1997). We extracted records of consortships from our longterm database. During every visit to a study group, all consortships are identified and data such as the identity of the consort pair and the beginning and ending times (from which we

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obtain duration of the consortship) are collected. These records enabled us to distinguish between males that obtained consortships in any given month from those that did not, and to calculate the amount of consortship time each male obtained in each month. We refer to these two measures as mating effort.

#### Paternal care: number of immature offspring as opportunities for paternal care

Genetic paternity results were available for only 148 of the 448 individuals that were immature during the study; for details on genetic paternity assignments, see Alberts et al. (2006). For the remaining 300 immature individuals we assigned paternity based on the proportion of consortship time a male obtained if consortship observations were available during the 5-day period of likely conception or on dominance rank of each male and the number of adult males present when the offspring was conceived. We assigned partial paternities for cases where mating records did not clearly identify a single father. This method of paternity assignment has previously been shown to match paternity assignment by molecular techniques in our study population (Altmann et al. 1996). The procedures we used to assign paternity based on mating records, male dominance rank and the number of adult males in the group is summarized by the equation below:

{ $(pCt \times Ct \max 300 \div 300) + [(RankAdultmalegroupsizeestimate) \times (1 - (Ct \max 300 \div 300)]}$ 

where

pCt = proportion of observed consortship time a male obtained;

Ct = observed consortship time, maximum value of which is set at 300 min or 5hrs; RankAdultmalegroupsizeestimate = paternity based on proportion of dominance rank and adult male group size

#### Seasonality of rainfall and variability in temperature

We examined the effect of seasonality in rainfall and variability in temperature because these two environmental factors have been shown to influence the secretion of T across many species of vertebrates (e.g. Smith et al., 1975; Cameron et al., 1993; Wahab et al., 2008; Gesquiere et al., 2010; Lynn et al., 2010). In Amboseli, seasonal differences in amount of rainfall strongly predict food availability, both in quantity and quality, (Alberts et al. 2005) such that individuals have a wide choice of foods during the wet season but resort to the so-called fall-back foods during the dry season (Alberts et al., 2005). Fallback foods are difficult to process and so animals spend more time foraging but less time resting time during the dry season. In addition, animals have to travel longer distances between foods resources, shade, or water during the dry season than they do during the wet season.

Annual precipitation in Amboseli averages 348mm but is highly variable from year to year, ranging from 150mm to 550mm (Altmann et al. 2002). However, rains predictably occur from November to end of April or May and as a result this period is wetter than the rest of the year (Alberts et al. 2005). The rest of the year, that is the months of June though October is characterized by a long dry season that is devoid of rain. In order to examine the effect of season on levels of T, we divided the study period into a dry and wet season as September to October and November to April respectively.

We have recently shown that concentration of T is higher during months with high temperatures than during months of low temperatures (Gesquiere et al. 2011). Consequently, we distinguished months as either cool or hot using the criterion

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established by Gesquiere et al. (2011) such that months with average daily maximum temperature lower than a cut-off of 34.5° C were categorized as cool, and those above the cut-off as hot.

#### Fecal sample collection, processing, and testosterone assays

We determined concentration of testosterone from 4552 fecal samples (the number of fecal samples per male was variable, ranging from 1 to 134). Fecal samples are routinely collected as part of the longterm project; methods for fecal sample collection, preservation, and processing have previously been validated (Khan et al. 2002; detailed protocol available at http://www.princeton.edu/~altlab/AltmannHormoneLabProtocols. Each fecal sample was collected a few minutes following observed defecation by a known individual. It was then thoroughly mixed after collection and preserved in vials pre-filled with 95% ethanol. At the end of each data collection day, fecal samples were stored in a charcoal fridge with a daily maximum temperature range of 20 to 25°C for a maximum of two weeks before they were sent to the University of Nairobi, where the ethanol was evaporated and the samples were freeze-dried. Freeze-dried samples were sifted, weighed to control for dietary differences across seasons and between individuals (Wasser et al., 1993), and steroids were extracted using methanol and subsequently using a solid phase extraction technique for further purification; and then kept in a freezer at -20°C until assay. Concentration of fT was determined as described in Gesquiere et al. (2011). In brief, we used the Equate <sup>125</sup>I Testosterone RIA kit (SolidPhase, Portland, ME) beginning 2000 until its production was discontinued in 2004. As a result, we switched to another commercial kit from Diagnostics Systems Laboratories (DSL) 1251 Testosterone, Beckman Coulter, Webster, TX. These two kits were previously validated for use in our study population (Equate: Lynch et al. 2003; DSL: Beehner et al. 2009). A comparison of fT levels from the two kits using a subset of samples showed a high correlation ( $R^2$ = 0.906, n = 124, p <0.001) in fT concentrations; this enabled us to adjust, using the equation  $T_{DSL} = 1.9676*T_{Equate}+16.9926$ , fT levels from the Equate kit so that samples obtained from the two tests could be pooled together and used in the same analysis (Gesquiere et al. 2011). We expressed levels of fT as ng/g dry feces. When a male had multiple fT samples in a given month, we obtained his average fT concentration for that month such that each male had one fT value for that month.

All methods and assay protocols were conducted in accordance with the requirements of scientific research by the Government of Kenya (Research Permit (MOEST 13/001/C351 Vol. II) and by Princeton University (IACUC 1547).

## Data analysis

For each month for which at least one hormonal sample was available for a male, we matched his average monthly level of fT to his consortship activity and the estimated number of immature offspring he had in the group that month. We also included in our analysis, measures of the four potentially confounding factors during that month: age, dominance rank, season, and average maximum daily temperature; for a total of six predictor variables. Our response variable was concentrations of fT, which were logtransformed to achieve normality. We used a mixed-effects model to determine the extent to which consortship activity and estimated number of immature offspring predicted variance in the concentrations of fT. We also included the four potentially confounding factors (age, dominance rank, season, and temperature) as fixed-effects. Finally, we nested the subject identity within group in the random effects structure. We fitted two separate models: in the first, we expressed mating effort as whether a male obtained consortships or not, and in the second, we expressed it as the amount of consortship time a male obtained in each month. Model fitting and evaluation was based on Akaike information criteria (AIC) and by elimination of insignificant terms (Pinheiro & Bates, 2000). All statistical tests were performed in R 2.9.2; statistical significance was set at 0.05.

# RESULTS

Table 1 summarizes results of the mixed-effect model. Both measures of mating effort were significantly correlated with fT: males that obtained consortships in a given month experienced higher fT than those that did not (t = 3.539, p = 0.0004), Fig. 1; furthermore, fT also increased significantly with the amount of consortship time that a male obtained (t = 3.433, p = 0.0006; analysis were performed separately for each measure of mating effort but the two models were not significantly different, AIC - 457.969 for binary mating effort vs -457.222 for continuous mating effort; consequently, tables and figures present only the results of the model using mating effort as binary variable). In contrast to the significant relationship between mating effort and fT, the

number of immature offspring a male had in the group was not significantly correlated with fT (t = 1.627, p = 0.1039).

Age of adult males was negatively correlated with fT such that young adults had higher concentrations than did old ones. Similarly, dominance rank also explained significant variance in fT such that high-ranking males had higher fT than did lowranking males. Although age and rank are correlated in our study population, the results reported for each are marginal, that is conditional on the other; further the results are consistent with predicted relationship between T on the one hand and age and dominance rank on the other.

We also found significant seasonal effects such that fT levels were higher during the wet than during the dry season (t= 8.048, p < 0.0001). Due to the strong seasonal effect, we conducted subsequent analyses to determine whether variability in fT was explained by mating effort, age, dominance rank, and temperature within each season treated separately. Results of these analyses, with mating effort as a binary variable, are summarized in Table 2. Analyses of the partitioned datasets showed that during the wet season, variance in fT due to the various predictor variables was generally similar to those from the entire dataset as summarized in Table 1. However, during the dry season, only age (t = -4.218, p < 0.0001) and temperature (t = 4.497, p < 0.0001) explained significant variance in fT. We found similar trends with mating effort as a continuous variable (wet season: t = 3.354, p = 0.0008; dry season: t = 0.480, p = 0.6313). Fig. 2 shows within-season differences in fT between males that obtained consortships in any given month and those that did not. Table 1: Amount of consort time, age, dominance rank, and season but not the number of immature offspring or temperature, predicted significant differences in fT. Estimate for covariates represents slope and that for categorical variable (i.e. season) represents difference in means between the dry and the wet season using the dry season mean as the reference.

Variable	Estimate	std. error	df	t-value	p-value
Intercept	2.334	0.042	2413	55.912	< 0.0001
Amount of consort time	0.031	0.009	2413	3.539	0.0004
Number of immature offspring	0.005	0.003	2413	1.605	0.1087
Age	-0.027	0.004	2413	-7.676	< 0.0001
Dominance rank	-0.008	0.002	2413	-3.459	0.0006
Season	0.069	0.009	2413	7.910	< 0.0001
Temperature	-0.014	0.011	2413	-1.270	0.2041

Table 2: Patterns of fT concentrations between the dry and wet season. Dry season values are in bold. Estimate for covariates represents slope and that for categorical variable (i.e. season) represents difference in means between the dry and the wet season using the dry season mean as the reference.

Variable	estimate	std. error	df	t-value	p-value
Intercept	2.155	0.059	896	36.629	<0.0001
_	2.459	0.049	1375	49.932	<0.0001
Amount of consort time	0.009	0.013	896	0.705	0.4811
	0.039	0.012	1375	3.246	0.0012
Number of immature offspring	0.006	0.004	896	1.455	0.1461
	-0.000	0.004	1375	-0.163	0.8708
Age	-0.020	0.005	896	-4.218	<0.0001
	-0.022	0.004	1375	-4.974	<0.0001
Dominance rank	-0.004	0.003	896	-1.201	0.2302
	-0.013	0.003	1375	-4.498	<0.0001
Temperature	0.122	0.027	896	4.497	<0.0001
	-0.037	0.012	1375	-3.008	0.0027

Figure 1: The average concentration of fT was lower among males that did not consort than among those that consorted.



Figure 2: Average fT concentration was lower during dry than during the wet season and among males that did not consort than among those that consorted.



Season and mating effort

#### DISCUSSION

In the present study, we have demonstrated that T is positively correlated with mating effort in male savannah baboons, which are polygynandrous and reproduce throughout the year. High T in males presumably facilitates mating activity (e.g. Hegner & Wingfield 1987; Brown et al. 1995; Ketterson & Nolan 1999; Reburn & Wynne-Edwards 1999). The positive correlation between fT and mating effort that we have reported here can arise from a suite of male competitive behaviors that enhance access to reproductive mates (Wingfield et al. 1990; Goymann et al. 2003; Goymann & Wingfield 2004; Muller & Wrangham 2004). Males in consortships not only display high levels of aggressive behavior, they are also recipients of such behaviors as they try to keep rival males from the female consort (Bercovitch 1983; Alberts et al. 1996). The results also suggest that male baboons do not maintain chronically elevated levels of T but instead experience increases in its concentrations when they are engaged in consortships. This apparent functional modulation of T such that T increases when opportunities of offspring production are highest is consistent with the 'challenge hypothesis', which suggests that T increases are associated with reproductive opportunities (Wingfield et al. 1990). Furthermore, in a population where reproduction occurs throughout the year, matching secretion of T to periods of reproductive opportunities may may be beneficial in two ways. First, it may facilitate access to reproductive opportunities, to the extent that T enhances male-male competition. Second, it may enable males to avoid the costs of maintaining chronically elevated levels of T (Folstad & Karter 1992; Wingfield et al. 2001).

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Recent findings from our study population have demonstrated that males care for their offspring and derive fitness benefits from doing so. Buchan et al. (2003) showed that fathers intervened favorably, during agonistic conflicts, on behalf of their immature offspring; furthermore, Charpentier et al. (2008) found that a father's presence during his offspring's juvenile period accelerated maturation among daughters regardless of the father's dominance rank and also his son's maturation if the father was high-ranking. Consequently, the absence of a significant correlation between opportunities for paternal care and fT in the present study is surprising. Given that male baboons in our study population provide care to their offspring, why is that care not reflected in the concentrations of fT in males?

The absence of a significant negative correlation between fT and opportunity for paternal care can be attributed to several factors. Two of these include, first, a potential decoupling of ways in which paternal care behavior is expressed from mechanisms responsible for the secretion of T (Wingfield et al. 2001; Hau 2007). Second, although it has been demonstrated that males in our study population care for the offspring (Buchan et al. 2003), immatures in the population don't face high risks from conspecifics thus contrasting sharply with populations where infants face high risks from infanticide (e.g. in chacma baboons: Palombit et al. 1997). In other words, in the absence of acute risks to immatures beyond dominance-based psychosocial stress (Onyango et al. 2008), selection should favor dissociation between behavioral mechanisms for paternal care and neuroendocrinological circuitry for the secretion of T in male baboons.

Declining T concentrations as males advance in age is consistent with findings from other primates including humans (reviewed in Kaufman & Vermeulen 2005) and has been demonstrated for the Amboseli baboons and other closely related taxa (Beehner et al. 2009; Altmann et al. 2010; Gesquiere et al. 2011). This gerontological pattern is thought to arise from diminished testicular capacity to secrete T and changes in how it is bound both in plasma as well as in end tissues (reviewed in Kaufman & Vermeulen, 2005). High T concentrations among high ranking males is not surprising in a species such as the savanna baboon where dominance rank is acquired and maintained by overt aggression and this pattern has been documented in other primates (e.g. ring-tailed lemur: Cavigelli & Pereira 2000; sifaka: Brockman et al. 2001; chimpanzees: Muller & Wrangham 2004; chacma baboons: Bergman et al. 2006).

High concentrations of fT during the wet season may arise from increased malemale competition for access to reproductive mates, whose number slightly increases during the wet season despite the lack of a pronounced breeding seasonality in our study population. Alternatively, it may be attributed to the fact that females are more likely to conceive and carry pregnancy to term during the wet season than they are during the dry season (Beehner et al. 2006a,b). In addition, and to the extent that chronically elevated levels of T is costly to males (Wingfield et al. 2001), increased food availability during the wet season may enhance recuperation such that the costs of maintaining high T are expectably lower during the wet season due to low energetic constraint during the wet season (reviewed in Magrath & Komdeur 2003).

In conclusion, the present study has shown that mating effort is positively correlated with concentrations of fecal T metabolites. In contrast, the study did not find a significant correlation between T and opportunities for paternal care. The strong age,

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dominance rank, and seasonal effects on fT suggest a role for both intrinsic and extrinsic energetic constraints on the secretion of T in male baboons.

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# CHAPTER FOUR: Male dispersal decisions: mating success, opportunities for paternal case, age, and dominance rank in savanna baboons

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# ABSTRACT

The association of adult males with permanent female groups, which is common among many non-human primates, is surprising from a strictly mating perspective. Male decisions to disperse from one group to another are subject to several factors such as inbreeding pressure, competition for mates and for ecological resources, and increased risks of mortality during transfer. When males derive fitness from care of their offspring, paternal care may influence male dispersal decisions. In the present study, we used a 13year dataset to test the hypothesis that opportunities for paternal care, which we measured as the number of immature offspring a male had in the group, predict dispersal decisions in 156 male savanna baboons distributed in 8 groups. We considered each month as a potential dispersal opportunity and conducted our investigation of the probability of dispersal within the context of reproductive tradeoffs by weighing a male's opportunities for paternal care against his mating success during the prior three months. We also controlled for male age and dominance rank, which are known to influence male dispersal decisions. The marginal probability to disperse was low among males experiencing high mating success, among older males, and among high-ranking males. However, opportunity for paternal care did not influence male dispersal decisions. Together, these results demonstrate that male dispersal decisions, thus the association between males and permanent female groups, are influenced by several factors.

# **INTRODUCTION**

The permanent association between non-monogamous males with permanent female groups that is a common phenomenon among cercopithecine primates is surprising from a strictly mating perspective. Indeed, the slow life histories and the highly predictable reproductive schedules of female primates makes it possible for males to track the distribution of fertile females (Kappeler & van Schaik 2002; Pereira et al. 2000). As a result, at least theoretically, and in the absence of fertile females in their present group, males are predicted to maximize paternity success by deserting females after fertilization to seek mating opportunities in other groups (Wrangham 1980; Clutton-Brock & Parker 1992; Dunbar 2000). However, when males accrue fitness benefits from offspring care, it can be expected that paternal care potentially influences male reproductive decisions including dispersal.

Decisions to disperse from one group to another are under push and pull forces. Push forces include inbreeding avoidance and competition for both reproductive mates and ecological resources (reviewed in Greenwood 1980; Johnson & Gaines 1990; Handley & Perrin 2007), whereas pull forces include high mortality and lost reproductive opportunities that males experience during dispersal (Johnson & Gaines 1990; Isbell et al. 1993; Alberts & Altmann 1995a).

Emerging evidence show that males in some non-monogamous primate species not only care for their offspring but that they also derive fitness benefits in the form of improved offspring quality and survival. Paternal care in male primates is expressed through behaviors such as active displacements of other males (Borries et al. 1999), carrying (Anderson 1992), or favorable intervention on behalf of their offspring during
agonistic interactions (Buchan et al. 2003). Offspring care is known to benefit the offspring through increased quality and survival (Anderson 1992; Charpentier et al. 2008). For example, co-residency of baboon fathers and their offspring during the offspring's juvenile period was associated with accelerated maturation in savanna baboons (Charpentier et al. 2008). Strategies to maximize offspring quality and survival have also been shown in species with female-biased dispersal such as langurs. Female langurs migrate to groups with younger adult males presumably to seek protection for their offspring from infanticidal males (Sterk et al. 1997; Borries et al. 1999). Consequently, for males that derive fitness benefits such as improved offspring quality and survival, opportunities for care may influence decisions to disperse.

A male's capacity to navigate risks associated with dispersal and his prospects in gaining access to fertile females in the new group may also influence his dispersal decisions. Across species, successful transfer and access to reproductive opportunities in the new group is strongly influenced by body condition (e.g. Clarke et al. 2008). As a result, patterns of dispersal may also change during a male's reproductive career, and such changes may also depend on distribution of reproductive opportunities. For example, males are known to disperse to groups with fewer competitors but to those with more fertile females than those in their present group (Packer 1979; Alberts & Altmann 1995a; Altmann, 1990, 2000; Dunbar 2000; Stoinski et al. 2009).

Here, we investigate whether the number of a male's immature offspring, indicative of his opportunities for paternal care, predicts male dispersal decisions in a wild population of savanna baboons, *Papio cynocephalus*. We conducted our investigation in a broader context of reproductive tradeoffs and thereby integrated other factors known to influence such tradeoffs. These factors include a male's recent reproductive success and his opportunities for paternal care. Finally, we also examined the effect of individual differences in male traits such as age and dominance rank.

## METHODS

We collated data used in the present study from our longterm database, Amboseli Baboon Research Project. The data included demographic variables, genetic paternity assignments, and records of mating histories collected over a 13year period, from 1996 through 2008. In baboons, dispersal from the natal group occurs when males are about 8.5 years old (Alberts & Altmann 1995b). Subsequent transfers, also called secondary or breeding dispersals, may follow and the frequency of these transfers is predicted by the distribution of mating opportunities (Alberts & Altmann 1995b). For example, males with low reproductive success in their present group are more likely to transfer; on average, males also transfer from groups with low number of reproductive females (Altmann 1990; Alberts & Altmann 1995a). Our study subjects included 156 individually known adult males in a total of 8 groups, some resulting from fission events that occurred during the study period.

#### **Predictors of dispersal**

#### **Opportunities for paternal care: the number of immature offspring**

We used the number of a male's living immature offspring in the group as a measure of his opportunity for paternal care. There were a total of 546 immatures over the 13-year period, and genetic paternity assignment was available for 227, see Altberts et al. 2006 for details on genetic paternity assignment. Paternity estimates for the 319 immatures for which genetic paternity results were not available was assigned based on a combination of mating behavior, male dominance rank, and the number of adult males in the group at the time of conception of each immature. Briefly, in the absence of genetic paternity assignments for all immatures, we took advantage of other available data to assign paternity. These data included information on mating history and prevailing group demography at the time each of the immatures for which genetic paternity assignment was not available for was conceived. Previous findings from our study population have demonstrated a strong match between behavioral and genetic paternity assignments (Altmann et al. 1996). Behavioral paternity assignments were estimated from the amount of consortship time a male obtained during the period of likely conception. When no consorts were observed, we based estimates of paternity on each adult male's dominance rank weighted by the number of adult males present in the group during the period when each immature was conceived. We assigned multiple paternities for when assignments could not identify a single clear father. The procedures we used to assign paternity in this way are summarized by the equation below.

{ $(pCt \times Ct \max 300 \div 300) + [(RankAdultmalegroupsizeestimate) \times (1 - (Ct \max 300 \div 300)]}$ 

where

pCt = proportion of observed consortship time a male obtained;

Ct = observed consortship time, maximum value of which is set at 300 min or 5hrs;

RankAdultmalegroupsizeestimate = dominance rank and adult male group size paternity

proportion

## **Recent mating history**

We quantified mating success from consortship activity, episodes of mate-guarding that strongly predict paternity success in many cercopithecines including savanna baboons in our study population (Altmann et al. 1996; Alberts & Altmann 1995a). Data on consortships are routinely collected as part of the longterm project. For each consortship, data on id of the male and female, and on the duration of the consortship are recorded. We used these records to determine whether a male obtained any consortships in a given month, and if he did, how much consortship time he obtained. We used these two measures, collected over 90 days prior to the month of dispersal, to represent male mating success. Differences in how long each group is studied over any given period of time will obviously account for variability in the amount of consort time among males across groups. We therefore adjusted consort time for the amount of time each group was studied during the 90 days prior to the month of dispersal.

### Age and dominance rank

We examined the effect of age on male dispersal decisions because of changing opportunities that may derive in part from the male's changing somatic capacity that may influence his success to competitively access reproductive mates or to overcome the rigors of dispersal. In addition, injuries incurred during male-male competition for reproductive mates may also hasten decline in a male's somatic capacity during his reproductive career. In our study population, for example, older males have a higher degree of body scarring and canines in poor condition than younger adults (Alberts & Altmann 1995b). Ages of males that were born into study groups were known to within several days because each study group is studied at least once, and usually several days, per week. We estimated ages of immigrant males by visually comparing their traits including size and other measures of physical condition such as coat condition, body scarring, and the state of their canines to those of males of known age (Alberts & Altmann, 1995b); the ages of subjects ranged from 5.6 to 21.7 years.

We also examined the extent to which male dominance rank predicted whether males transferred from one group to another because dominance predicts the distribution of mating opportunities in our study population (Alberts et a. 2003, 2006). We scored dominance ranks from records of agonisms between males (Hausfater 1975); assigning a 101 rank score of 1 to the highest-ranking individual, 2 to the second one, and so on. These rank assignments are done every month.

## Determining male dispersal

For each month, we examined census records to determine which males dispersed and which did not. A census of all group members is conducted during each visit to a study group. Males that dispersed received a score of 1 and those that did not a score of 0. We defined this qualitative variable as a dispersal event. In other words, we considered each month as an opportunity to stay or to disperse. In order to determine whether a male's number of immature offspring, indicative of his opportunities for paternal care, mating success, age, and dominance rank predicted male transfer decisions, we examined the nature of these four variables during 90 days preceding each month during the 13 years. We obtained each male's average age and dominance rank during the 90 preceding dispersal.

Finally, we controlled for differences in access to reproductive mates between the highest-ranking male and those of other ranks (Alberts et al. 2003) by restricting our dataset to group-months for which at least one consortship occurred during the prior 90 days. This way, we did not overestimate the probability to obtain consortships among low-ranking males: although a low-ranking male is less likely to obtain a consortship when there are few receptive females, they would also obtain none when there are no receptive females in the group, these two phenomena may be very different for male decision-making and might be confounded in an analysis using all months. As a result of

working with this reduced dataset, our final sample size was 5406 male-months and 221 dispersal events.

### Data analysis

We used mixed-effects models to determine whether the number of a male's immature offspring predicted whether a male dispersed. We entered the estimated number of a male's immature offspring, his age and dominance rank, and mating effort as fixed effects; group and individual id as random effects. Dispersal event was the response variable, and the model was fitted with binomial errors. Model parsimony was based on comparisons of Akaike information criteria (AIC), and statistical significance set at the 0.05 threshold was evaluated using Markov chain Monte Carlo (MCMC) simulation of the posterior distribution (Baayen et al. 2008). These tests were performed in R version 2.6.2 using the lme4 and languageR packages.

# RESULTS

Results of the mixed model using mating effort as the amount of consort time a male obtained are summarized in Table 1; the model with mating effort as a binary variable, between males that obtained some consortship and those that did not also produced similar results. The number of a male's immature offspring did not predict probability of dispersal, (p= 0.4017), Table 1). In contrast, probability of dispersal decreased with increase in the amount of consortship time a male obtained during three months prior to

the month in which they dispersed. Raw mean consort time (min/hr) was  $5.016\pm0.080$  among those who stayed vs  $2.274\pm0.245$  among those who dispersed, Figure 1. Males that obtained at least one consortship were also less likely to disperse (p < 0.0001). In addition, the probability of dispersal significantly decreased with male age (p<0.0001); the raw average age of males who stayed was  $12.105\pm0.043$  compared to  $11.763\pm0.218$  among those who dispersed, Figure 2. Lastly, high-ranking males were less likely to disperse than their low-ranking counterparts, mean dominance rank among males who stayed was  $5.273\pm0.048$  and  $6.901\pm0.262$  respectively, Figure 3.

Table 1: Probability to disperse was low among males experiencing high mating success, among older males, and among low-ranking males. HPD = Bayesian highest posterior density, at 95 confidence interval; pt-statistic is the p value associated with the marginal or conditional hypothesis testing (Pinheiro & Bates 2000; Baayen et al. 2008). Estimate for covariates represents slope.

Predictor variable	Estimate	MCMC	HPD95	HDP95	рМСМС	pt-
		mean	lower	upper		statistic
Intercept	0.122	0.116	0.076	0.157	0.004	<0.0001
Number of immature	-0.001	-0.002	-0.005	0.001	0.2816	0.4017
offspring						
Mating effort	-0.002	-0.022	-0.003	-0.001	0.0001	<0.0001
Age	-0.008	-0.008	-0.011	-0.005	0.0001	<0.0001
Dominance rank	0.010	0.010	0.0076	0.012	0.0001	<0.0001

Figure 1: Males experiencing low mating success (min/hr  $\pm$  standard error) are more likely to disperse. Mating success represented as consort time (min) in minutes adjusted for how long (hr) each group was studied over the 90 days preceding the month of dispersal.



13.0 12.5 12.0 12.0 11.5 11.5 11.0 **Stayed** dispersed

Figure 2: Older males are less likely to disperse than younger ones, (mean age, years  $\pm$  standard error).

Figure 3: High-ranking males are less likely to disperse, (mean rank  $\pm$  standard error). Note that high-ranking males have low rank scores and vice versa.



### DISCUSSION

Male baboons, as is typical of males of many non-monogamous primates, are found in association with permanent female groups even during times when opportunities for mating are limited. In the absence of mating opportunities, these prolonged associations have been explained in terms of ecological constraints such as predation pressure (Isbell et al. 1993; Alberts & Altmann 1995a) and social ones such as risks of infanticide to a male's offspring (reviewed in Janson 2000). In this study, we investigated whether opportunities for paternal care influence male dispersal decisions.

In the present study, opportunities for paternal care did not influence male dispersal decision in male baboons. Although baboon fathers derive fitness benefits by protecting their immature offspring from sources of psychosocial stress resulting from conflicts with conspecifics (Altmann 1980; Buchan et al. 2003; Nguyen et al. 2009; Onyango et al. 2008), the intricate matrilineal system in this species and population may buffer immatures from social stressors thereby limiting the father's role in offspring survival. Furthermore, the tight link between gerontological patterns and reproductive success (Alberts et al. 2003, 2006) and individual differences therein make it difficult to disentangle the role of opportunities for paternal care in male dispersal decisions at a population level. Comparative studies in populations or closely related species with high incidence of infanticide, such as chacma baboons (Palombit et al. 1997), langurs (Sterck 1997; Borries et al. 1999), and geladas (Beehner & Bergman 2008), are needed to provide insights on the nature of paternal care in male dispersal decisions.

Our results suggesting that males experiencing low mating success in their present group were more likely to disperse are consistent with predictions of male dispersal

decisions across many species (e.g. patas monkeys: Harding & Olson 1986; samango monkeys: Henzi & Lawes 1987; baboons: Rasmussen 1979; Altmann et al. 1988; Alberts & Altmann 1995a; Clarke et al. 2008; macaques: van Noordwijk & van Schaik 2001; spotted hyena: Höner et al. 2007). Similarly, our results documenting that high-ranking males were less likely to disperse than low-ranking males are also consistent with previous findings from our study population (Alberts & Altmann 1995a). This is not surprising because dominance is a strong predictor of the distribution of mating opportunities and ultimately paternity success among male baboons (Alberts et al. 2003, 2006).

Changes in reproductive opportunities during a male's reproductive career may explain the effect of age on male dispersal decisions suggested by our results. First, the low probability to disperse among older males may arise if females prefer them as reproductive mates. Female spotted hyenas, for example have been shown to prefer older males (Höner et al. 2007). Second, for older males that face limited opportunities to access reproductive mates on their own, opportunities to form coalitions, as a mating tactic (Bercovitch, 1988; Silk 1994; Noë & Sluitjer 1990), may also entice older males to stay. Third, given the general correlation between age and body condition, older males may be at a substantial disadvantage to overcome challenges such as high predation risk during dispersal (Isbell et al. 1993). In addition, older males may not endure increased conspecific aggression because dispersers across many taxa are known to experience increased aggression from conspecifics in the new group (Ydenberg et al. 1988).

Among younger adults, in contrast, a combination of factors including capacity to endure the risks associated with dispersal (e.g. Clarke et al. 2008) may explain the high

probability to disperse. In addition, although 50% of males reproduce in their natal group, natal males may be under a strong pressure from inbreeding avoidance (Greenwood 1980; Johnson & Gaines 1990; Alberts & Altmann 1995a; Handley & Perrin 2007) either singly or in combination with the absence of opportunities for paternal care.

In conclusion, the combination of mating success, age, and dominance influence male dispersal decisions in ways that may involve within and between sex interaction in reproductive strategies and opportunities. These results have important implications for studies of behavioral ecology and draw attention to the need for a more integrative model of primate socioecology.

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#### **GENERAL DISCUSSION**

Theory predicts that males in multi-male multi-female societies maximize their fitness by mating with as many females as possible (Bateman 1948). In mammals, paternal care is rarely observed due in part to limited opportunities for males to offer valuable care in the presence of internal gestation and lactation (Clutton-Brock 1989; Trivers 1972). In addition, low paternity certainty associated with many polygynandrous mating systems (Swedell & Saunders 2006) may reduce a male's ability to discriminate his offspring and thus to provide discriminate care. Nonetheless, paternal care has been observed in primates more commonly than in other mammalian groups (Borries et al. 1999; Buchan et al. 2003; Charpentier et al. 2008). Where offspring recognition occurs and paternal care benefits the offspring, the extent to which intensity of paternal care may limit a male's chances to simultaneously access mating opportunities and thus produce additional offspring remains largely unknown for mammalian males in non-monogamous mating systems.

Paternal care is expected to evolve when it confers fitness benefits to fathers (Woodroffe & Vincent 1994). In order to realize such benefits, fathers must also have the capacity to recognize their own offspring (Trivers 1985; Queller 1997). Recent evidence from our study population (Buchan et al. 2003; Charpentier et al. 2008) and from other cercopithecine primates (Borries et al. 1999) suggests that fathers in these species care for their offspring and improve their fitness by doing so (Charpentier et al. 2008).

## Per capita paternal care, mating effort, and body condition

In this study, I have demonstrated that male baboons provide care to their offspring. This result is consistent with previous findings from the same population (Buchan et al. 2003; Charpentier et al. 2008). However, the results of my study extend the previous findings in suggesting that paternal care in the polygynous male savanna baboon is on a per capita basis, Chapter 1. Specifically, I have documented that the proportion of time a male spent in proximity to immatures and females with young increased with the number of immature offspring a male had in the group; suggesting that the number of a male's immature offspring is indicative of his opportunities for paternal care.

# Resolution of conflict between mating effort and paternal care in savanna baboons

The apparent incremental, per capita, care of offspring may influence a male's investment in offspring production. However, I did not find evidence in support of a tradeoff between paternal care and mating effort, Chapter 1. As expected, my study showed that high-ranking males were more likely to gain access to fertile females and also spent more time in consortships than low-ranking females. These results, discussed in Chapter 1, are not surprising, per se, indeed they are consistent with previous findings demonstrating that dominance rank predicts the partitioning of mating opportunities and ultimately paternity among males in many species (reviewed in Ellis 1995) including baboons (Bulger 1993; Alberts et al. 2003, 2006).

However, an apparent paradox emerges when our results on the relationships between the number of immature offspring and paternal care and male dominance rank

and mating effort are taken together. Thus the puzzle. I found that young adult males had higher mating success than older males across all ranks, which suggests that young highranking males presumably in good body condition have the somatic capacity to invest in offspring production without constraining their investment in the care of offspring. In other words, results of the present study suggest that body condition may mediate the resolution of conflict between mating effort and paternal care in male baboons. Young adult male baboons may be able to successfully compete mating opportunities while remaining vigilant on the locations of their offspring.

### Energetic constraints and female reproductive quality pattern mating effort

The specific context of mate guarding in baboons enabled me to determine the extent to which opportunities for paternal care may constrain mating effort at a fine scale. My study demonstrated that during consortships, mating effort was a function of both how much resources are available to a male and of the female consort's reproductive quality. In contrast, a male's opportunities for paternal care, his age and dominance rank did not explain significant differences in intensity of mate guarding, Chapter 2. Two key and interesting ideas emerge from these results. First, the results suggest a role for energetic constraints on mating effort during consortship. Second, the fact that characteristics of the male such as his dominance rank and opportunities for paternal care did not account for significant differences in mating effort during consortship suggest a possible role for an interaction between male and female reproductive strategies. Although the role of female behavioral strategies was beyond the scope of this study, females play important role in maintaining a consortship (Bercovitch 1995).

#### **Evolutionary dissociation between reproductive behavior and testosterone**

My results demonstrated a strong positive correlation between mating effort and fecal concentrations of testosterone, which is consistent with the stimulatory effect of T on mating or sexual behavior and activity, Chapter 3. The results also demonstrated a gerontological pattern in T such that concentrations declined with male age during adulthood. Such a pattern is consistent with previous findings from the study population (Altmann et al. 2010; Gesquiere et al. 2011). Furthermore, I found that T concentrations during the wet season were higher than those during the dry season. This suggests that energetic constraints may impact male reproduction as it does in females across many primate species including humans (Bronson 1995; Brockmann et al. 1998; Strier et al. 2001; Lynch et al. 2002; Bales et a. 2006; Gesquiere et al. 2008).

In evolutionary terms, however, the absence of a significant relationship between T and opportunities for paternal care suggest an interesting pattern. Alongside increasing focus on the role of T in mediating reproductive tradeoffs is the question of covariation between T and reproductive behavior. Interest in this question focuses primarily on whether the physiological pathways responsible for the secretion of T have evolved in concert with or decoupled from those responsible for the expression of reproductive behavior (reviewed in Hau, 2007). A potential constraint on the coevolution of T and reproductive behavior is the fact that chronically elevated levels of T are associated with increased mortality, reduced fat stores, and suppressed immune system (Wingfield et al. 2001). Among non-seasonal breeders, such as the study population, these costs would be

particularly exacerbated among males that pursue a strategy that primarily focuses on offspring production.

Potential decoupling of T and reproductive behavior may explain the lack of significant covariation between T and opportunities for paternal care. To this extent, therefore, our results contrast findings that have reported quick male response to social cues (e.g. common marmoset: Ziegler et al., 2009; California mouse: Becker et al. 2010).

#### Cost-benefit analysis of male dispersal decisions

The phenomenon of sex-biased dispersal offers, perhaps, the ultimate test of the nature and extent of tradeoffs between mating effort and paternal care. To what extent do opportunities for paternal care influence male dispersal?

Results of this study, detailed in Chapter 4, showed, not surprisingly, that males experiencing low mating success are more likely to disperse, which is consistent with previous findings from the study population (Altmann et al. 1988; Alberts & Altmann 1995). In addition, I showed that older males who are presumably at a great disadvantage to disperse due to increased risk of predation (Isbell 1993) and the rigors of dispersal per se were less likely to disperse than younger adults. Taken together, these results suggest that dispersal decisions in male baboons are influenced by a number of factors whose nature and combination potentially change during a male's reproductive career. The combination of such factors, and a possible role for within and between sex interactions, make it difficult to disentangle any tradeoffs between mating effort and paternal care at the population level.

# Implications

A fundamental concept, and the basis of many empirical and theoretical studies, in behavioral ecology is the socioecological model. In its basic form, it postulates that the distribution of females follows the distribution of ecological resources whereas the distribution of males follows that of females (Wrangham 1980). The basic idea here is that ecological resources limit fitness among females whereas females are the limiting resource for males (Wrangham 1980). In many species of non-human primates, however, the ecological model has not been adequate in explaining the longterm association between adult males and permanent female groups. These associations occur even in the absence of mating opportunities. Several reasons have been postulated to explain these associations: predation avoidance and lost opportunities for reproduction (reviewed in Johnson & Gaines 1990; Isbell et al. 1993). Results of my study suggest that male life history traits and how these change during a male's adult life are equally important. For example, I have demonstrated that older males are less likely to disperse presumably due to reduced somatic capacity to overcome the challenges of transferring from one group to another and to successful compete for reproductive mates in the new group. My study thus demonstrates the need to integrate male life history traits in formulating a more complete socioecological model.

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