"FOLLOWING," AN ALTERNATIVE MATING STRATEGY OF MALE OLIVE

BABOONS (*PAPIO HAMADRYAS ANUBIS*)

By

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ABSTRACT OF THE DISSERTATION

"Following," an Alternative Mating Strategy of Male Olive Baboons (*Papio hamadryas*

anubis)

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Recent studies revealing the limitations of the Priority of Access model suggest

the evolutionary significance of alternative mating strategies. The olive baboon's (*Papio

hamadryas anubis*) social system provide a valuable opportunity to examine a little

studied alternative mating strategy- "following." The most well known mating strategy

of male baboons is individual aggressive competition for a consortship, a temporary

relationship between a male and fertile female (Bercovitch 1995). What is less often

appreciated about this phenomenon, however, is that the consorting pair is typically

shadowed by a retinue of "followers" that maintain proximity to the consort pair for

extended periods of time. Despite qualitative observations in several primate species, we

know virtually nothing about the functional significance of this common male behavior,

although it has been proposed as an alternative mating strategy. My dissertation

addresses the following three questions regarding the factors influencing the expression

of alternative male mating strategies: (1) what are the fitness costs and benefits of

alternative mating strategies for males?; (2) how does male condition impact the

expression of alternative mating strategies?; and (3) do intersexual interactions influence

these strategies? I examined these questions using behavioral data and genetic data collected on olive baboons during a 19 month field study in Laikipia District, Kenya.

My research indicates that following is an alternative mating strategy and can be directly linked to deviation from the Priority of Access Model, as observed through both behavior and infant paternity. Followers do not experience costs related to activity budget or feeding bout length, although they do face an increased risk of injury due to involvement in agonistic interactions with the consort male and spend less time interacting with other individuals. Following particularly provides lower ranking males with more opportunities to mate as theoretically predicted, although higher ranking males also use this strategy, depending on the distribution of reproductive opportunities. Female choice and male coercion also influence the expression of following, indicating the importance of intersexual interactions.

My dissertation expands our understanding of alternative mating strategies by incorporating a little studied and behaviorally flexible taxon, and has implications for models of social evolution and our understanding of human evolution.

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I am grateful that I discovered Robert Scott was familiar with a statistical analysis I was working on my third year; his help then and since has made my analyses better. Rob has also been a voice of reason, helping me control my perfectionist tendencies (the result of which is the short and sweet introduction, as opposed to a monograph).

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right track in my work. Erin also shared her code and advice on GLMMs, which have found their way into every chapter.

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INTRODUCTION

Explanations of male mating success in primates have historically focused heavily on a single attribute: dominance rank (Smuts 1987; Bulger 1993; de Ruiter and van Hooff 1993; Weingrill et al. 2000). Dominance rank often predicts male mating success, with higher ranking individuals having a priority of access to fertile females (Cowlishaw et al. 1991; Bulger 1993; de Ruiter and van Hooff 1993; Weingrill et al. 2000). Recent data from a number of primate taxa, however, reveal the limits of this priority of access model (Berard et al. 1993; Alberts et al. 2003; Wroblewski et al. 2009; Bissonnette et al. 2011; Dubuc et al. 2011). Furthermore, male dominance status is less correlated with reproductive success in species with larger neocortex ratios, which Pawlowski et al. (1998) interpret as evidence for alternative mating strategies based on increased cognitive ability. These studies, therefore, direct our attention to the potential evolutionary significance of alternative mating strategies in primates.

Alternative Mating Strategy Theory

There is widespread behavioral, morphological, physiological, and life history variation within both sexes in many taxa (Maynard-Smith 1979; Dawkins 1980; Caro and Bateson 1986; Andersson 1994; Repka and Gross 1995; Gross 1996; Brockmann 2001; Shuster and Wade 2003). Where variation in a trait or set of traits is discontinuous, the different phenotypes may reflect "alternative strategies" to solving a particular problem (Caro and Bateson 1986). Thus, rather than giving rise to a single "most fit" phenotype, selection has resulted in distinctive phenotypic diversity. Such alternative strategies are relevant to understanding disparate behaviors, ranging from foraging to mating; I will focus on alternative mating strategies in males, as these are relevant in understanding

"following" behavior. Shuster and Wade (2003) propose that alternative mating strategies will be favored whenever there is reproductive skew. Since male reproductive success is typically variable (Bateman 1948; Trivers 1972; Emlen and Oring 1977; Kvarnemo and Ahnesjö 1996), the occurrence of such strategies is expected to be widespread, suggesting that alternative mating strategies are evolutionary significant phenomenon.

A strategy is referred to an "evolutionarily stable strategy" (ESS) if no alternative strategy, among those specified, has higher average fitness, provided that a threshold percentage of the population adopts this strategy (Dawkins 1980). Alternative strategies are characterized by genetic polymorphism and the strategies with equal average fitness maintained by frequency-dependent selection (Gross 1996). Thus, there exists an evolutionary stable frequency at which the average fitness of individuals expressing the alternative strategies is equal. An example of alternative strategies is the alternative strategies of the lek breeding ruff (*Philomachus pugnax*); there are two distinct male morphs, resulting from two alleles at a single locus (Lank et al. 1995). "Resident" males have dark plumage and defend territories on the lek, while "satellite" males have white plumage and do not defend territories, but seek sneak copulations.

These alternative strategies are classified as "irreversible" or "Mendelian" strategies (Brockmann 2001; Shuster and Wade 2003) and are genetically determined polymorphisms fixed over an individual's lifetime or developmental trajectory. Irreversible alternative strategies are expected to occur when the costs of phenotypic plasticity are high for example, if specialized adaptations are required or there are

constraints on phenotypic plasticity. Irreversible alternative strategies, however, constrain individuals' responses to their environment (Jones and Agoramoorthy 2003).

"Reversible" alternative strategies based on dynamic, facultative response to environmental conditions are expected when temporal variation in fitness favors individuals able to express multiple phenotypes (Brockmann 2001; Shuster and Wade 2003). Such phenotypic plasticity is expected when environmental changes impacting fitness occur between reproductive opportunities and cues regarding these changes are available. Reversible strategies can be further divided into two categories: simultaneous reversible and sequentially reversible alternative strategies. Simultaneous reversible alternative strategies are the most flexible, as it is more likely that an individual can switch between strategies more rapidly. Sequentially reversible strategies are those where an individual can switch from one strategy to another at a particular point in its life. If the fitness associated with a particular alternative strategy is influenced by phenotype or environmental conditions, and the individual can detect and respond to these conditions, then selection will favor individuals switching from one strategy to another in a manner that maximizes individual fitness.

Evolutionary theory argues that such reversible strategies may be "status-dependent" or conditional (Gross 1996), allowing individuals to maximize reproductive success by dynamic expression of alternative strategies based on conditions both intrinsic to the individual and extrinsic (i.e., environmental, including social environment) (Maynard-Smith 1979; Dawkins 1980; Andersson 1994; Repka and Gross 1995; Gross 1996; Brockmann 2001). Conditional strategies are characterized by genetic monomorphism (in regard to strategy decision), and the average fitnesses of the

alternative tactics are not equal, except at the switchpoint. Since the fitness benefit of the tactics depends on individual condition, the phenotypes have fitness-dependent functions; the point where these functions intersect is the switchpoint. Thus, the switchpoint is the condition where the tactic with the highest fitness benefits changes. Alternative phenotypes therefore have condition-dependent fitness functions: depending on a particular individual's condition, a particular alternative strategy will result in the highest fitness for that individual. The switchpoint is located where the fitness of the tactics intersects; at this point, the phenotype showing the highest fitness changes. Conditional strategies allow individuals to express the phenotype that maximizes its reproductive success based on information available. Repka and Gross (1995) indicate that both individual phenotype and the population frequency of an alternative strategy both influence the fitness of the strategy. Horseshoe crabs (*Limulus polyphemus*) provide an illustrative example, with males pursuing either an attached or satellite conditional alternative mating strategy (Brockmann 1990; Brockmann 2001). Males pursuing the attached strategy attach to females using modified claw-like legs, while satellite males locate and position themselves in close proximity to attached pairs. Strategy success is based on male age, which is associated with male physical condition. Thus, the optimal strategy for a particular male is age-dependent; younger males rely on the attached strategy, while older males rely on the satellite strategy. At a particular age, the fitnesses accrued by the use of the two strategies are equal; this is the switchpoint and we expect younger males to use the attached strategy and older males to use the satellite strategy.

Alternative mating strategies are also influenced by the nature of environmental conditions, particularly the spatial and temporal distribution of reproductive opportunities

(Brockmann 2001; Shuster and Wade 2003). Shuster and Wade (2003) propose that when there are no environmental cues, irreversible or Mendelian strategies will be favored. On the other hand, when environmental cues are present, more flexible strategies will result. Such environmental cues include cues regarding reproductive opportunities. An example of such a reproductive cue is seen in many catarrhine primates: sexual swellings of cycling females (Nunn 1999; Deschner et al. 2003; Gesquiere et al. 2007; Higham et al. 2008; Higham et al. 2009).

Two terms are used in discussing this subject: strategy and tactic. Both terms, however, are used interchangeably in the literature and are often difficult to distinguish in practice (Dixson 1998). A strategy is genetically based, resulting in the allocation of an organism's somatic and reproductive effort among alternative phenotypes; strategies operate through physiological, neurological, or developmental cues from the organism. Thus, the strategy is the genotype that codes for the decision rule (Gross and Repka 1998). A tactic is a phenotype that results from a strategy and will have behavioral, morphological, physiological, or life history features that distinguish it from alternative tactics (Gross 1996). Tactics are the alternative phenotypes an individual may adopt; for conditional strategies, all individuals will have any underlying genetic material for each tactic regardless of expression (Gross and Repka 1998).

Conditional strategies are thought to be the most common form of discrete variation within a species, and alternative mating strategies in primates are often facultative (Jones and Agoramoorthy 2003; Tomkins and Hazel 2007). Most research on alternative male mating strategies has been conducted on insects, fish, birds, and non-primate mammals (Andersson 1994). Flexibility is a key feature of alternative male

mating strategies in most primate taxa. Thus, facultative alternative strategies are thought

to be most significant for understanding alternative strategies in primates (Gross 1996;

Brockmann 2001).

Studies of alternative strategies in primates are relatively rare; one well studied

alternative pre-mating strategy is sexual bimaturism in mandrills (*Mandrillus sphinx*)

(Setchell and Dixson 2002; Setchell 2003) and especially the orangutan (*Pongo*

pygmaeus). For example, "flanged" male orangutans exhibit a "sit, call, and wait"

strategy centered on sedentary residency in an area, accompanied by long calling, while

"unflanged" males adopt a more mobile "search and find" strategy based in part upon

forced copulations with encountered females (Schürmann and van Hooff 1986;

Maggioncalda et al. 2000; Utami et al. 2002; Utami Atmoko and van Hooff 2004). For

primates living in multi-male, multi-female groups, two well-studied conditional

alternative mating strategies are sneak copulations and coalition formation (Bercovitch

1988; Kuester and Paul 1989; Noë 1989, 1994; Brereton 1992; Berard et al. 1994; Noë

and Sluijter 1995, Soltis et al. 1997; Soltis et al. 2001; Alberts et al. 2003; van Schaik et

al. 2004). There is also some evidence of more subtle, but potentially significant,

manifestations of alternative mating strategies in primates. For example, Eberle and

Kappeler (2004) recently proposed that male gray mouse lemurs (*Microcebus murinus*)

differentially invest in mate guarding and sperm competition based on male condition.

This dissertation examines a potential "status-dependent" reversible alternative mating

strategy consisting of behavioral polymorphism in olive baboons (*Papio hamadryas*

anubis).

"Following," a Proposed Alternative Mating Strategy of Olive Baboons

In multi-male multi-female groups, male competition for females involves mate guarding females during consortships (Small 1990; Bercovitch 1995). The term "consortship" refers to an association between a male and a fertile female that is characterized by the maintenance of close proximity and copulation between the pair (Small 1990). Obtaining a consortship will generally correlate with access to a fertile female. The most well known mating strategy of male baboons is individual aggressive competition for a consortship.

What is less often appreciated about this system, however, is that the consorting pair is typically shadowed by a retinue of "followers" (Hall and DeVore 1965; Hausfater 1975; Strum 1982, 1987, 1994; Bercovitch 1988; Sapolsky 1990; Forster and Strum 1994). Anywhere from one to eight adult males may maintain proximity at variable distances from the consort pair and each other, coordinating their activities with the consort pair, and thereby consistently "shadowing" the pair for extended, but variable, periods of time. These follower males interact affiliatively and aggressively with other follower males and the consort male. Following has been observed in olive baboons (*Papio hamadryas anubis*, Hall and DeVore 1965; Strum 1982, 1987, 1994; Bercovitch 1988; Sapolsky 1990; Forster and Strum 1994), yellow baboons (*P.h. cynocephalus*, Hausfater 1975), Barbary macaques (*Macaca sylvanus*, Kuester and Paul 1989), crested black macaques (*Macaca nigra*, Engelhardt pers.com.), long tailed macaques (*M. fascicularis*, Engelhardt et al. 2006) and rhesus macaques (*M. mulatta*, Kaufmann 1965). Despite many qualitative observations (Hall and DeVore 1965; Hausfater 1975; Strum

1982, 1987, 1994; Bercovitch 1988; Sapolsky 1990; Forster and Strum 1994), we know virtually nothing about the functional significance of this common male behavior.

In their pioneering study of olive baboons (*Papio hamadryas anubis*), Hall and DeVore (1965) suggested that following behavior may facilitate the formation of a coalition among two follower males, who cooperatively oust the consort male from his position, after which one of these males becomes the new consort ("Coalitionary Challenge"). While coalitions are well studied, the link, if any, between coalition formation and following, remains unknown.

That point is further emphasized by observations that two males' coalitionary challenge to a consort male may result in a *third* follower male, uninvolved in the coalition, taking over the consort, whereupon the two coalitionary males follow *him*, as may the original consort male ("Opportunistic Takeover"). In fact, the first male to reach the consort female during an aggressive interaction or following an abandonment generally becomes the consort male, at least for a short period of time (Strum 1987; Noë 1992; Bercovitch 1995). As approximately 50% of new consort males mate with the female within the first five minutes after a consort changeover, even a short consortship can be beneficial to the male (Bercovitch 1995). Strum (1982) found that a majority of consort turnovers are not the result of aggression between the new consort male and the former consort male; this class only represents 26% of consort turnovers. Rather, an uninvolved follower who had monitored the situation from a distance would "rush the female and claim her without any agonistic interactions with the other males" (Strum 1982: 194). An uninvolved follower sometimes incites other follower males into *initiating* these aggressive interactions with the consort male. Strum (1994) indicates that

75% of takeovers involve social manipulation, rather than direct aggression, though the links to following remain unknown.

Additionally, consortship turnover may occur when a consort male apparently "spontaneously" abandons the female and a follower male takes over without a preceding overt challenge by any male ("Abandoned Consort"). Bercovitch (1988) indicates that over half of observed consort takeovers occur after the consort male abandons the female. Such abandonment is less likely during the period of most likely ovulation. Sapolsky (1990) argues that abandonment is not "spontaneous," but the result of the subtle threat of simply the presence of one or more follower males. Additionally, harassment by follower males may decrease the rate of copulation of the consort male. However, consort males have been observed to mate while follower males are involved in agonistic interactions amongst themselves (Danish pers. obs.). The consort male sometimes attempts to herd the female away from follower males, particularly when the follower males are interacting affiliatively with one another or have formed a coalition against him. Indeed, the threat posed by a follower male may result in the consort male himself starting an aggressive interaction with one or more follower males- which may result in a consort turnover (Strum 1987). In contrast, agonistic interactions amongst follower males may result in increased duration of the current consortship.

Following can thus be viewed as a possible strategy that provides males with opportunities to pursue one of several tactics that increase their likelihood of obtaining access to fertile females. Preliminary observations suggest that there is also a high degree of flexibility in following tactics, with rapid shifting between tactics occurring.

This dissertation therefore examines the functional significance of this little studied behavior in light of alternative mating strategy theory.

Description of Study Site and Subjects, and Previous Work at the Site

<u>Study Site</u>

This study took place on the 20,250ha Segera Ranch and communally owned land known as Thome-B in Laikipia District (36°50'E, 0°15'N), Kenya near the town of Nanyuki, approximately 260km north of Nairobi (FigI.1) (Lemasson et al. 2007; Shur 2008; Palombit unpublished data). The Laikipia plateau is a semi-arid ecosystem comprising two major habitat types: 1) riverine woodlands along rivers and streams dominated by *Acacia xanthophloea*, but also including dense shrub layers; and 2) *A. drepanolobium*-dominated scrub and grasslands away from waterways. The study site is at an altitude of 1,700m and the mean annual temperature ranges from 10-20°C. The mean annual rainfall prior to this study was 500mm (Shur 2008; Palombit unpublished data); however, in 2009 during my study, the area experienced a drought (Danish pers. obs.; Huho et al. 2011). This drought has been linked to El Niño-Southern Oscillation and the Indian Ocean Dipole (reviewed in Ogotu et al. 2011). This was followed by an extended period in which it rained every month, with a mean *monthly* rainfall of 851mm (see Table I.1). Much of my data collection occurred during this rainy period.

<u>Study Subjects</u>

Two groups of habituated olive baboons (*Papio hamadryas anubis*) have been studied at this site since 1999 (KAT) and 2000 (TDM) by Ryne Palombit and colleagues (Table I.2) (Palombit 2003; Lemasson et al. 2007; Shur 2008; Shur et al. 2008a,b).

Lions, leopards, hyenas and jackals were present at the site as potential predators (Danish pers. obs.).

When I began fieldwork in April 2009, only one group, TDM, was sleeping in their habitual *A. xanthophloea* sleep trees at the site of a dam on Thome-B (see FigI.1). The individual names and identity codes for all adult individuals of TDM are listed in Tables I.3 and I.4. In January 2010, TDM underwent a what appeared to be the onset of a group fission event which continued throughout my study, resulting in two sister subgroups, TDM and SUB (see Tables I.5, I.6, I.7, and I.8 for group composition of the two subgroups). As I was observing a SUB female (DI) in January 2010, while other observers remained with TDM, I was able to obtain detailed data on the ranging behavior of the two sister subgroups. The subgroups regularly moved in differing directions, often moving at least an estimated one to four or more kilometers apart. SUB was comprised of seven females (CI, DI, HZ, JU, LU, PA, VN) and six males (EM, FD, JE, LY, MK, NA). Notably, these many of the possible male-female dyads were qualitatively identified as friends (Smuts 1985; Palombit 2003), and there were no observed friendships between individuals that became members of the two subgroups. The females of SUB (and TDM) remained consistent with one exception; female PA moved to TDM in April 2010. Male movements were similar to typical emigration/immigration patterns, with males remaining with a particular subgroup for an extended period of time. Males FD and LY moved back to TDM in April 2010, while male EM emigrated to WAZ in February 2010 and male NA emigrated to KAT in May 2010; notably, all SUB females were pregnant at this time and thus unlikely to be cycling for more than one year. In September 2010, male MK began consorting with TDM female MA in the mornings,

with SUB ranging closer to TDM than usual; MA joined SUB soon after. Notably, MA is thought to be SUB female HZ's daughter, based on affiliative behavior (Danish pers. obs.), but had a dependent infant when fissioning began and was friends with a TDM male. Male LY also returned to SUB in September 2010. Other than male BO from TDM, who moved into SUB on two observation days when female DI was consorting, movement between the sister subgroups was of a duration of months, and thus semi-permanent.

KAT group had only been observed infrequently over the three years preceding my study, in part due to their ranging away from the usual sleeping site into an area that was too far away for the project field assistants to access regularly on foot. At the start of my field study, I located the group, which was in the process of an apparent group fissioning event. The group composition of the two daughter groups, KAT (larger) and WAZ (smaller), was fairly consistent over my study (see Tables I.9, I.10, I.11, and I.12). When I first located the groups, WAZ had only two adult males (DM and KL) and five adult females (CM, DV, FI, MT, VD). Male HM moved to WAZ and subadult female FG was identified as a member of WAZ in December 2009. Male CT also immigrated from TDM in December 2009. Both KAT and WAZ used a large number of known sleep sites along the Sugoroi River (see FigI.1), and often could not be found at any of 12 known sleep sites. The unpredictable ranging of these nascent daughter groups resulted in less observation time from August through November 2009 until the groups began using the sleep trees by the dam. In February 2010, male EM immigrated from SUB to WAZ. The same adult females remained in WAZ, with RS (known subadult female of WAZ) being promoted to adult status and female ZN identified as a pregnant WAZ

female (previously unknown, but likely a subadult in WAZ) in 2010. The five WAZ males remained in WAZ for the duration of my study, other than EM's disappearance, which was associated with a period of known predation events. Two KAT males, LE and SS, occasionally moved into WAZ for several days at a time; this typically corresponded to the presence of a consorting female in WAZ. Both males were older, low ranking males; they sometimes followed the consortship, but infrequently consorted. If these males left KAT in the morning, they typically were with WAZ for the entire observation day, as the groups foraged independently. Since they freely moved between the subgroups, I treated them accordingly in analyses, particularly when considering time available in Chapter 3. Notably, this group has a history of fission/fusion events prior to my study; several years ago, a subgroup of KAT left in an apparent fissioning event (Palombit unpublished data). This subgroup later returned, along with unknown animals of all age/sex classes, and fused with the remainder of KAT.

In summary, group fissioning effectively resulted in four social groups: TDM, SUB, KAT, and WAZ. Of these, I studied TDM, SUB, and WAZ since KAT had no cycling females for most of my study. The analysis for Chapter 1 relied on data from TDM (before and after fissioning), SUB, and WAZ. The analysis for Chapter 2 relied on data from TDM only, since I only had data on WAZ for a short period around the consortships of two females and there was no definitive alpha male in SUB, as MK and JE appeared to be vying for dominance. The analysis for Chapters 3, 4, and 5 relied on data from TDM (before and after fissioning), SUB, and WAZ. I treated male movement between these subgroups as an emigration/immigration, such that males were present only in one subgroup on a given day in analysis, but could switch subgroups on different

observation days. I typically refer to these subgroups as groups since they were semi-independent entities, though the final outcome of the group fissioning remained unclear at the end of my study.

<u>Previous and Ongoing Work at the Site</u>

This field site was formed as part of a comparative study by Ryne Palombit, comparing "friendships," affiliative bonds between lactating females and males, of olive and chacma baboons (Palombit et al. 1997; Palombit et al. 2001; Palombit 2003). Approximately 37% of infant mortality is due to male infanticide in chacma baboons; data suggests that these friendships function as an anti-infanticide strategy in this species (Palombit et al. 1997). Notably, the risk of infanticide is much lower in olive baboons, and friendships in olive baboons are less cohesive and investment in the relationship is more male biased than those of chacma baboons (Palombit 2003). Evidence from playback experiments suggests that friendships in olive baboons function to reduce female harassment by conspecific females, rather than infanticide (Lemasson et al. 2007). Female olive baboons with at least one high ranking friend, however, had lower glucocorticoid levels than females with no high ranking male friends; this finding is consistent with male harassment, rather than female harassment (Shur et al. 2008a). Additional endocrine data indicate that male friends have lower levels of testosterone during the period their female friend is lactating, compared to control males (Shur et al. 2008b).

Objectives and Hypotheses

Chapter 1: Since following has been suggested as an alternative mating strategy, but had not been quantitatively shown to provide males with access to fertile females, I

examined follower behavior and determined that following provided males with access to fertile females. I first asked 1) how does the behavior of followers differ from nonfollowers? Since followers may be more likely to be involved in agonistic interactions with the consort male as a result of competition for access to fertile females, I predicted that a) followers will have a higher rate of agonistic interactions, particularly with the consort male, compared to nonfollower males, controlling for number of males. Since followers may cooperate in forming coalitions to challenge the consort male, b) I expected followers to have a higher rate of affiliative interactions, particularly with other followers, compared to nonfollowing males, controlling for the number of males. 2) Is following an effective alternative mating strategy? Based on my preliminary observations and descriptions of following in the literature, I predicted that males would gain access to females via following, particularly that a majority of consort takeovers would be carried out by followers. If following in fact functions as an alternative mating strategy, 3) what tactics do followers use to obtain access to fertile females?; I predicted the following: a) followers would use these tactics at a higher rate than nonfollowers: Coalitionary Challenge, Opportunistic Takeover, Takeover of Abandoned Consort Female, and Sneak Copulations, since these are the typically discussed alternative strategies of olive baboon males; and b) nonfollowers would use Individual Aggressive Challenge at a higher rate than followers, since Individual Aggressive Challenge is typically thought of as the "primary" mating strategy. I then asked 4) if dominance rank and female cycle day influenced the tactic used by males. I predicted that a) high-ranking males would use the Individual Aggressive Challenge more than lower ranking males, since high-ranking males are more likely to be successful at these challenges; b) mid- and

low-ranking males would use the Coalitionary Challenge, Opportunistic Takeover, and Takeover of Abandoned Consort Females more than high-ranking males, since mid- and low-ranking males will be less successful at Individual Aggressive Challenge and most coalitions are formed by mid-ranking males. I did not have any a priori predictions regarding the direction of differences related to female cycle day. This chapter in revision for publication as: "L.M. Danish and R.A. Palombit, "Following," an alternative mating strategy used by male olive baboon (*Papio hamadryas anubis*): quantitative behavioral and functional description" in the International Journal of Primatology.

Chapter 2: I examined the influence of following on mating and direct reproductive success, to determine the efficacy of this alternative mating strategy. Since following results in a majority of consort takeovers, particularly during the period of likely ovulation I asked the following questions: 1) does the priority of access model account for patterns of mating in my study?; and 2) is there reproductive skew, as measured by consorting and infant paternity?   I additionally asked 3) if following was responsible for deviation from the priority of access model, predicting that increases in the duration of time spent following results in increases in the duration of time spent consorting.

Chapter 3: Since alternative mating strategy theory indicates that the expression of such strategies is influenced by male condition and reproductive opportunities, my objective was to examine the factors influencing the expression of following, by examining both intrinsic and extrinsic factors: dominance rank and the number of available females. I predicted that lower ranking males would spend more time following compared to higher ranking males, although I expected this difference to decrease during

the period of likely ovulation since mating is more likely to result in conception during this time. Since the number of consorting females may influence male strategy, I also examined the percent of time spent following by relative dominance rank. I then examined whether dominance rank predicted male success in taking over a consortship from a consorting male while using the alternative strategy following. I additionally examined the operational sex ratio in all groups and the proportion of observation days with multiple consorting females in each group. I had no a priori predictions regarding the influence of the available number of females, which was dependent on group size. This chapter has been resubmitted to Behavioral Ecology and Sociobiology as "L.M. Danish and R.A. Palombit, Influence of Dominance Rank and Group Size on the Expression of "Following," an Alternative Mating Strategy of Male Olive Baboons (*Papio hamadryas anubis*)

Chapter 4: Since costs are critical to any functional analysis of behavior, I examined the potential costs of following. My objectives were to examine the costs incurred by followers, examining energetic costs and social costs. For energetic costs, I examined the length of time spent feeding and traveling, as well as feeding bout duration. I hypothesized that followers would experience energetic constraints in the form of both a decrease in time spent feeding and a decrease in feeding bout length, since most previous studies found some reduction in feeding time and Alberts *et al.* (1996) found shorter feeding bouts for mate guarding males in the closely related yellow baboon. If followers experience a foraging cost, I expect this cost to be less than that incurred by consorting males since followers are less constrained in their movements. Since males attend to cues of the likelihood of female ovulation and alter their behavior in response to such

cues, I predicted that followers would incur greater feeding costs on the most likely days

of ovulation since I expect followers to increase their mating effort, which will further

constrain normal activities, more during the period of likely ovulation. Followers are

involved in agonistic interaction with the consort male (Danish and Palombit submitted),

and I expect such interactions to be more frequent when the dyad is in closer proximity.

As a result, I expect followers to spend more time involved in aggressive interactions or

monitoring of the consort male, and less time feeding, as proximity between the consort

male and follower decreases. I therefore predicted that proximity to the consort male

would influenced the time the costs incurred by followers, particularly that the length of

time spent feeding and feeding bout duration of followers would decrease with increasing

proximity to the consort male. Finally, I hypothesized that following would constrain

males' ability to interact with other individuals, by constraining their ability to move

around the group and interact with social partners; I predicted that followers would spend

less time grooming compared to nonfollowing males. This chapter has been submitted to

Behavioral Ecology and Sociobiology as "L.M Danish and R.A. Palombit, Male Olive

Baboon (*Papio hamadryas anubis*) "Followers" Incur Time, But Not Energetic, Costs.

Chapter 5: Recent evidence regarding sexual conflict (Smuts and Smuts 1993;

Muller et al. 2011) underscores the importance of examining the influence of intersexual

interactions, including female preference and male aggression, on following. Since

recent studies have suggested that measures of female preference are correlated to male

aggression directed at females, I tested this prediction. While both female preferences

and male coercion are thought to influence the evolution of alternative mating strategies,

the influence of these selective forces on the expression of alternative mating strategies

remain little studied despite the potential for such an influence on a flexible alternative strategy. I therefore predicted that the proportion of time a male spent following a particular female's consortships would be increase with increasing female proceptivity and male aggression towards that female. I additionally predicted that follower success would be increase with increasing female proceptivity and male aggression.

Table I.1: Monthly Rainfall During Study Period

Year	Month	Total Rainfall (mm)
2009	Jan	0
2009	Feb	0
2009	Mar	0
2009	Apr	0
2009	May	0
2009	Jun	80
2009	Jul	10
2009	Aug	76
2009	Sep	233
2009	Oct	905
2009	Nov	840
2009	Dec	638
2010	Jan	511
2010	Feb	777
2010	Mar	1349
2010	Apr	601
2010	May	1296
2010	Jun	444
2010	Jul	1025
2010	Aug	1447
2010	Sep	375

From Aronoff, Danish, Moinde, and Palombit unpublished data

Table I.2: Group Composition History

	KAT		TDM		
Date	Number of Females	Number of Males	Number of Females	Number of Males	Source
Feb-04 to Jul-04	NA	NA	25	19-23	Lemasson et al. 2007
Sep-04 to Aug-05	18-20	9-11	26-30	19-21	Shur 2008
Sep-05 to Dec-05	NA	NA	24-25	18-24	Palombit unpublished data
2006	NA	NA	25-26	18-19	Danish, Moinde, and Palombit unpublished data
Jun-07 to Jul-07	16	9	25	15-16	Aronoff, Danish, Moinde, and Palombit unpublished data
Apr-09 to Dec-09	NA[1]	NA[1]	30-31	17-19	Danish, Moinde, and Palombit unpublished data

1- KAT had begun to fission, see Table I.3.

Both KAT and TDM were in the process of fissioning in 2010, see Tables I.3-I.12

Table I.3: TDM Adult Males 2009, Prior to Group Fissioning

Name	ID	Notes
Barack	BK	Immigrated from unknown group in 2008
Bob	BO	Present as adult at start of long term study in 2000
Elmer	EM	Present in KAT group at start of long term study in 1999, immigrated to TDM in 2005, left and returned in 2006, immigrated to KAT from TDM in 2010
Fred	FD	Present as adult at start of long term study in 2000
Hector	HC	Immigrated from Finafran (unhabituated group)
Henry	HY	Subadult male in 2005 (presumed natal)
Judd	JD	Subadult male in 2005 (presumed natal)
Jake	JE	Subadult male in 2005 (presumed natal)
Larry	LY	Present as adult at start of long term study in 2000
Mark	MK	Immigrated as an young adult from KAT in 2007 (not natal to KAT)
Monty	MO	Named as a juvenile in 2006 (presumed natal)
Murray	MR	Present as adult at start of long term study in 2000
Noah	NA	Presumed natal, considered an adult prior to 2005
Nelson	NL	Named as a juvenile in 2006 (presumed natal), subadult in 2007
Otis	OS	Named as a juvenile in 2005 (presumed natal)
Rambo	RM	Named as a juvenile in 2006 (presumed natal)
Roy	RO	Present as adult at start of long term study in 2000
Seymour	SE	Present as adult at start of long term study in 2000
Sylvestor	SV	Named as a juvenile in 2006 (presumed natal)
Ted	TD	Present as adult at start of long term study in 2000

From Aronoff, Danish, Moinde, and Palombit unpublished data

Table I.4: TDM Adult Females 2009, Prior to Group Fissioning

Name	ID	Estimated Age Class
Ashanti	AT	Old
Bernice	BE	Old
Cassie	CA	Old
Camilla	CI	Young
Diana	DI	Young
Doris	DO	Old
Euphemia	EU	Old; estimated at 25 years of age or older by Dr. Rikoi (Institute of Primate Research) when darted for radio collaring
Eve	EV	Young; had independent yearling (believed to be her first) in 2009 when named as an adult.
Florence	FL	Old
Hazel	HZ	Old
Judy	JU	Old
Katerina	KR	Young; had dependent infant (believed to be her first) in 2009 when named as an adult.
Kate	KT	Old
Lorraine	LO	Young; had dependent infant (believed to be her first) in 2009 when named as an adult.
Lucille	LU	Old
Makayla	MA	Young; had dependent infant (believed to be her first) in 2009 when named as an adult.
Norma	NO	Old
Olivia	OV	Young; had dependent infant (believed to be her first) in 2009 when named as an adult.
Priscilla	PA	Young; had dependent infant (believed to be her first) in 2009 when named as an adult. Possible she is older since she was not well habituated.
Rachel	RC	Young; had dependent infant (believed to be her first) in 2009 when named as an adult
Sandy	SA	Young
Stella	SL	Old
Thelma	TL	Old
Ulrike	UL	Young; pregnant with first known infant in 2009
Velma	VL	Old
Vanessa	VN	Young
Victoriya	VY	Young; named as an adult in 2009
Whoopi	WH	Young; gave birth to first known infant in 2009
Yolanda	YO	Old
Zelda	ZA	Old

From Aronoff, Danish, Moinde, and Palombit unpublished data

Table I.5: TDM Adult Males 2010, After Fissioning

Name	ID	Notes
Barack	BK	
Bob	BO	Moved into SUB for one day twice (when female DI was consorting). Disappeared Aug-10[1]
Fred	FD	Moves from SUB to TDM Apr-10
Hector	HC	
Henry	HY	
Judd	JD	
Larry	LY	Moves from SUB to TDM Apr-10, returns to SUB in Sep-10
Monty	MO	
Murray	MR	Disappears Jul-10
Nelson	NL	
Rambo	RM	
Roy	RO	Disappears Sep-10[2]
Seymour	SE	Disappears Apr-10
Ted	TD	Disappears Aug/Sep-10[2]
Zorro	ZR	Transient member of multiple groups

1- Associated with sleep site changes after predation event, BO was seen (one day each) with WAZ, then KAT, then disappeared
2- Disappearances occurred during a period with evidence of multiple predation incidents at the sleep trees

From Aronoff, Danish, Moinde, and Palombit unpublished data

Table I.6: TDM Adult Females 2010, After Fissioning

Name	ID	Notes
Ashanti	AT	Disappeared Aug/Sep-10[1]
Bernice	BE	Disappeared Sep-10[1]
Cassie	CA	
Doris	DO	Disappeared Sep-10[1]
Euphemia	EU	
Eve	EV	Disappeared Aug/Sep-10[1]
Florence	FL	
Katerina	KR	
Kate	KT	Disappeared Aug/Sep-10[1]
Lorraine	LO	
Makayla	MA	Moves from TDM to SUB Sep-10
Norma	NO	
Olivia	OV	
Priscilla	PA	Moves from SUB to TDM Jun-10
Rachel	RC	
Sandy	SA	
Stella	SL	Disappeared May-10
Thelma	TL	Disappeared Aug/Sep-10[1]
Ulrike	UL	Disappeared Sep-10[1]
Velma	VL	
Victoriya	VY	
Whoopi	WH	Disappeared Sep-10[1]
Yolanda	YO	
Zelda	ZA	Disappeared Aug/Sep-10[1]

1- Disappearances occurred during a period with evidence of multiple predation incidents at the sleep trees

From Aronoff, Danish, Moinde, and Palombit unpublished data

Table I.7: SUB, Smaller Daughter Group of TDM After Fissioning, Adult Males 2010

Name	ID	Notes
Elmer	EM	Emigrates to WAZ Feb-10
Fred	FD	Moves from SUB to TDM Apr-10
Jake	JE	
Larry	LY	Moves from SUB to TDM Apr-10, returns to SUB in Sep-10
Mark	MK	
Noah	NA	Emigrates to KAT May-10
Zorro	ZR	Transient member of multiple groups

From Aronoff, Danish, Moinde, and Palombit unpublished data

Table I.8: SUB, Smaller Daughter Group of TDM After Fissioning, Adult Females 2009

Name	ID	Notes
Camilla	CI	
Diana	DI	
Hazel	HZ	
Judy	JU	
Lucille	LU	Disappears Feb-10
Makayla	MA	Moves from TDM to SUB Sep-10
Priscilla	PA	Moves from SUB to TDM Jun-10
Vanessa	VN	

MK and MA began consorting in Sep-10, MA had been friends with BK and was thought to be HZ'a daughter
From Aronoff, Danish, Moinde, and Palombit unpublished data

Table I.9: KAT Adult Males 2009-2010

Name	ID	Notes
Dick	DC	Immigrates from TDM as a subadult prior to 2005
Hamson	HM	Moves to WAZ Dec-09, returned to KAT Sep-10
Leo	LE	Present as adult at start of study in 1999, moves into WAZ when there is a consorting female
Noah	NA	Immigrates from SUB May-10 (assumed TDM natal male)
Otis	OS	Immigrated from TDM (assumed natal group) in Dec-09
Peregrine	PR	Newly adult, thought to be natal to KAT
Sebastian	SS	Immigrated to TDM in 2005, then KAT in 2006 (unknown natal group), moves into WAZ when there is a consorting female
Wingard	WN	Present as adult at start of study in 1999, disappears in Sep-10[1]

1- Disappearances occurred during a period with evidence of multiple predation incidents at the sleep trees

From Aronoff, Danish, Moinde, and Palombit unpublished data

Table I.10: KAT Adult Females 2009-2010

Name	ID	Estimated Age Class, Notes
Carbenek	CB	Old
Gwynedd	GW	Old
Ilyena	IY	Young; pregnant with first known infant in 2010
Linnet	LT	Old
Nivetta	NV	Young; had dependent infant (believed to be her first) in 2009 when named as an adult.
Orkney	OY	Old
Ragnell	RG	Old, disappearred in Aug-10[1]
Tintagel	TN	Old

1- Disappearance occurred at the beginning of predation incidents, remains of a adult female/large juvenile baboon found same day RG was not found with the group

2- Disappearances occurred during a period with evidence of multiple predation incidents at the sleep trees

From Aronoff, Danish, Moinde, and Palombit unpublished data

Table I.11: WAZ Adult Males 2009-2010

Name	ID	Notes
Christopher	CT	Emigrated from TDM in Dec-09, named as a juvenile in TDM in 2006 (assumed natal). Age estimated by Dr. Rikoi (IPR) as 7-8 years old in 2010 when darted for radio collaring
Damas	DM	Known subadult male in 2007 in KAT (assumed natal)
Elmer	EM	Emigrates from SUB Feb-10, disappeared in Sep-10[1]
Hamson	*HM*	Moved to WAZ Dec-09, returned to KAT Sep-10
Kurwenal	KL	Known subadult male in 2007 in KAT (assumed natal)
Leo	LE	Present as adult at start of study in 1999, moved into WAZ when there is a consorting female
Sebastian	SS	Immigrated to TDM in 2005, then KAT in 2006 (unknown natal group), moved into WAZ when there was a consorting female
Zorro	ZR	Transient member of multiple groups

1- Disappearances occurred during a period with evidence of multiple predation incidents at the sleep trees

From Aronoff, Danish, Moinde, and Palombit unpublished data

Table I.12: WAZ Adult Females 2009-2010

Name	ID	Estimated Age Class, Notes
Camelot	CM	Young; had dependent infant (believed to be her first) in 2009
Dover	DV	Young
Firiel	FI	Old, disappeared Sep-10[1]
Fudge	FG	Becomes adult May-10
Meliot	MT	Young
Rosette	RS	Young; pregnant with first known infant in 2010
Varda	VD	Old
Zarine	ZN	Young; pregnant with first known infant in 2010 when named

1- Disappearance occurred during the period with evidence of multiple predation incidents at the sleep trees and followed shortly after an apparent stillbirth of FI's infant

From Aronoff, Danish, Moinde, and Palombit unpublished data
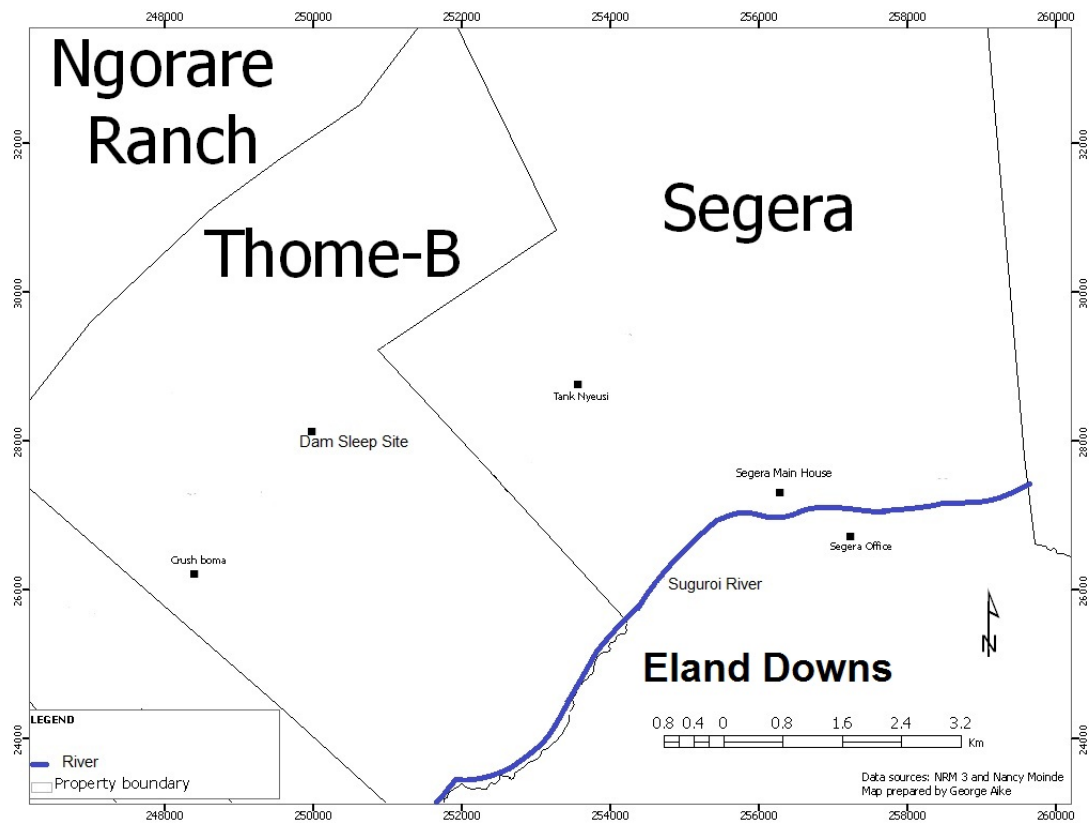
FigI.1: Map of the Study Site

Modified from map prepared by George Aike, Mpala Research Center, Laikipia, Kenya. Includes Moinde unpublished data.

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CHAPTER ONE

DEMONSTRATION OF FOLLOWING AS AN ALTERNATIVE MATING STRATEGY

Introduction

Explanations of male mating success in primates have historically focused heavily on a single attribute: dominance rank (Cowlishaw et al. 1991; Bulger 1993; de Ruiter and van Hooff 1993; Weingrill et al. 2000). Dominance rank often predicts male mating success, with higher ranking individuals having a priority of access to fertile females. Recent data from a number of primate taxa, however, reveal the limits of the priority of access model (Berard et al. 1993; Alberts et al. 2003; Wroblewski et al. 2009; Bissonnette et al. 2011; Dubuc et al. 2011) suggesting the potential evolutionary significance of alternative strategies across many taxa. Thus, such alternative strategies are a means for lower ranking individuals to sire offspring, resulting in a reduction in the ability of high ranking males to monopolize access to females and deviation from the priority of access model.

Conditional alternative mating strategies allow individuals to maximize reproductive success by dynamic expression of alternative strategies based on conditions (both intrinsic to the individual and extrinsic [i.e., environmental]) (Maynard-Smith 1979; Dawkins 1980; Andersson 1994; Repka and Gross 1995; Gross 1996; Brockmann 2001). Gross (1996) outlines "status-dependent selection" of alternative strategies, in which the alternative phenotypes have fitness functions that are dependent on an aspect of the individual's condition (e.g., physical condition, dominance rank). In order for alternative strategies to be selected for, these fitness functions must intersect at a

"switchpoint" where the fitness of the two strategies is equal. Therefore, one of the strategies will have a higher fitness benefit to an individual depending on their condition; provided the costs of flexibility are not prohibitive, individuals that express the alternative strategy favored by their condition will maximize their fitness.

Shuster and Wade (2003) additionally suggest that the number and distribution of reproductive opportunities experienced by males, as well as cues regarding these reproductive opportunities, are important in understanding alternative strategies. They propose that more flexible, conditional strategies will evolve when there are cues regarding reproductive opportunities. An example of such a cue is seen in many catarrhine primates: sexual swellings of cycling females (Nunn 1999; Deschner et al. 2003; Gesquiere et al. 2007; Higham et al. 2008; Highham et al. 2009). During the follicular stage, the swelling increases in size; following ovulation, the swelling rapidly decreases in size. Conception is most likely during the four days prior to the detumescence of the sexual swelling (Higham *et al.* 2008). These sexual swellings, therefore, provide information regarding the probabilistic likelihood of conception (Nunn 1999; Deschner *et al.* 2003; Gesquiere *et al.* 2007; Higham *et al.* 2008; Higham *et al.* 2009).

For primates living in multi-male, multi-female groups, two well-studied conditional alternative mating strategies are sneak copulations and coalition formation (Bercovitch 1988; Kuester and Paul 1989; Noë 1989, 1994; Brereton 1992; Berard et al. 1994; Noë and Sluijter 1995, Soltis et al. 1997; Soltis et al. 2001; Alberts et al. 2003; van Schaik et al. 2004). Notably, data support the use of these strategies as an alternative to individual aggressive competition for consortships by lower ranking males. For example,

middle-ranking males participate in the majority of the coalitions in olive and yellow baboons, and these coalitions most often target higher ranking males (Bercovitch 1988; Noë 1989, 1994; Noë and Sluijter 1995; Alberts et al. 2003). The use of sneak copulations exhibits a similar pattern, with subadult (adolescent males, lower ranking as a result) or subordinate males and males of low status relying on sneak copulations (Kuester and Paul 1989; Kuester and Paul 1992, Alberts et al. 2003; Bissonnette et al. 2010). These males are observed mating rapidly, often covertly when consort males are distracted often by an ongoing fight for access to the female (Kuester and Paul 1989).

The most well known mating strategy of male baboons is individual aggressive competition for a consortship, a temporary relationship between a male and fertile female (Bercovitch 1995). What is less often appreciated about this system, however, is that the consorting pair is typically shadowed by a retinue of "followers" (Hall and DeVore 1965; Hausfater 1975; Strum 1982, 1987, 1994; Bercovitch 1988; Sapolsky 1990; Forster and Strum 1994). These follower males maintain proximity at variable distances from the consort pair and each other, coordinating their activities with the consort pair, for extended periods of time. These males interact both with one another and the consort pair. Following has been observed in olive baboons (*Papio hamadryas anubis*, Hall and DeVore 1965; Strum 1982, 1987, 1994; Bercovitch 1988; Sapolsky 1990; Forster and Strum 1994), yellow baboons (*P.h. cynocephalus*, Hausfater 1975), Barbary macaques (*Macaca sylvanus*, Kuester and Paul 1989), crested black macaques (*Macaca nigra*, Engelhardt pers.com.), long tailed macaques (*M. fascicularis*, Engelhardt et al. 2006) and rhesus macaques (*M. mulatta*, Kaufmann 1965). Despite many qualitative observations (Hall and DeVore 1965; Hausfater 1975; Strum 1982, 1987, 1994; Bercovitch 1988;

Sapolsky 1990; Forster and Strum 1994), we know virtually nothing about the functional significance of this common male behavior.

Current theory and these limited qualitative observations generate an array of potential fitness benefits, which suggest that following functions as a means for males to gain access to fertile females and is thus an alternative mating strategy to individual aggressive competition for consortships. Notably, individual followers may pursue different tactics and males may flexibly change tactics in a short period of time. Thus, following may not be a unitary phenomenon, but rather comprise multiple behavioral tactics used in the context of a broader following behavior. Moreover, qualitative observations suggest that the expression of following is flexible, with males able to switch strategies within a day (Danish pers. obs.), which suggests that following is likely to be a conditional alternative strategy. In their pioneering study, Hall and DeVore (1965) suggest that following may facilitate the formation of a coalition by two or more followers, who aggressively oust the consort male, whereupon one of the coalition partners takes over the consortship ("Coalitionary Challenge"). While coalitions are well studied, the link, if any, between coalition formation and following, remains unknown. Such Coalitionary Challenges or other distractions to the consort male may provide followers with an opportunity to affect a consort takeover while the consort male is distracted ("Opportunistic Takeover"); in such instances, the first male to reach the contested female often becomes the new consort male, at least for a brief time. Additionally, following may provide males with the opportunity to takeover a consortship after the previous consort male abandons the female ("Abandoned Consort Female Takeover"); following is thus a means of remaining in close proximity to be the first male

to reach an abandoned female. Finally, it is possible that following provides males with an opportunity to obtain a sneak copulation, without any consort takeover (Sneak Copulation).

While following has been described qualitatively, I have examined following quantitatively for the first time. I first asked 1) how does the behavior of followers differ from nonfollowers? Since followers may be more likely to be involved in agonistic interactions with the consort male as a result of competition for access to fertile females, I predicted that a) followers will have a higher rate of agonistic interactions, particularly with the consort male, compared to nonfollowing males, controlling for number of males. Since followers may cooperate in forming coalitions to challenge the consort male, b) I expected followers to have a higher rate of affiliative interactions, particularly with other followers, compared to nonfollowing males, controlling for the number of males. 2) Is following an effective alternative mating strategy? Based on my preliminary observations and descriptions of following in the literature, I predicted that males would gain access to females via following, particularly that a majority of consort takeovers would be carried out by followers. If following in fact functions as an alternative mating strategy, 3) what tactics do followers use to obtain access to fertile females?; I predicted the following: a) followers would use these tactics at a higher rate than nonfollowers: Coalitionary Challenge, Opportunistic Takeover, Takeover of Abandoned Consort Female, and Sneak Copulations, since these are the typically discussed alternative strategies of olive baboon males; and b) nonfollowers would use Individual Aggressive Challenge at a higher rate than followers, since Individual Aggressive Challenge is typically thought of as the "primary" mating strategy. I then asked 4) if dominance rank

and female cycle day influenced the tactic used by males. I predicted that a) high-ranking males would use the Individual Aggressive Challenge more than lower ranking males, since high-ranking males are more likely to be successful at these challenges; b) mid- and low-ranking males would use the Coalitionary Challenge, Opportunistic Takeover, and Takeover of Abandoned Consort Females more than high-ranking males, since mid- and low-ranking males will be less successful at Individual Aggressive Challenge and most coalitions are formed by mid-ranking males. I did not have any a priori predictions regarding the direction of differences related to female cycle day.

Methods

Data derive from 393 and 50 hours of focal data from 26 males from two groups of habituated olive baboons (Segera/Mutara) (Lemasson et al. 2008; Shur et al. 2008a, 2008b). These data derive from TDM (before and after the apparent onset of fissioning described in the Introduction), TDM's sister group SUB, and WAZ. Research complied with the protocols of the Rutgers University Institutional Animal Care and Use Committee (Protocol 09-004) and the legal requirements of Kenya (National Council of Science and Technology Research Permit NCST/5/002/R/348).

I selected adult females, specifically selecting females of varying ages and dominance ranks, as opposed to random selection. I observed 13 females over 19 cycles. These females were observed throughout their entire estrous cycle and for consecutive cycles until conception. I observed male mating behavior for an entire female cycle, recording the identity of all consort and follower males, descriptions of all consort takeover attempts, and the onset of detumescence of the female's sexual swelling.

When observing a particular female's consortships, I collected ten minute focal animal samples, rotating between all males following the female's consortships. I also collected focal animal samples (Altmann 1974) on all adult males when not consorting or following (hereafter nonfollowing); these focal samples were collected when none of the focal females was consorting. Thus, I collected data on both following and nonfollowing males and all focal samples could be categorized as a focal sample of a following male, or nonfollowing male. Agonistic and affiliative behaviors were recorded continuously during focal samples. These affiliative behaviors included behaviors typically seen in "greetings" (e.g., mounting, touching of genitals), which Smuts and Watanabe (1990) have suggested as the only context in which males engage in affiliative interactions. Behaviors not separated by more than ten seconds were treated as a single interaction in analysis (Berghänel et al. 2011).

Follower Status

For each consortship, males were classified as either "consort males," "followers," or "nonfollowers." This classification was determined independently for each consortships and observation day, such that a male was a follower of one consortship could be a nonfollower or consort male for another consortship. Consort males were identified based on their extended proximity maintenance with a female with a sexual swelling; consort males stayed within sight of the female, following her as she traveled. I categorized the remaining males in the group using a male proximity score (MP-score) modified from Smut's (1985) composite proximity score (or "C-score"), which was calculated for each male separately. I calculated the MP-scores from spatial data collected via scan samples at 15 minute intervals throughout the observation day, in

which I collected distances of all visible adult males to the consort male using a Nikon

Prostaff 550 rangefinder accurate to 0.5m within 100m. Since the rangefinder obtains the

distance between itself and the target, the observer stood between the consort male and

target male, such all three were in a straight line. The observer than used the rangefinder

to measure the distance between themselves and each male; the distance between the

males was therefore the sum of these two distances. The MP score is calculated as below

for each consort male-male dyad, for n scan sample intervals:

$$MP = (1/\text{distance}_1) * ([1/\text{number intervals}]*100) + \ldots (1/\text{distance}_n) * ([1/\text{number intervals}]*100)$$

The component parts of the MP-score were calculated from each scan sample interval by

taking the product of the reciprocal of the distance between the males and the percentage

of time at that distance (the product of the reciprocal of the number of scan sample

intervals and 100). The MP-score is the sum of all such components, from the first scan

sample to the nth scan sample. Based on preliminary research from a dataset not

included in this analysis (Danish and Palombit 2008), I classified males that were seen

during more than 25% of scan samples and with a MP-score of 1.9 or higher as

"followers," while males with a MP-score less than 1.9 were classified as

"nonfollowers." In this preliminary study, I recorded the distance of all males to the

consort male as described here, and additionally recorded the identity of males I

qualitatively identified as followers. I then examined the MP-scores of all males, and

compared these scores to our qualitative assessment. I tested different values of the MP-

score, to determine which criterion resulted in classification of males that matched our

qualitative assessment of follower status. I thereby obtained an objective measure of

follower status that matched our qualitative assessment of follower status for the preliminary dataset.

<u>Consort Takeover Attempt Classification</u>

Sneak copulations, extended aggression (lasting more than five minutes) directed at the consort male (indicative of a potential takeover), and consort turnovers were recorded *ad libitum*. Consort takeover attempts were classified as one of four tactics based on observed male behavior: 1) Individual Aggressive Challenge, 2) Coalitionary Challenge, 3) Takeover of an Abandoned Female, and 4) Opportunistic Takeover during the distraction provided by a third party's interaction. I operationally defined Individual Aggressive Challenge if a single male directed prolonged aggression at the consort male. A Coalitionary Challenge was defined as the concurrent direction of aggression towards the consort male by two or more males (Noë and Sluijter 1995). A Takeover of an Abandoned Female occurred when the consort male moved away from the consort female, without any overt aggression, and a new male began consorting. Opportunistic Takeovers occurred when the new consort male gained access to the consort as the result of some form of distraction, but did not directly interact with the consort male and the consort male had not abandoned the female. In Table 1.1, I additionally subdivided the Opportunistic Takeover category to identify the cause of consort male distraction as: coalitionary challenge by other males, other aggressive interaction with another follower, other aggressive interaction with a nonfollower male, and other. Other included female-female aggression and distraction by herders or domestic animals. I recorded all attempted sneak copulations *ad libitum,* as well as whether the attempt was successful. I recorded the follower status of the male attempting a consort takeover, as well as the

success or failure of the attempt. This protocol yielded a dataset of 99 successful and 59 unsuccessful consort takeover attempts by 24 adult males, for which detailed data regarding male behavior and follower status were collected. The proportion of successful takeovers by followers was calculated by dividing the number of takeovers by followers by the total number of observed takeovers.

Female Cycle Day

Female cycle day can retroactively be determined using the deflation day (D-day), with preceding days denoted as D-1, D-2, etc. The proportion of successful consort takeovers by followers was calculated for each cycle day as described above. I did not calculate the proportion of successful consort takeovers by followers separately for each day for cycle days before D-4 since these days are not likely days of conception and females vary in how many of these days they consort during; I treated cycles days D-5 and earlier as a single day.

Dominance Rank

I determined dominance rank from decided dyadic agonistic interactions; only supplants and submissive behaviors and vocalizations were used (e.g., bare-teeth display, fear bark). Elo-ratings were determined for each male throughout the study period (starting value = 1000, k = 100 as described in Neumann *et al*. 2011); the value of the Elo-rating increases with increasing competitive ability so that males with higher Elo-ratings are higher ranking. Elo-rating has several advantages over matrix based methods that are particularly useful in determining male dominance, which is dynamic in olive baboons. Elo-ratings can be used to derive a linear hierarchy by listing males by their Elo-ratings in descending order. For my analyses, I used a male's Elo-rating on the day

of the particular consort takeover attempt, which allowed us to account for changes in individual males' dominance throughout the study.

Data Analysis

Since I predicted that followers will have more agonistic interactions with the consort male, I compared the rate of agonistic interactions with the consort male while following with the rate of all agonistic interactions with males while not mating. From my focal data, I determined the mean rate of agonistic interactions, in which the focal was either the actor or the recipient, for each male when following and nonfollowing. Each male was thus represented once in each behavior type. I divided the rate by the number of potential interactors; the number was one for followers (e.g., the consort male) and the number of other males in the group for nonfollowing males. By controlling for the number of interactors I were able to examine the rate of agonism experience by a male per interactor and thus specifically compare followers' rates of agonism with the consort male with a "baseline" rate of agonism with any one male. The same principle applies for the rate of affiliative interactions below. I used a Welch's Two Sample T-test to determine if the rate of agonism differed between following and nonfollowing males. I also ran a Welch's Two Sample T-test to test the prediction that followers to have more affiliative interactions with other followers than with males when not mating. From my focal data, I determined the mean rate of affiliative interactions, which included behaviors in which the focal was the actor or the recipient, for each male when following and nonfollowing. As above, I divided the rate by the number of potential interactors; the number was the number of other followers for followers and the number of other males in the group for nonfollowing males. I therefore only included data from followers when

there was more than one follower, and thus at least one potential individual to interact with. I tested a post hoc prediction that higher ranking followers would direct more aggression at the consort male using a Spearman's rank correlation between the mean rate of agonistic interactions directed at the consort male by the focal, examining only focal samples of followers, and the mean Elo-rating for each male. The Elo-rating for a male on the day of the focal sample was determined, and I used the mean of the Elo-ratings from all focal samples of that male in this analysis. I used the Holm-Bonferroni Method to account for multiple testing (Levin 1996; Wright 2012), which results in three different p values; both sets of p-values are ranked in ascending order and the calculated p-value must be less than its corresponding adjusted p-value to be considered significant. The three adjusted p-values were 0.050, 0.025, and 0.017.

In order to determine if males gained access to female by following, I examined all observed consortship takeovers (n = 99) and determined the proportion carried out by followers. I then examined the proportion of consort takeovers by followers over female cycle day, since conception is most likely on D-1 and D-2. I used Chi-squared tests for each cycle day, testing whether the number of takeovers by followers was significantly different from the overall mean, to determine if the proportion of consort takeovers by followers differed on different cycle days.

To determine which behavioral tactics followers used to obtain access to fertile females, I ran a Generalized Linear Mixed Model (GLMM) in the statistical software R v2.1.5.1 (R Development Core Team 2010).   My response variable was the number of consort takeover attempts, successful and unsuccessful, for each individual male during each individual female cycle. These data and the standard errors of the data were Poisson

distributed, as confirmed by a Goodness-of-Fit test. The fixed effects were: male behavior (following or nonfollower), consort takeover type (Abandoned Consort, Coalitionary Challenge, Individual Aggressive Challenge, or Opportunistic), and the interaction of male behavior and consort takeover type. Since the amount of time observing each female cycle varied, I included observation time as a fixed effect as well. My random effects were male and female identity, with female cycle as a nested effect of female identity to account for the observation of multiple cycles for some females.

To determine if male dominance rank and female cycle day influenced the consort takeover tactic used by males, I ran a second GLMM with takeover type as the response variable and male Elo-rating and female cycle day as fixed effects. A Shapiro-Wilk normality test was run to ensure that the data were normally distributed. The following random effects were included in the model: observation day, male identity, consort male identity, consort female identity, and social group. I applied a Bonferroni correction to this model and the preceding model; the calculated p-values for both models were required to be less than 0.0250 to be significant.

Results

Considering only interactions with the consort male, followers had a higher rate of agonistic interactions compared to nonfollowing males ($t_{23} = 3.8887$, $P = 0.0007$) (Fig1.1). Considering only interactions with other followers, followers also had more affiliative interactions, compared to nonfollowing males, as predicted ($t_{27} = 2.4276$, $P = 0.0225$) (Fig1.2). Anywhere from zero to eight males may follow a consortship on a given day (mean = 2.3). Followers of differing ranks did not differ in their expression of

aggression towards the consort male, contrary to my prediction ($r = -0.0700$, $n = 24$, $P = 0.7494$) (Fig1.3).

Overall, 74% of consort takeovers were executed by males who were followers of the targeted consortships. Notably, the percentage of consort takeovers by followers increased (up to 92%) during the periods of likely ovulation (Fig1.4). Chi-squared tests showed that the the number of takeovers by followers was less than the mean of 75% on D-5 and earlier ($X^2 = 7.3$, $df = 1$, $P < 0.0100$) and more than the mean on D-2 ($X^2 = 4.7$, $df = 1$, $P < 0.0500$). Thus, as predicted, a majority of consort takeovers were by followers; this was particularly true on D-2, one of the two most likely days of conception.

Each of the four consort takeover tactics were used by both follower and nonfollower males (Table 1.1). For Abandoned Consort Takeovers, which made up 38% of all consort takeovers, followers and nonfollowers used this tactic a similar number of times, contrary to my prediction (Fig1.5a). As predicted, Coalitionary Challenges, which made up 10% of all consort takeovers, were carried out more often by followers ($P = 0.0004$) than nonfollowers (Fig1.5b). Notably, when both successful and unsuccessful Coalitionary Challenges are considered, 94% of coalitions were made up of at least one follower; on average, 78% of the members of a particular coalition were followers (Danish unpublished data). Contrary to my prediction, Individual Aggressive Challenges, which made up 19% of all consort takeovers, were carried out less often by nonfollowers ($P = 0.0442$) than followers (Fig1.5c). Finally, Opportunistic Takeovers were carried out equally by followers and nonfollowers, contrary to my prediction (Fig1.5d). I observed sneak copulation attempts in 7% of consort takeovers, however,

these attempts were always made by subadult, not adult, males for whom I do not have quantitative data on follower status. Of these sneak copulations attempts, two were successful, three were unsuccessful (no completed copulation), and the remaining two were uncertain.

The fixed effect Cycle day was not a significant factor in understanding variation in consort takeover type (P = 0. 5080, Table 1.2). Male Elo-rating was significant (P = 0.0040), with male dominance rank influencing takeover type as predicted (Fig1.6). Abandoned Consort Takeovers were primarily carried out by both low-and high-ranking males, which partially supported my prediction. As predicted, Coalitionary Challenges were predominately attempted by low- and mid-ranking males. Individual Aggressive Challenges were attempted primarily by higher ranking males and Opportunistic Takeovers were carried out by low- and mid-ranking males, as predicted.

Discussion

My results indicated that the behavior of followers can be distinguished from nonfollowing males. By engaging in more agonistic interactions, followers face an increased risk of injury; these interactions therefore represent a cost incurred by followers. While injury is estimated to occur in less than 1% of agonistic interactions (Drews 1996, yellow baboon *Papio hamadryas cynocephalus*), the potential cost of a severe injury is expected to exert selective pressure on males. In addition, involvement in agonistic interactions has additionally been suggested to contribute to the foraging costs incurred by consort male (Alberts et al. 1996); thus, the increased rate of agonism I observed suggests that, like consort males, followers may also face additional costs due to a loss of foraging time similar to consort males. The potential cost of following

indicates that following will be selected against unless there is a counter balancing benefit.

Followers were involved in more affiliative interactions with other followers compared to nonfollowing males. I propose that such affiliative interactions mediate the formation of coalitions against the consort male. While Coalitionary Challenges comprise only 10% of successful consort takeovers, a further 7% of all consort takeovers are Opportunistic Takeovers where the coalitionary challenge of a third party provides a distraction. In addition, since only 29% of Coalitionary Challenges succeed, coalition formation is in fact involved in more than 17% of takeover attempts. Therefore, I suggest that following provides males with an increased opportunity to find and communicate with potential coalitionary partners, as well as familiarizing themselves with the current status of the consortship and consort male. If following increases the opportunity for coalition formation, I predict that species that exhibit following will also have a higher rate of coalition formation in the context of competition for fertile females, compared to species in which following is not described.

Following provides males with access to fertile females; my data therefore support the conclusion that following is an effective alternative mating strategy. Individual Aggressive Challenge has historically been thought of as the primary mating strategy of male olive baboons and our understanding of alternative strategies typically focuses on alternatives to this strategy. Coalitionary challenge with another male has been well-studied in baboons (Alberts et al. 2003, Noë and Sluijter 1995) as such an alternative strategy. Interestingly, despite their proposed importance, Individual Aggressive Challenges only made up 19% of successful consort takeovers and

Coalitionary Challenges made up 10% of consort takeovers, with an additional 7% of Opportunistic Takeovers involving failed third party Coalitionary Challenges. Thus, these commonly studied tactics only account for 36% of all consort takeovers, consistent with Strum's (1982) suggestion that social manipulation is an alternative strategy to Individual Aggressive Challenge; my findings indicate that this tactic is equally available to followers and nonfollowers and is common (33% of consort takeovers). Surprisingly, both of these consort takeover tactics were used more by followers than nonfollowers, suggesting following is an important component of these strategies. Notably, Coalitionary Challenges were primarily carried out by low and mid ranking males, consistent with previous study of coalition formation (Bercovitch 1988; Noë 1989, 1994; Noë and Sluijter 1995; Alberts et al. 2003). While coalition formation is a frequently studied alternative mating strategy, the links, if any, to following remained unknown prior to my study. Much of our understanding of coalition formation focuses on the relative fighting ability of the coalition and target as a crucial parameter (Noë 1994; Noë and Sluijter 1995; Pandit and van Schaik 2003); Noë (1994) notes that relative fighting ability constrains the number of viable partners, but males have options for partners within that constraint. My finding that followers make up a majority of coalition participants implies that coalition formation requires time spent in proximity to either the target or coalition partners. While familiarity with coalition partners and experience have been resisted as factors in coalition formation, observation of the current conflict has yet to be evaluated.

Contrary to my predictions, Opportunistic Takeovers and Abandoned Consort Female Takeovers were used equally by followers and nonfollowers; I suggest that this

pattern is due to the nature of such consort takeovers, which are categorized by seizing a chance to obtain access to a female, not causing the opportunity- something any male in the vicinity is able to do. Opportunistic Takeovers were used more often by low and mid-ranking males as predicted, suggesting that, as with coalition formation (Bercovitch 1988; Noë 1989, 1994; Noë and Sluijter 1995; Alberts et al. 2003), higher ranking males gain less from attending to such events since they are able to succeed in Individual Aggressive Challenges without waiting for such an opportunity to arise. Finally, no sneak copulations attempts by adult males were observed. Only subadult males attempted sneak copulations and these attempts always took place during takeover attempts by adult males. Since consort males typically remained in close proximity to the consort female (Danish pers. obs.), there appeared to be little opportunity for sneak copulations, supported by other studies of baboons (e.g., Alberts et al. 2003). During takeover attempts, adult males appeared to be attempting to gain more permanent access to the fertile female than a single copulation; thus, I conclude sneak copulations are primarily a subadult strategy.

High ranking males used the Abandoned Consort Female Takeover tactic more often than predicted, although low ranking male also used this tactic more often as predicted. I hypothesized that high-ranking males may provoke consort female abandonment by intimidating or threatening the consort male, however, my data indicate that higher ranking followers do not direct more aggression towards the consort male than lower ranking followers. Sapolsky (1990) suggests an alternative, indicating that a male that remains in proximity to a consort male may prompt the consort male to abandon the female without any overt threat; he causes abandonment simply by

"maintain[ing] pressure on the courting male" (p. 117). I argue that the presence of a high ranking follower will be more stressful to the consort male than a lower ranking follower due to the likelihood of greater dominance rank disparity, even if there is no overt aggression.

High-ranking males use Individual Aggressive Challenge as expected, although surprisingly followers, as opposed to nonfollowers, used this tactic. These tactics are expressed differentially by males of differing dominance ranks, suggesting males flexibly adjust their behavior as theoretically expected (Gross 1996, Brockmann 2001) even at a level beyond the choice of following or not following. I am further examining the influence of dominance rank on the expression of following (Chapter 3). Notably, cycle day did not influence the behavioral tactic used to effect a consort takeover, suggesting that these tactics are available and effective throughout the cycle.

Based on my findings, I propose that following is an alternative mating strategy, and suggest individuals likely flexibly express follow based on dominance rank. While males of all dominance rank gain access to fertile female by following, my data indicate that following provides mid- and low-ranking males, who would otherwise be excluded from mating, with access to females. I suggest that strategy use by low- and mid-ranking males has impacted the strategies of high-ranking males, resulting in their adoption of the following strategy. I propose that the occurrence of following accounts for the well documented deviation from the priority of access model (Berard et al. 1993; Alberts et al. 2003; Wroblewski et al. 2009; Bissonnette et al. 2011; Dubuc et al. 2011) in olive baboons, and potentially other species in which following has been observed. That following is an important part of the overall system of competition and challenge has

important implications when considering the benefits and costs of mating strategies, particularly since following involves a greater time investment than the time involved in the takeover attempt itself. Though under-studied, following is a critical part of mate competition that challenges the historical view of mate competition and mating strategies in male olive baboons.

Table 1.1 Summary of the Number of Consort Takeovers and Takeover Attempts of Different Types by Followers and Nonfollowers

Takeover Type	Number by Followers	Number by Non-followers	Total Number	Proportion of all Takeovers	Number of Unsuccess-ful Attempts (followers)	Proportion of Takeover Type by Followers
Abandoned Consort	23	14	37	0.38	4 (4)[b]	0.62 (0.66)
Coalitionary Challenge	10	0	10	0.10	24 (22)	1.00 (0.94[d])
Individual Aggressive	16	3	19	0.19	12 (11)	0.84 (0.87)
Opportunistic	23	9	32	0.33	19 (12)[c]	0.72 (0.67)
Third Party Coalition	*3*	*4*	*7*	*0.07*		*0.43*
Consort-follower Aggression	*12*	*3*	*15*	*0.15*		*0.80*
Consort-nonfollower aggression	*2*	*2*	*4*	*0.04*		*0.50*
Other	*6*	*0*	*6*	*0.06*		*1.00*
Total	73[a]	26	99		59	0.73 (0.77)

a- One takeover by a follower not observed well enough to classify.

b- Likely an underestimate since we could only classify a failed attempt if the consort male moved away and the male clearly moved towards the female

c- Underestimated due to logistics of data collection during a takeover attempt; we prioritized observing the consort pair and immediate challenger, so we likely failed to record the attempts of some males. Once a takeover attempt began, other males would sometimes run towards the consort pair, but our primary attention was on males in the immediate vicinity of the consortship

d- Where at least one member of the coalition was a follower

Table 1.2 Summary of GLMMs

Model	Model/Effect	Estimate	Standard Deviation	P-value	Result as Predicted?
Question 3: which tactics do followers use?	Fixed effects: Male behavior (following)	0.7376	0.3686	0.0454	YES
		0.0242	0.0074	0.0011	
	Time Female Observed	0.1671	0.4119		YES
	Nonfollower Coalitionary Challenge	0.9249	0.2477	0.5516	
	Follower Coalitionary Challenge	0.1209	0.4197	0.0004	NO
		0.1176	0.2906	0.7727	
	Nonfollower Opportunistic			0.6857	
	Follower Opportunistic	-1.3324	0.6549		NO
				0.0419	
	Nonfollower Individual Aggressive Challenge	-0.0332	0.2966	0.9110	
	Follower Individual Aggressive Challenge				NO
	Abandoned Consort			NS	
Question 4: do male dominance rank and female cycle day influence consort takeover tactic?	Overall Model	1.1678	0.1868	0.0440	
	Fixed Effects: Elo-rating	0.0012	0.0005	0.0040	YES
	Female Cycle Day	-0.0324	-0.1243	0.5080	NO
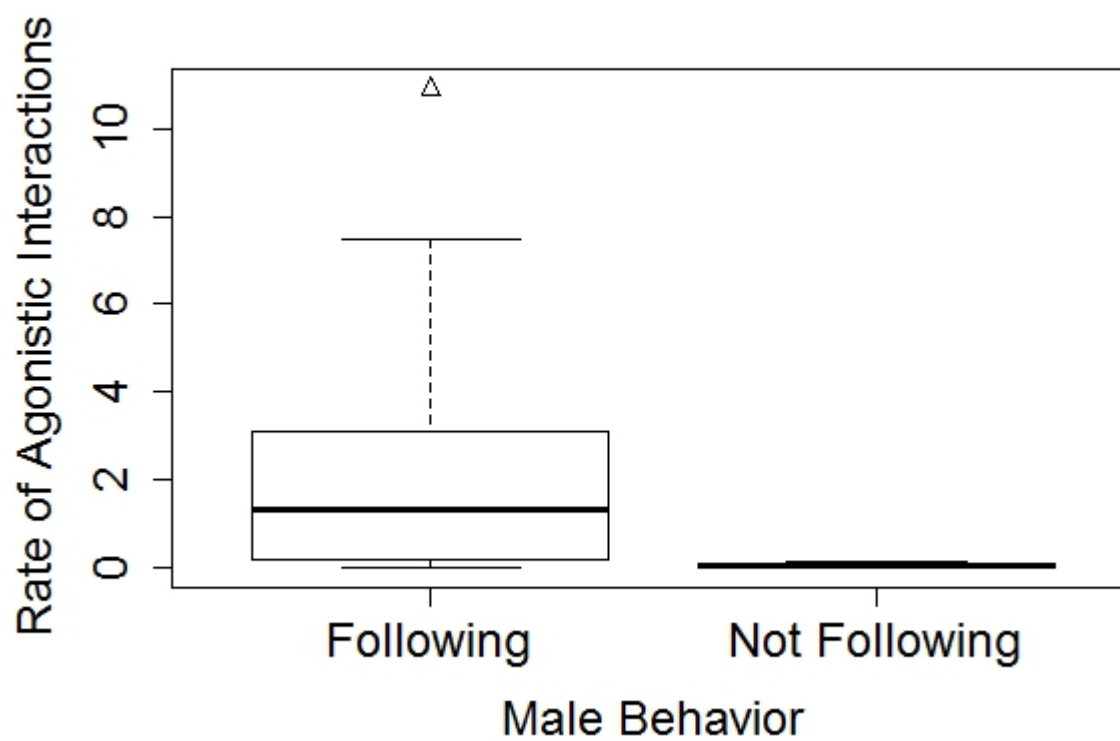
Fig1.1 Comparison of the Number of Agonistic Interactions with Males when Following and Nonfollowing
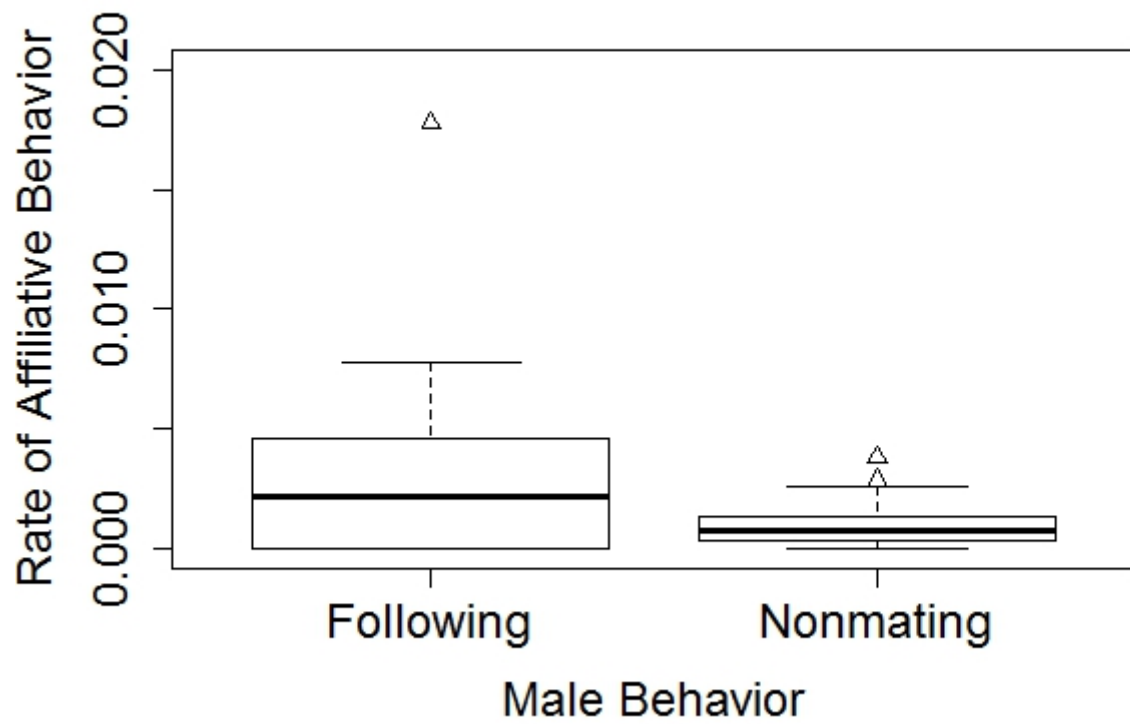
Fig1.2 Comparison of the Number of Affiliative Interactions with Males when Following and Nonfollowing
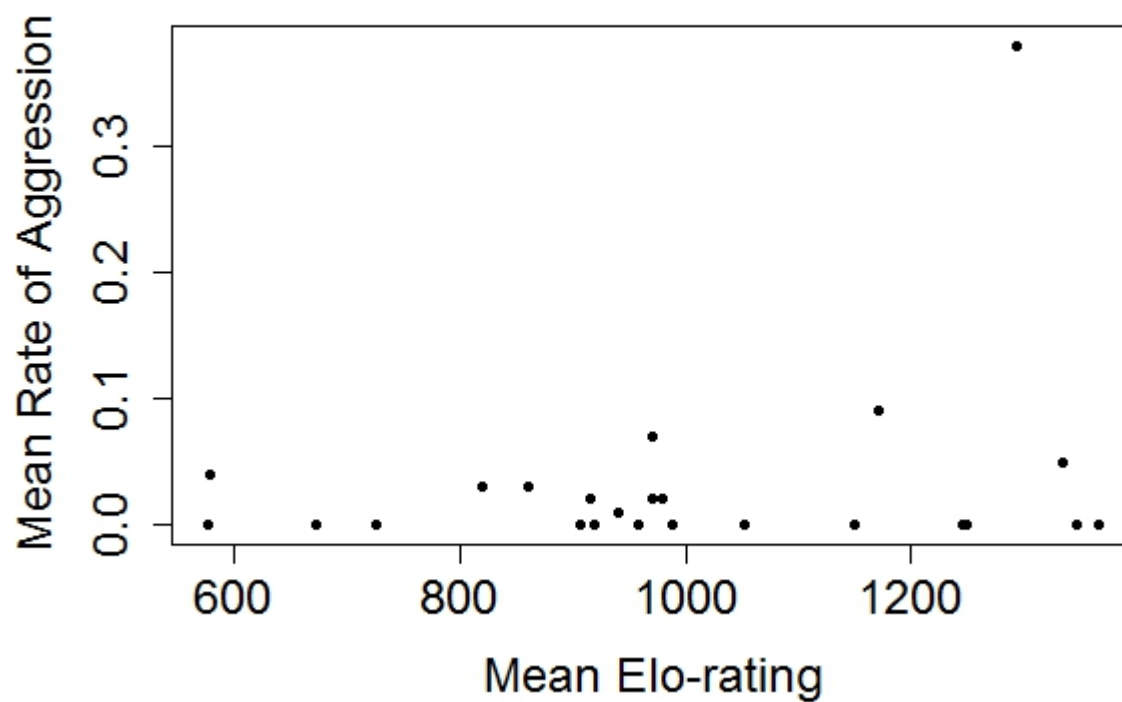
Fig1.3 Number of Agonistic Interactions with Other Followers by Male Elo-rating

Mean values for individual males.
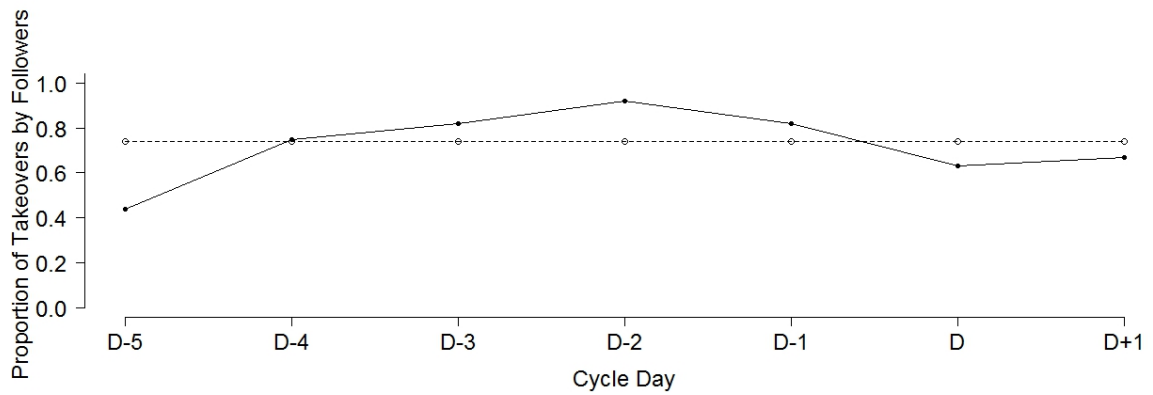
Fig1.4 Proportion of the Total Number of Consort Takeovers by Carried Out by Followers on a Particular Female Cycle Day

The dashed line is the mean of all cycle days (0.74). One asterisk- $p < 0.0500$; two asterisks- $p < 0.0050$
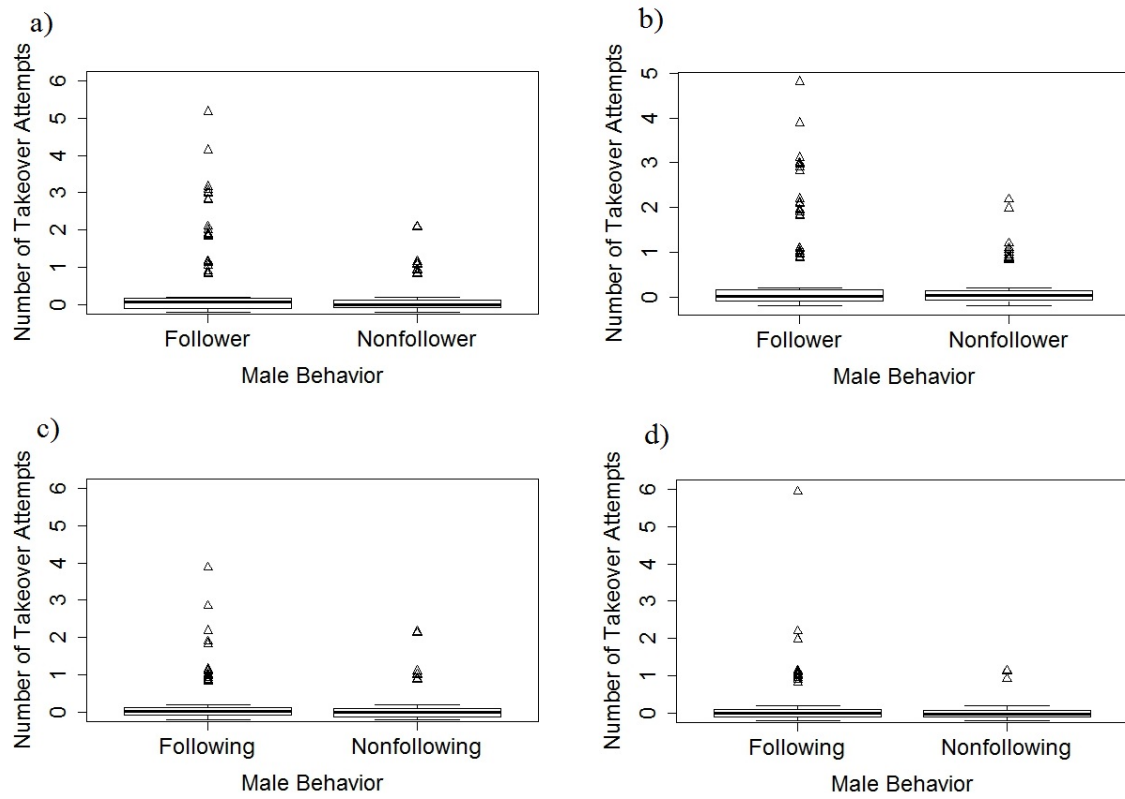
Fig1.5 Number of Consort Takeover Attempts by Followers and Nonfollowers by Consort Takeover Type

a- Abandoned consort, b- coalitionary challenge, c- opportunistic, d- individual aggressive
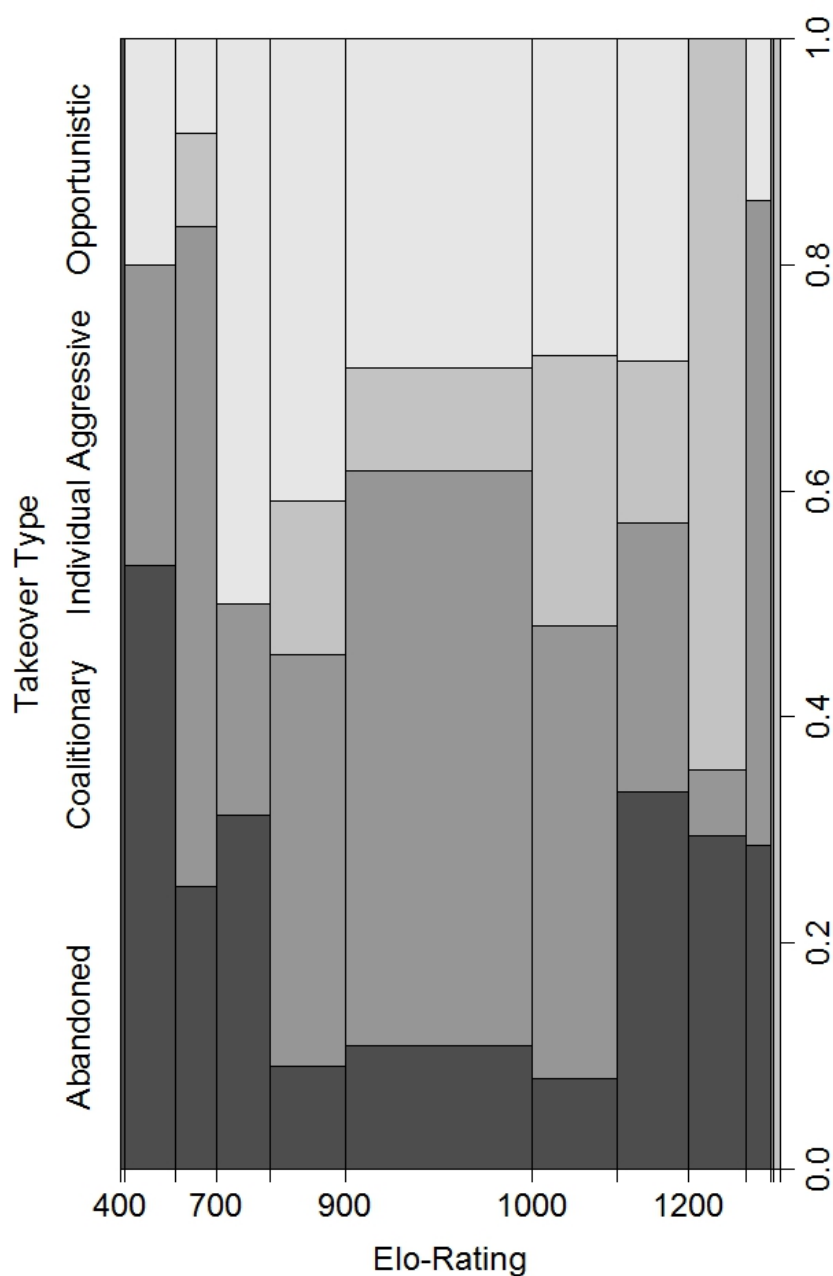
Fig1.6 Proportion of Consort Takeover Attempts by Takeover Type by Male Elo-rating

Abandoned consort- dark grey, coalitionary challenge- medium grey, individual aggressive- light grey, opportunistic- lightest grey. The width of the column corresponds to the number of consort takeovers by males of the specified Elo-rating range.

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CHAPTER TWO

DEVIATION FROM THE PRIORITY OF ACCESS MODEL AND REDUCED

REPRODUCTIVE SKEW AS A RESULT OF FOLLOWING

Introduction

Due to the marked greater difference in parental investment by females of most mammalian species (Trivers 1972), male reproductive success is expected to be highly variable and limited by access to females (Bateman 1948; Emlen and Oring 1977; Kvarnemo and Ahnesjö 1996). We therefore expect males to compete for access to females, resulting in an opportunity for sexual selection when males differ phenotypically. Males are expected to gain access to females based on the outcome of competition, which is reflected in the dominance hierarchy common in most social mammals (Parker 1974; de Ruiter and van Hooff 1993). The distribution of reproduction amongst individuals in a social group is known as reproductive skew (Keller and Reeve 1994).

Compromise models of reproductive skew postulate that observed reproductive skew is the outcome of the relative competitive abilities between dominant and subordinate individuals (Reeve *et al.* 1998). Primates violate several assumptions of these models, and therefore the use of queueing Priority of Access (PoA) models has been suggested for primates (Altmann 1962; Alberts *et al.* 2003; Port and Kappeler 2010). The PoA model predicts reproductive skew by assuming that the dominance hierarchy functions as a queue. Thus, when there is one fertile female, the highest ranking male has priority of access to that female, when there are two fertile females the two highest ranking males have access to one female, etc. Kutsukake and Nunn (2006)

have argued that this model is similar to the tug-of-war model (Reeve *et al*. 1998),

although the tug of war considers the number of males as it influences competitive

ability, not female receptivity and lacks the functional aspects of compromise models

(/Port and Kappeler 2010). In a multi-male, multi-female species like many primates, the

ability of the alpha male to monopolize access to is limited by female cycle synchrony

(Alberts *et al*. 2003; Ostner *et al*. 2008). I therefore consider the PoA model a valuable

tool to examine reproductive skew in primates.

Recent data from a number of taxa suggest that there is considerable variation in

fit to this PoA model (reviewed in Alberts 2012), and suggest that the expression of

alternative strategies is potentially relevant in understanding variation in reproductive

skew (Wroblewski *et al*. 2009; Bissonette *et al*. 2011; Dubuc *et al*. 2011). The

connection between reduced reproductive skew and male alternative strategies remains

little tested, however. I quantitatively examined reproductive skew and deviation from

the PoA model using olive baboons (*Papio hamadryas anubis*), and the influence of a

little studied alternative mating strategy, "following" (Hall and DeVore 1965; Bercovitch

1988; Forster and Strum 1994; Chapter 1) as a model system. The "primary" mating

strategy of male olive baboons is individual aggressive competition for the well known

"sexual consortship," a temporary relationship between a male and an estrous female

characterized male mate guarding (Hall and DeVore 1965; Bercovitch 1988). The

consorting pair is typically accompanied by a retinue of "followers" that maintain contact

at variable distances with the consorting pair and with each other, attempting to gain

access to the consorting female.

Since the majority of consort takeovers are by male followers, particularly during the period of likely ovulation (Chapter 1) I asked the following questions: 1) does the priority of access model account for patterns of mating in my study?; and 2) is there reproductive skew, as measured by consorting and infant paternity? I additionally asked 3) if following was responsible for deviation from the priority of access model, predicting that increases in the duration of time spent following results in increases in the duration of time spent consorting.

Methods

One habituated group of olive baboons were studied from September 2009 to July 2010 in Laikipia District, Kenya (Segera/Mutara 36°50'E, 0°15'N). I recorded female reproductive state and all observed consortships *ad libitum* each observation day. In addition, I observed select females, and associated consort and follower males, closely throughout their entire estrous cycle and for consecutive cycles until conception. I observed nine females over ten cycles.

<u>Period of Likely Ovulation</u>

Cycling female baboons develop sexual swellings, which change in size throughout their cycle. Ovulation occurs around the time when the sexual swelling undergoes rapid detumescence (Nunn 1999; Higham *et al*. 2008). I recorded the day of deflation for all females. The day of deflation and the four preceding days are the most likely days of ovulation (Alberts *et al*. 2003; Higham *et al*. 2008). All analyses were restricted to consortships occurring during this period.

Consort and Follower Status

Males were classified as either "consort males," "followers," or "nonfollowers" with respect to the focal female's consortships. Consort males were identified based on extended proximity maintenance, staying within sight of the female and following her as she travels, with a female with a sexual swelling. I categorized the remaining males in the group using a male proximity score (MP-score) modified from Smut's (1985) composite proximity score (or "C-score"), which was calculated for each male separately. I collected distances of all visible adult males to the consort male via scan samples at 15 minute intervals throughout the observation day. I used a Nikon Prostaff 550 rangefinder accurate to 0.5m within 100m. The MP score is calculated as below for each consort male-male dyad, for n scan sample intervals:

$$MP = (1/\text{distance}_1) * ([1/\text{number intervals}]*100) + \ldots (1/\text{distance}_n) * ([1/\text{number intervals}]*100)$$

The component parts of the MP-score were calculated from each scan sample interval by taking the product of the reciprocal of the distance between the males and the percentage of time at that distance (the product of the reciprocal of the number of scan sample intervals and 100). The MP-score is the sum of all such components, from the first scan sample to the nth scan sample. Based on previous studies (Danish and Palombit 2008), I classified males that were seen during more than 25% of scan samples and with a MP-score of 1.9 or higher as "followers," while males with a MP-score less than 1.9 were classified as "nonfollowers."

Observed and Expected Proportion of Consortships Obtained by Individual Males

Since I did not have exact durations of consortships observed *ad libitum*, I determined the observed and expected proportion of consortships by treating all consortship days as equivalent. If more than one male consorted with a female, I assigned each consort male half of a consortship for the day, if three males consorted with a female, I assigned each consort male one third of a consortship for the day, etc. Males' scores were divided by the total possible score. I used the same method to determine the expected proportion of consortships for each male. If there was one fertile female, the alpha male was assigned the consortship day, for two females the alpha and beta male both were assigned a consortship day, etc. For Model 1 (see Data Analysis), I used the time (in minutes) spent consorting with the focal female using the duration of the observed consortships, since I had precise data on all consort turnovers in this dataset. For the expected time consorting for this analysis, I accounted for female synchrony; if one female was consorting, the highest ranking male was expected to consort for the entire duration of consortships, if two males were consorting, each was expected to consort for half the duration of consortships, etc.

Expected and Observed Proportion of Infants Sired

The expected proportion of infants sired was the same value as the expected proportion of consortships for a male since this represented the proportion of females a male was expected to access to. The observed proportion of infants sired was determined from paternity data (see below).

Proportion of time spent following an existing consort

I calculated proportion of time spent following for all males for each focal female and cycle for each male by determining the sum of the male's time spent following (in minutes) based on MP-score and the total amount of time a male was present in the group (Chapter 3). Since consorting males cannot follow at the same time, I excluded any time a male spent consorting from the amount of time a male was present in the group.

Dominance Rank and Alpha Male Periods

I determined dominance rank from decided dyadic agonistic interactions; only supplants and submissive behaviors and vocalizations were used (e.g., bare-teeth display, fear bark) (Hall and DeVore 1965). Elo-ratings were determined for each male throughout the study period (starting value = 1000, k = 100) (Neumann *et al.* 2011); the value of the Elo-rating increases with increasing dominance rank. The rating process begins with all individuals at the same starting value, with the ratings being updated after each successive interaction. The winner gains points and the loser loses points; the number of points depends on the calculated probability of a particular outcome between the two individuals, with the maximum value set as k. This method has several advantages over the traditional dominance matrix based methods, including the ability to handle sparse data sets and detect changes in dominance rank. Comparisons have validated the robustness and reliability of this method, and even suggested that this method may increase the power of analyses. These Elo-ratings can be used to derive a linear hierarchy by listing males by their Elo-ratings in descending order, which I did for a given observation day for most analyses. Further, Neumann *et al.* (2011) indicate that the sequence of the interactions is particularly important, and that approximately nine

observations, including one with a dominant and one with a subordinate individual, are needed to calculate an accurate initial Elo-rating. These Elo-ratings can be used to derive a linear hierarchy by listing males by their Elo-ratings in descending order.

There were two alpha males during my study: JD from August 2009-December 2009, and RM from February 2010-July 2010. I therefore examined each of these periods separately and excluded any consortship data from January, during the alpha male changeover.

<u>Genetic Paternity Analysis</u>

I noninvasively collected at least two fecal samples from all adult males and adult females. Fecal samples were immediately preserved in RNAlater ® and frozen at -8°C at the end of the observation day, prior to transport to the United States.

The following measures were taken to reduce contamination: 1) separation of laboratory areas for pre- and post-PCR work; 2) the use of separate pipettes and aerosol-resistant pipette tips; 3) the use of negative controls to monitor reagents and the exclusion of all PCRs in which there was amplification in the negative control; and 4) multiple amplifications and closer examination of anomalous alleles with additional fecal extractions, using a different sample when possible, as needed (Taberlet *et al*. 1996; Fernando 2003).

DNA was extracted from fecal samples using a Qiagen DNA Stool Mini Kit, using a modified version of the Isolation of DNA from Stool for Human DNA Analysis protocol available from Qiagen (pp. 22-24). The sample was vortexed and 200μL of the sample were separated for DNA extraction. The stool samples were first lysed in Buffer ASL during a 24 hour incubation at room temperature, then impurities and PCR

inhibitors were adsorbed to InhibitEX tabelets. Proteins were digested with Proteinase K during a 30 minute incubation at 70°C, rather than the ten minutes recommended by Qiagen (Moscovice et al. 2009; Strier et al. 2011). Buffering conditions were adjusted by adding 100% ethanol, then DNA was bound onto a QIAamp silica-gel membrane. DNA was purified through the use of two wash buffers, then eluted in 100μL of Buffer AE. If previous extractions had not yielded an extraction that amplified well, I ran this extraction procedure on multiple 200μL aliquots from the same fecal sample, combining them in the binding stage.

The use of a "multi-tubes" approach has been recommended as this facilitates the detection of allelic dropout, false alleles, and contamination; this approach consists of multiple amplifications of a single DNA extract (Taberlet et al. 1996). A multi-samples multi-extracts approach is recommended as an extension of the multi-tubes approach; multiple samples are collected for each individual, with multiple extractions for each sample, in addition to a multi-tubes approach (Goosens 2000). Therefore, I used the multi-tubes approach (Taberlet et al. 1996) and used extractions from more than one fecal sample when possible.

I identified potential microsatellite loci by screening loci used in previous study of chacma and yellow baboons (Di Fiore pers. comm.; Buchan et al. 2005; Moscovice et al. 2009; Moscovice et al. 2010). Since false alleles are more common in dinucleotide repeat microsatellites, compared to di- and tri-nucleotide repeats, I preferentially screened tetranucletide repeat microsatellite loci (Taberlet et al. 1996; Morin et al. 2001; Fernando 2003). I initially screened these loci using five to ten individuals from my population that were thought to be unrelated; if these individuals were monomorphic, I considered the

locus uninformative and did not use such loci in my analysis. I continued screening loci until I had ten variable loci (Table 2.1); I genotyped all individuals at a minimum of nine of ten of these loci.

Since multiplex PCR is recommended to obtain more results from limited DNA (Taberlet *et al*. 1996), I tested different combinations of loci. I first ran loci singly, then paired loci that had size disparity and tested these combinations on samples with known genotypes at both loci. I tested different annealing temperatures, relying on protocols from previous study as well (Burell pers. comm.; Di Fiore pers. comm.; Moscovice et al. 2009; Moscovice et al. 2010). If there was extraneous amplification or it was difficult to call alleles, the loci combination was not used. All Multiplex reactions used primers with different fluorescent labels.

The PCR mix for the ten microsatellite marker loci was as follows: 1) 2.5uL of 2X Multiplex ® Mix (from Qiagen Multiplex PCR Kit), 2) 0.5uL of Bovine Serum Albumin (5.5mg/mL), 3) 1.0uL of Primer Mix with 0.2μL of each 10mmol primer and remaining volume of RNAase free water, and 4) 1.0-2.0 uL of DNA template. Bovine Serum Albumin (BSA) was included since it binds compounds that reduce the amplification of target DNA that are often present in feces (e.g., polysaccharides, pigments, RNA) (Morin *et al*. 2001; Fernando 2003). I varied the volume of DNA template based on previous PCR results, increasing the volume if amplification was low. The cycling conditions were as follows: 1) initial denaturation was 95 º C (hot start) for 15 minutes; 2) Annealing was at variable temperatures (Table 2.1), and repeated 36-40 times, depending on DNA concentration of extraction: a) 94 º C for 30 seconds, b)

annealing temperature for 1.5 minutes, and c) 72°C for one minute; and 3) final extension was 72 ºC for 30 minutes.

The PCR products were separated and visualized on an ABI 3730 DNA Analyzer (Applied Biosystems) using GeneScan 500 ROX[TM] size standard (Applied Biosystems) and POP-7[TM] polymer (Applied Biosystems). The raw data were analyzed by GeneMapper v4.0 (Applied Biosystems). I determined the size of all alleles for a locus, and assigned alleles only if a datum was within one base pair in length of that allele and if the peak height was higher than the size standard; I ran a new PCR to confirm findings that did not fit these criteria.

When working with DNA extracts of low concentration, stochastic sampling errors when pipeting template DNA may occur (Tberlet et al. 1996). In this instance, it is possible for only one allele of a heterozygote to be amplified and detected. DNA degradation may exacerbate this problem. As a result, an individual may be incorrectly identified as a homozygote; this failure to detect a true heterozygote is referred to as allelic dropout. The concentration of the extract affects the rate of allelic dropout; allelic dropout is more frequent in amplifications of low concentration extracts (Morin *et al*. 2001). To account for allelic dropout and the influence of DNA concentration, all heterozygous genotypes were confirmed after a minimum of two replicates and all homozygous genotypes were confirmed after a minimum of seven replicates (Taberlet *et al*. 1996).

I assigned paternity using maximum likelihood methods, as implemented in the program CERVUS 3.0 (Kalinowski *et al*. 2007). Classic paternity analyses rely on exclusionary methods; genetic data are used to exclude putative fathers and paternity is

assigned (if possible) to a single nonexcluded male (Marshall *et al*. 1998). This method is limited in its use, particularly in cases where multiple males are not excluded; this method is only able to unambiguously assign paternity for a small percentage of offspring (Chakraborty *et al*. 1997). Likelihood methods like CERVUS 3.0 (Kalinowski *et al*. 2007), however, assign paternity to the male with the highest log-likelihood ratio (LOD score) (Thompson 1986; Meagher 2013). The likelihood of paternity for a particular male divided by the likelihood of paternity for a random male comprises the likelihood ratio. The LOD score is the logarithm of this ratio. When multiple loci are used in the analysis, likelihood ratios are derived at each locus and multiplied together before the natural log is taken.

Microsatellite loci commonly have nonamplifying or null alleles, which occur when there are mutations in the flanking sequence of the microsatellite locus, resulting in changes in the priming site (Pemberton *et al*. 1995). Notably, the occurrence of null alleles varies across both loci and populations (Di Fiore 2003). Null alleles can be detected by lowering primer stringency to account for sequence mismatches at the priming site or by redesigning primers (Pemberton *et al*. 1995). Null alleles can also be accounted for during the analysis itself. Allowing a certain level of mismatch between individuals prevents excluding potential parents due to an apparent mismatch, when the individuals actually share a null allele. In addition, null alleles can be detected through mismatches between known mother-offspring dyads and deviations from Hardy-Weinberg equilibrium. In my dataset, I found one mother-offspring mismatch at one locus (female FL and infant FK), but as both individuals were heterozygous, this mismatch is not consistent with the presence of a null allele. I also tested all loci for

deviation from Hardy-Weinberg equilibrium using CERVUS 3.0 (Kalinowski *et al*. 2007); all loci were at Hardy-Weinberg equilibrium, indicating the likely absence of null alleles at these loci. At lower frequencies, such null alleles are more difficult to detect, but may be accounted for in the error rate, which accounts for null alleles. In my CERVUS simulations, I assumed the proportion of loci mistyped was 0.02, based on observed mother-infant mismatch rates from my dataset.

In my simulation, I assumed that 95% of potential fathers had been genotyped. All mothers were sampled since the success rate of CERVUS (Kalinowski *et al*. 2007) is increased when the mother is genotyped; in particular, at least twice as many loci are needed to compensate for the lack of the maternal genotype (Marshall et al. 1998). I also collected fecal samples from nine of eleven infants conceived during my study that survived to at least six months of age. All infants were conceived during JD's alpha period. I also examined mother-infant mismatch at individual genotypes; there was a single mismatch, in a pair that was assigned maternity in all simulation. I ran an analysis of maternity using CERVUS 3.0, setting the percent of potential mothers samples as 27% based on number of adult females in the population genotyped. Six infants were correctly matched to their putative mother, three at strict confidence and three at relaxed confidence. One infant could not be matched since I was unable to obtain a viable extraction from the putative mother's fecal samples, but my simulation was unable to assign a different female as most likely mother for this infant. One infant was assigned to a female not thought to be the putative mother, however, this assigned mother's infant was of different age and sex (and so unlikely to be mistaken identity) and the next most likely mother assigned by CERVUS (with a positive LOD) was the putative mother.

Data Analysis

I used Spearman's rank correlations to examine the relationship between the observed and expected proportion of consortships for both alpha male periods to examine fit with the priority of access model. I also calculated Departure-from-Model (Alberts *et al*. 2003); the higher this value, the greater the deviation from the priority of access model.

I also used Spearman's rank correlations to examine the relationship between the actual proportion of infants sired and the expected proportion of infants sired and between the proportion of infants sired and the observed proportion of time spent consorting during JD's tenure as the alpha male. Since I ran three Spearman's rank correlations for JD's tenure, I used the Holm-Bonferroni Method to account for multiple testing.

I examined reproductive skew using several methods, in order to allow my results to be compared with other studies. First, I determined the correlation between numerical dominance rank and the proportion of time spent consorting using a Spearman's rank correlation. I additionally calculated two indices of mating skew calculated with the Skew Calculator 2003 (https://www.eeb.ucla.edu/Faculty/Nonacs/shareware.htm): lambda (Kokko *et al*. 1997) and the binomial skew index (B index) (Nonacs 2000; Nonacs 2003). These indices examine reproductive skew without considering dominance rank.

I used a Generalized Linear Mixed Model (GLMM) to examine the factors that influenced the observed proportion of consortships obtained by a male for the female cycles we observed closely using the glmmPQL package (part of MASS library) in the

statistical software R v2.1.5.1 (R Development Core Team 2010) to account for overdispersion, since there was more variance in the model than predicted by other modeling packages (Bolker *et al*. 2008). These data and the standard errors of the data were Poisson distributed, as confirmed by a Goodness-of-Fit test. The response variable for the GLMM was the time (in minutes) spent consorting (n=141, 9 females, 10 female cycles, 21 males). There were two fixed effects: 1) the expected time (in minutes) spent consorting as predicted by the PoA Model; and 2) time (in minutes) spent following. Values for the response variable and fixed effects were calculated for each male and female/cycle. The random effect was male identity.

Results

The proportion of observed consortships and the expected proportion of consortships were correlated during RM's alpha period (r=0.6500, p=0.0067, Fig2.1), but not JD's alpha period (r=0.23, p=0.3352, Fig2.2). Deviation-from-Model Alberts *et al*. 2003 was 1.97 for JD and 1.21 for RM. As a comparison with Alberts et al.'s (2003) dataset of 64 six month group periods, the highest Deviation-from-Model reported in this study was approximately 1.55, suggesting that my study population deviated from the priority of access model during both alpha male periods. In particular, the alpha male obtained a lower proportion of consortships and lower ranking males obtained a higher proportion of consortships than expected, with even the lowest ranking male often consorting at least occasionally.

The proportion of infants sired was not correlated with the expected proportion of infants sired (r=0.3200, p=0.1774) or the observed proportion of consortships (r=0.2300, p=0.0571). Infants were sired by males of all dominance ranks, and no male

sired more than 22% of the infants (see Table 2.2, Fig 2.3). Moreover, the current alpha male sired no infants, although the future alpha male sired 22% of infants.

There was a negative correlation between dominance rank and the proportion of time spent consorting during both alpha male tenures (JD -0.52, RM -0.68), indicating that higher ranking males consorted more than lower ranking males. The B index for both periods were significantly positive (JD 0.0416, RM 0.0766, p<0.0500), indicating that mating was skewed. The low lambda values (JD 0.1632, RM 0.2522) and B indices indicated that the reproductive skew was low, however, and higher during RM's alpha male period.

The expected proportion of consortships based on the predictions of the PoA Model did not influence the amount of time males consorted (t=1.3, p=0.1859). As the proportion of time spent following increased, so did the observed time consorting (t=7.5, p<0.0001) (Fig2.4). In addition, my observations indicated that all sires were observed to follow during the relevant conceptive cycle (n=6).

Discussion

My findings indicate that, while there is reproductive skew in olive baboons, it is low and there is considerable deviation from the Priority of Access Model. I also demonstrate variation in the fit to the PoA model during different time periods in my study group, consistent with previous study (Alberts *et al*. 2003; reviewed in Alberts 2012). Departure-from-Model at the end of one alpha male's tenure (JD) was higher than Departure-from-Model at the beginning of the other alpha male's tenure (RM). In addition, the expected proportion of consortships obtained by a male was not correlated with the observed proportion of consortships during JD's alpha male period, but was

during RM's alpha male period, suggesting that the PoA model better predicted the observed proportion of consortships during RM's alpha male period. Since Departure-from-Model is expected to decrease as the alpha male's tenure increases (Alberts *et al.* 2003), this was unexpected. I suggest that the period of time in which the alpha male's rank is declining will result in lower reproductive skew as a result of the increased ability of lower ranking males to compete with the alpha male.

Notably, there were differences in the maximum number of females cycle synchronously during the two alpha male periods (JD, n=5; RM, n=3). While the influence of female synchrony on the expected proportion of consortships is accounted for in the predictions of the PoA model, the influence of synchrony on following is not. Previous study indicated that both dominance rank and the number of times a male followed influenced male success at obtaining a consortship via a takeover as a follower (Chapter 3). I suggest that followers may be more likely to encounter a consort male with lower rank disparity as female cycle synchrony increases, resulting in a greater likelihood of obtaining a consortship and reduced reproductive skew.

My paternity analysis indicates that direct reproductive success matches the low reproductive skew determined from behavioral observations. While high ranking males sired more offspring than lower ranking males, lower ranking males also sired more offspring than expected. Previous study of yellow baboons (*Papio hamadryas cyncephalus*) indicates that dominance rank is strongly linked to the number of offspring sired; in particular, males ranked below fifth in the dominance hierarchy experienced the sharpest decline in infants sired (Alberts *et al.* 2006). While Moscovice *et al.* (2009) report that 14 of 18 chacma baboon (*P .h. ursinus*) infants born over a three year period

were sired by males that dominated a high proportion of other males in the group (0.86-1.00), while only four infants were sired by lower ranking males. While it is not possible to ascertain fit to the priority of access model or the degree of alpha male monopolization from the information provided, the high concentration of paternity in high ranking males suggests higher reproductive skew than in this study. Dominance rank predicted male's ability to sire offspring in chimpanzees (*Pan troglodytes schweinfurthii*), although lower ranking males did sire more offspring than expected and the most successful male sired 30% of infants (Wroblewski *et al.* 2009). My findings are similar to Dubuc *et al.*'s (2011) finding in rhesus macaques (*Macaca mulatta*); the male with the highest proportion of infants sired only one third of infants and paternity was not related to male dominance rank. In addition, Strier *et al.*'s (2011) study found that the most successful male northern muriqui (*Brachyteles hypoxanthus*) sired only 18% of infants. Therefore, my findings differ from those of other *Papio hamadryas* subspecies, but recent studies of other species suggests that a similar pattern may be found more widely in the primates

One consequence of reduced reproductive skew is that cohorts of infants in some species will not be likely to be related paternally as previously suggested (Alberts 1999; Widdig *et al.* 2001; Smith *et al.* 2003). Comparative data presented above suggests that even closely related species may differ in this regard. Notably, individuals are often predicted to bias their affiliative behavior towards similar aged individuals, since they are more likely to be paternally related. My findings do not support this prediction, however, and suggest that phenotypic matching, rather than an association cue, would be necessary for kin recognition in this species. Additionally, if males stay in a group and are able to

reproduce in multiple years as suggested by my findings, I do expect individuals to be paternally related across age cohorts.

Reproductive skew potentially influences male-infant and male-female relationships, particularly since baboons are known for their distinctive male-female "friendships (Palombit *et al.* 1997; Palombit 2003). Data suggests that these friendships function as an anti-infanticide strategy in chacma baboon (Palombit *et al.* 1997). Notably, the risk of infanticide is much lower in olive baboons, and friendships in olive baboons are less cohesive and investment in the relationship is more male biased than those of chacma baboons (Palombit 2003). Evidence from playback experiments suggests that friendships in olive baboons function to reduce female harassment by conspecific females, rather than infanticide (Lemasson *et al.* 2007). There is contradictory data regarding the influence of paternity on male-infant interactions, however. Buchan *et al.* (2003) indicate that yellow baboon males defend their genetic offspring more than putative offspring (based on male consort behavior) and unrelated juveniles. On the other hand, Nguyen *et al.* (2009) study, in the same population as Buchan *et al.* (2003) indicate that only 50% of male friends are the father of their female friend's infant. Chacma baboon males also provide paternal care to unrelated infants; Moscovice *et al.* (2010) suggest that males pursue a "bet hedging" strategy, caring for infants they may have sired, since the cost of failing to protect an infant are high due to infanticide. If males form friendships based on consortship activity, reduced reproductive skew may result in reduced competition between females for access to male friends (Palombit *et al.* 2001). Forming friendships with unrelated infant's mothers would also have a higher likelihood of success when male sexual access to females is

determined less by the outcome of male intrasexual competition (Smuts 1985; Palombit *et al.* 1997).

My study provides quantitative behavioral and genetic evidence that following, an alternative mating strategy of olive baboons, directly influences reproductive skew, independent of the dominance rank and female cycle synchrony dependent expectations of the Priority of Access Model. Moreover, males that sired offspring followed during the conceptive cycle. My analyses also indicate that the time allocated to following influenced a male's time consorting. Thus, following is directly linked to both consortship and paternity success. Such alternative mating strategies provide lower ranking males with an alternate means of competing with higher ranking males (Anderrson 1994). Tug-of-war models of reproductive skew (Reeve 1998) base their predictions on male competition and allocation of resources; alternative strategies alter the relative competitive abilities of males. Thus, alternative strategies need to be considered in models of reproductive skew. Reproductive skew models provide a framework for understanding the factors that shape social groups and are thought to direct the evolution of key aspects of sociality; understanding causes for variation in such models are therefore critical to my understanding of understanding social evolution (Keller 1994). My findings particularly suggest that paternal kinship can not be simply estimated based on age cohorts, which alters our predictions relating to paternal kin selection.

Table 2.1 Loci and Annealing Temperatures

Locus	Repeat Type	Number of Alleles	Size range	Multiplex PCR Group	Annealing Temperature for PCR	Deviation from Hardy-Weinberg Equilibrium?
D1s548	Tetranucleotide	5	196-212	A	57°C	NO
D2s119	Dinucleotide	5	207-221	B	53°C	NO
D2s1326	Tetranucleotide	9	245-272	A	57°C	NO
D3s1766	Tetranucleotide	6	209-234	C	57°C	NO
D4s243	Tetranucleotide	6	154-178	C	57°C	NO
D5s111	Dinucleotide	11	143-171	D	55°C	NO
D5s1457	Tetranucleotide	7	109-142	E	55°C	NO
D10s611	Tetranucleotide	11	148-194	E	55°C	NO
D11s2002	Tetranucleotide	9	249-282	D	55°C	NO
D14s306	Tetranucleotide	6	166-182	B	53°C	NO

Table 2.2 Dominance Rank and Behavior of Genetically Identified Most Likely Sire

infant	dominance rank of father (of 19 males)	confidence level	did genetically identified most likely sire follow during the female's conceptive cycle?
CV	14	95%	YES (50%)[a]
CZ	13	95%	YES (100%)
EC	4	95%	YES (100%)
FK	2	95%	Not well observed
NY	5	95%	YES (50%)
OD	11	80%	Not well observed
SC	5	95%	Not well observed
VH	8	95%	YES (25%)
YT	2	95%	YES (78%)[a]

Percent of time that the father followed was estimated from the number of consortships (from D-4 to D in the mother's cycle) the male was qualitatively observed to follow divided by the total number of consortships observed (excluding those where the father was the consort). Percents marked "a" were derived from exact durations. For consortships I did not collect spatial data, I identified followers qualitatively.
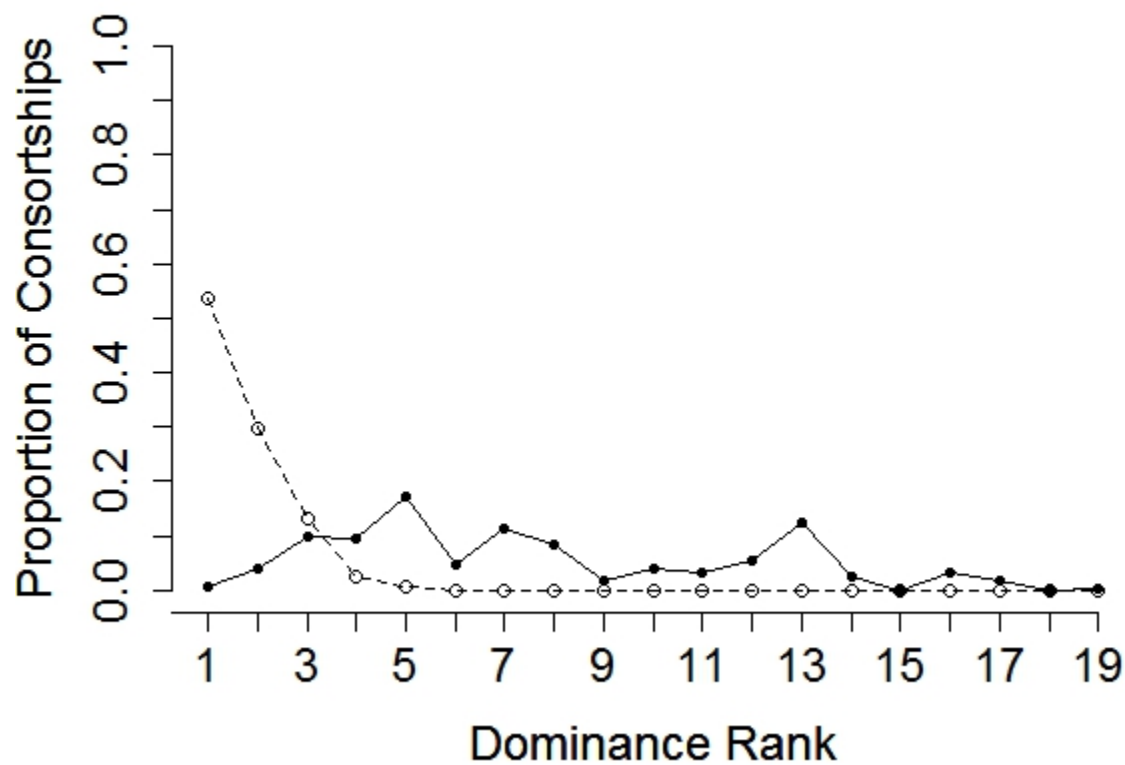
Fig2.1 Observed and expected proportion of consortships by dominance rank

(Alpha Male JD)

The expected proportion of consortships is the dashed line.
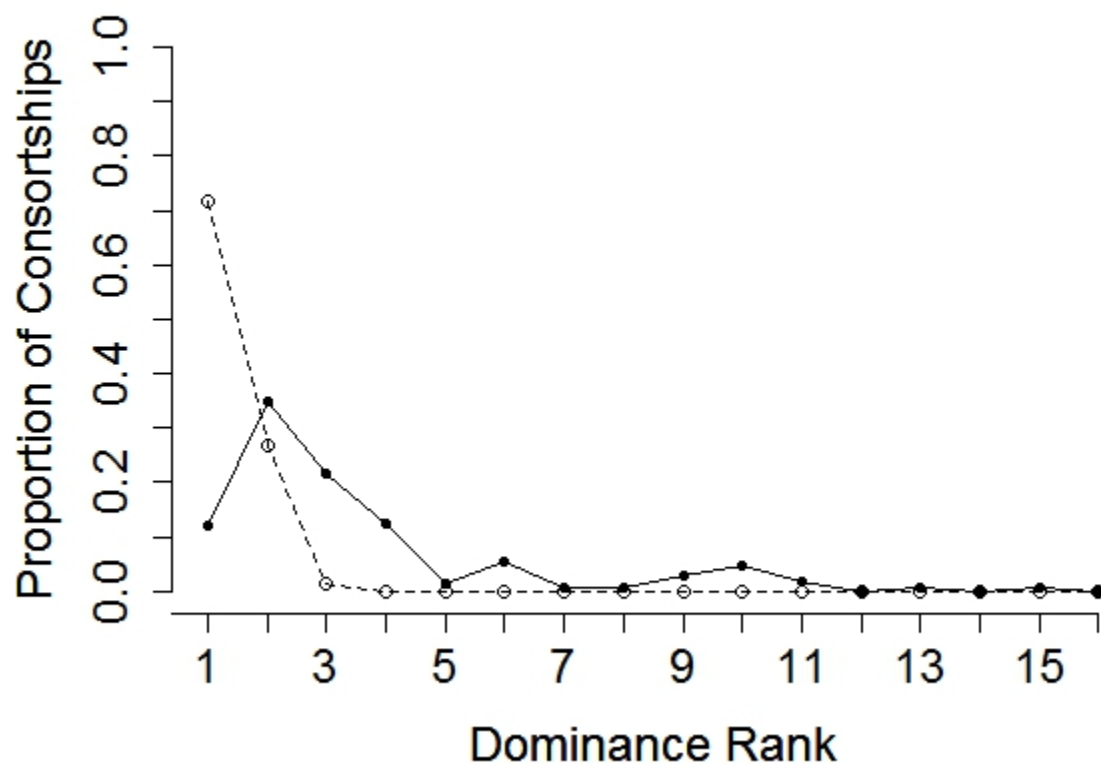
Fig2.2 Observed and expected proportion of consortships by dominance rank

(Alpha Male RM)

The expected proportion of consortships is the dashed line.
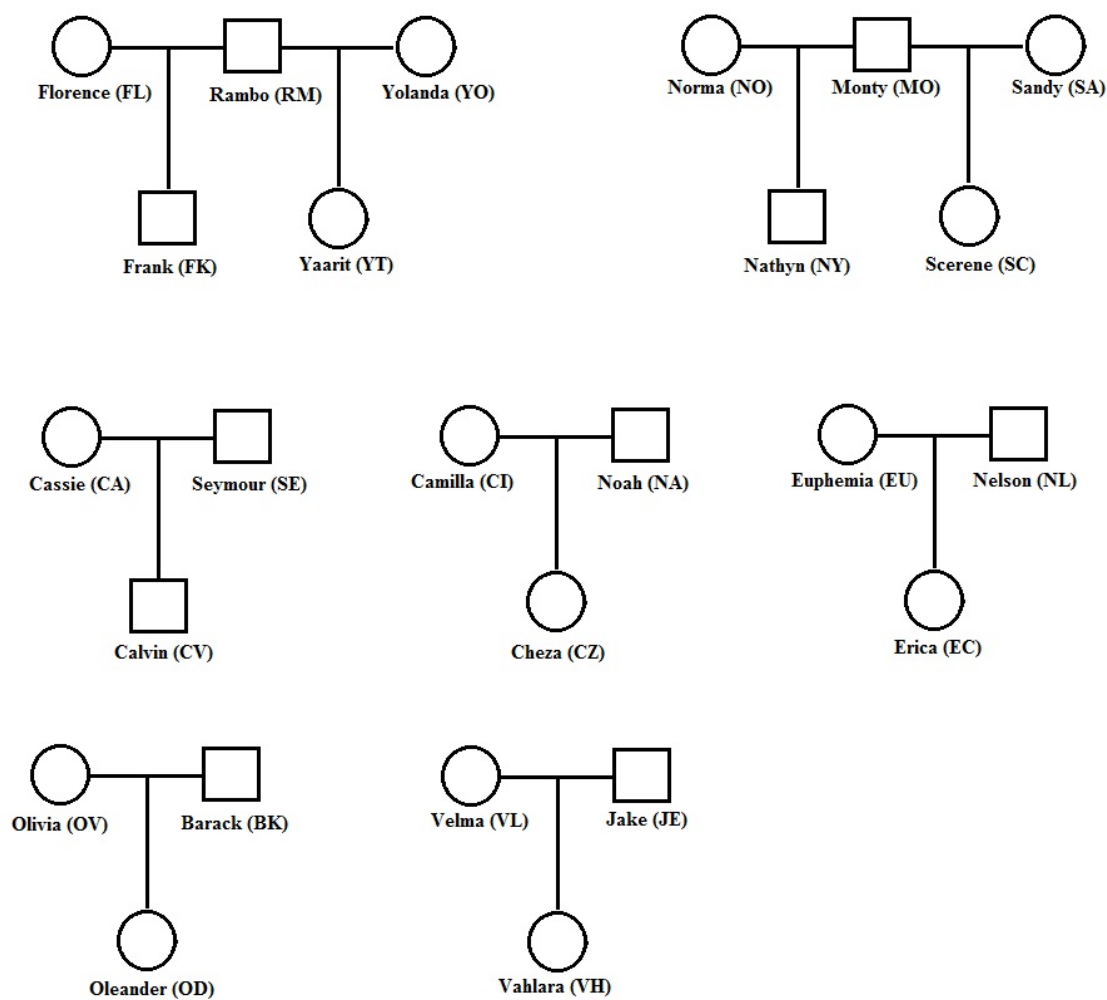
Fig2.3 Pedigree of Infants
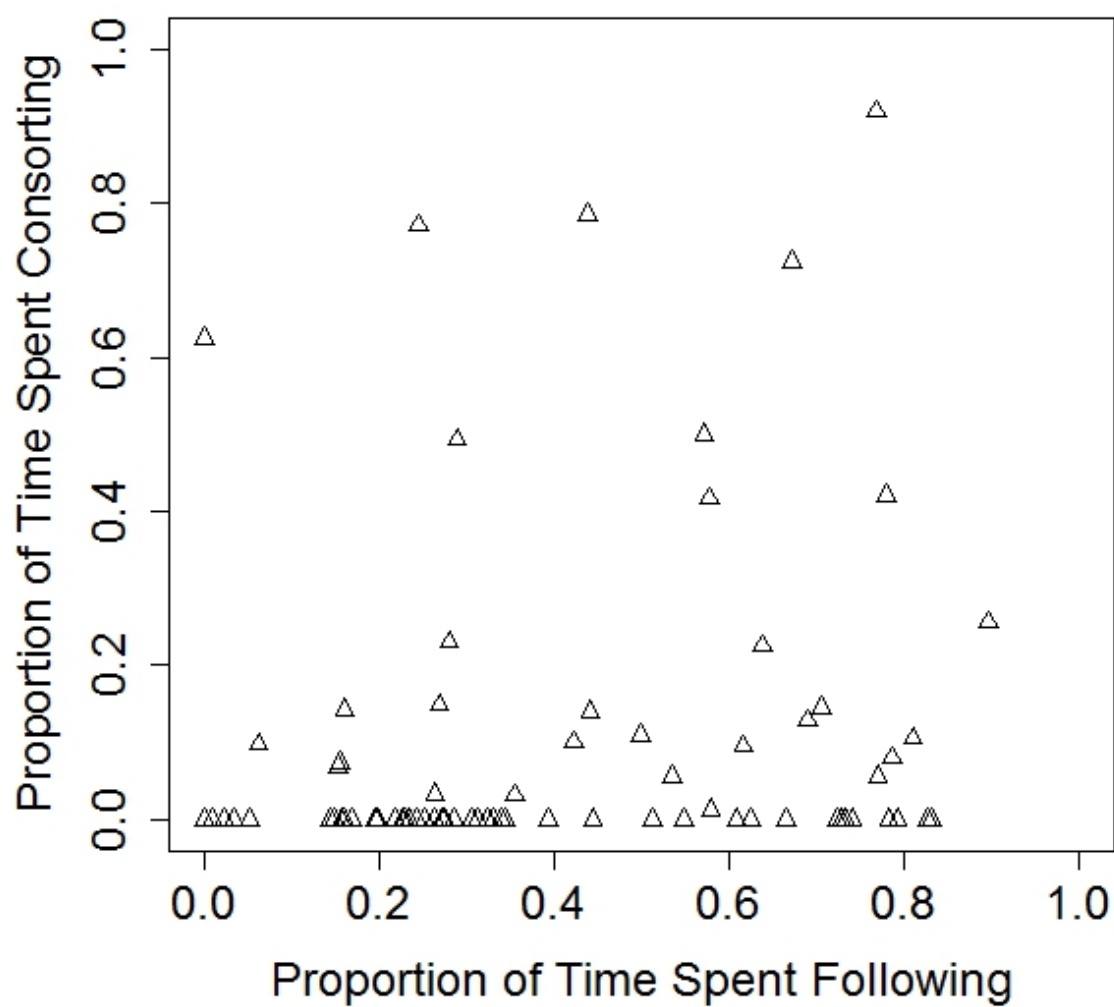
Fig2.4 Influence of the proportion of time spent following on the observed proportion of consortships

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CHAPTER 3

INFLUENCE OF DOMINANCE RANK AND GROUP SIZE ON THE

EXPRESSION OF FOLLOWING

Introduction

Alternative mating strategies, a subset of alternative reproductive strategies, which involve the behaviors related to the acquisition and retention of fertile females, are thought to arise in response to intense sexual selection (Bercovitch 1997; Andersson 1994; Gross 1996; Brockmann 2001). Thus, as reproductive success becomes more skewed there is increased selective pressure for individuals attaining low or no reproductive success to increase their individual reproductive success (Neff 2001; Shuster and Wade 2003). Gross (1996) argues that "status-dependent" alternative mating strategies allow individuals to maximize reproductive success by the dynamic expression of alternative strategies based on conditions that are both intrinsic (i.e., condition) to the individual and extrinsic (i.e., environmental) (Maynard-Smith 1979; Dawkins 1980; Andersson 1994; Repka and Gross 1995; Gross 1996; Brockmann 2001). Thus, the choice of alternative strategy depends on the individual's condition as an individual's phenotype affects the potential fitness benefits of alternative strategies.

Such conditional alternative mating strategies are observed throughout many taxa (reviewed in Oliviera *et al*. 2008). For example, male Italian tree frogs (*Hyla intermedia*), like many anurans, rely on either an advertising or satellite strategy at a lek (Castellano *et al.* 2009). The expression of these strategies is size dependent, with large males defending a lek and advertising their presence vocally, while smaller males adopt a "satellite" strategy, attempting to intercept females. An alternative strategy to territory

defense observed in both fish and sexually dichromatic birds is female mimicry

(Taborsky 1994; Slagsvold and Sætre 1991; reviewed in Krüger 2008). In the pied

flycatcher (*Ficedula hypoleuca*), for example, younger males may not develop adult

plumage, instead retaining a juvenile female-like plumage and remaining in the territories

of older territorial males and attempting to obtain surreptitious copulations from females.

While alternative mating strategies do not necessarily generate equivalent

benefits, the particular strategy adopted is predicted to maximize an individual's fitness

in light of individual condition or phenotype (Andersson 1994; Gross 1996; Brockmann

2001; Shuster and Wade 2003). Since individuals can potentially switch between

alternative strategies, and therefore exhibit phenotypic plasticity, these strategies are

considered "reversible" (Brockmann 2001; Shuster and Wade 2003). Shuster and Wade

(2003) predict that the most flexible strategies, in terms of rapidity and reversibility of

strategy switches will be behavioral strategies. They additionally predict that such

behavioral strategies are selected for when males experience many reproductive

opportunities and have access to environmental cues regarding these opportunities.

Thus, the nature of environmental conditions, particularly the spatial and temporal

distribution of reproductive opportunities, influences the expression of alternative mating

strategies (Brockmann 2001; Shuster and Wade 2003). The operational sex ratio (OSR)

provides a relative measure of the number of females available to a male and is expected

to influence the evolution of alternative mating strategies, since the intensity of sexual

selection will increase as OSR becomes more male-biased (Emlen and Oring 1977;

Kvarnemo and Ahnesjö 1996). Notably, since the number of reproductive opportunities

is important in alternative mating strategy theory (Shuster and Wade 2003), the absolute

number of fertile females may be important as well. Female synchrony will also influence male behavior, as males may be unable to monopolize access to multiple females concurrently. Female synchrony is expected to increase as the number of females increases, due to the increased likelihood of a greater number of females' cycles overlapping (Cowlishaw and Dunbar 2001). Little is known about the interaction of the spatio-temporal availability of females and male condition, but it is expected to influence the expression of alternative strategies as well as the evolution of behavioral strategies.

The foundation of alternative mating strategy theory derives primarily from studies of nonmammalian taxa (Andersson 1994; Brockmann 2001; Shuster and Wade 2003). Studies of alternative mating strategies in primates are relatively rare; two alternative strategies that have been suggested for primates living in multi-male, multi-female groups are the formation of coalitions and sneak copulations (Bercovitch 1988; Kuester and Paul 1989; Noë 1989, 1994; Brereton 1992; Berard *et al*. 1994; Noë and Sluijter 1995, Soltis *et al*. 1997; Soltis et al. 2001; Alberts *et al*. 2003; van Schaik *et al*. 2004). Notably, data support the use of these strategies as an alternative to solo competition by lower ranking males; middle-ranking males participate in the majority of the coalitions in olive baboons (*Papio hamadryas anubis*), and yellow baboons (*P.h. cynocephalus*). These coalitions also most often target higher ranking males (Bercovitch 1988; Noë 1989, 1994; Noë and Sluijter 1995; Alberts *et al*. 2003). The use of sneak copulations exhibits a similar pattern, with subadult (adolescent males, lower ranking as a result) or subordinate males and males of low status using this strategy (tufted capuchin monkeys *Cebus apella nigritus*, Alfaro 2005; yellow baboons *P.h. cynocephalus*, Alberts *et al*. 2003; Barbary macaques *Macaca sylvanus*, Kuester and Paul 1992, Bissonnette *et*

al. 2010, and Kuester and Paul 1989; stumptail macaques *Macaca arctoides*, Brereton 1992; Japanese macaques *M. fuscata* Soltis *et al.* 2001). These males are observed mating rapidly, often covertly, when consort males are distracted often by an ongoing fight for access to the female (Kuester and Paul 1989). Sneak copulations have also been observed in fish (Anderrson 1994), which differ from the primates due to the occurrence of external fertilization in fish. A similar influence of dominance rank on alternative strategy expression has been found in other mammalian species (e.g., fox squirrel *Sciurus niger* Koprowski 1993; eastern gray squirrel *Sciurus carolinensis* Koprowski 1995; fallow deer *Dama dama* Moore *et al.* 1995; Antarctic fur seals *Arctocephalus gazella* Gemmel *et al.* 2001; feral goat *Capra hircus* Saunders et al. 2005; mountain goat *Oreamnos americanus* Mainguy *et al.* 2008).

As discussed above, a commonly examined aspect of an individual's condition for group living species, particularly in primates, is dominance rank. The outcome of individual competition is determined mostly by dominance relationships, which reflect enduring differences in competitive ability or resource holding potential (Parker 1974; de Ruiter and van Hooff 1993; Martin and Bateson 1993). Dominance rank is the outcome of a series of agonistic and submissive interactions with other males; a male's rank informs us about his relative competitive abilities within his current social group. Dominance rank often predicts male mating success in primates, with higher ranking individuals having a priority-of-access to fertile females, particularly when the outcome of individual competition is determined primarily by dominance relationships (Smuts 1987; Bulger 1993; de Ruiter and van Hooff 1993; Weingrill et al. 2000; Alberts *et al.* 2003; Majolo *et al.* 2012).

Recent data from a number of primate taxa, however, reveal the limits of this priority-of-access model (Berard *et al.* 1993; Alberts *et al.* 2003; Bissonnette *et al.* 2011; Dubuc *et al.* 2011; Wroblewski *et al.* 2009; this current study Ch.2), indicating that high ranking males do not always monopolize mating and suggesting that lower ranking males rely on an alternative strategy to increase their reproductive success. In addition, female ovarian cycle synchrony has been found to reduce male ability to monopolize these cycles; female synchrony will determine the maximum male monopolization potential (Albert *et al.* 2003; Bissonette *et al.* 2011). A larger number of females are likely to cycle concurrently as the number of females in the group increases (Cowlishaw and Dunbar 2001). Alberts *et al.* (2003) determined that as the number of males, but not females, increased, there was an increase the in the degree of deviation from the priority of access model, a finding consistent with Mills and Reynold's (2003) work on the European bitterling (*Rhodeus sericeus*). As the number of males increases, it will be more difficult for high ranking males to monitor the mating attempts of lower ranking males; thus, more rivals results in a reduction of mating skew (Cowlishaw and Dunbar 1991; Pawlowski et al. 1998; Alberts *et al.* 2003; van Noordwijk and van Schaik 2004; Kutsukake and Nunn 2006). Since the number of males in a group tends to be correlated with the number of females in multi-male, multi-female groups (Andelman 1986; Mitani et al. 1996; Nunn 1999; Altmann 2000), separating the influences of male and female number is difficult. Regardless, we expect the largest deviation from this model in larger groups (Cowlishaw and Dunbar 2001; Alberts *et al.* 2003; reviewed in Alberts 2012), although the influence of alternative mating strategies on this established difference in

deviation from the priority of access model between groups of different sizes is little studied.

The olive baboon (*Papio hamadryas anubis*) is a useful model species to examine phenotypically plastic alternative strategies, as the males of this species experience many reproductive opportunities that may vary in an individual's life because the group size among *P.h. anubis* varies from twenty to more than one hundred individuals in a single population (e.g., Rowe 1996; Danish pers. obs., see Table 3.1 for study population). Thus, an individual male will have access to a varying number of females in their lifetime as they emigrate to new groups. In addition, females cycle throughout the year, which results in a varying number of females being receptive at any given time (e.g., Melnick and Pearl 1987; Bercovitch 1991, 1995).

In addition, males have access to environmental cues regarding spatial and temporal distribution of these reproductive opportunities. Female fertility in many Cercopithecine primates is advertised by conspicuous sexual swellings, which are reliable indicators of the timing of various stages of the ovulatory cycle (Nunn 1999; Deschner *et al.* 2003; Gesquiere *et al.* 2007; Higham *et al.* 2008; Highham *et al.* 2009). Such sexual swellings are among the most studied female ornamentations or signals, making this an ideal system for further study. During the follicular stage, the swelling increases in size; following ovulation, the swelling rapidly decreases in size. Conception is most likely during the four days prior to this detumescence of the sexual swelling (Higham *et al.* 2008). These sexual swellings, therefore, provide a broad cue of female sexual receptivity, as well as information regarding the probabilistic likelihood of conception (Nunn 1999; Deschner *et al.* 2003; Gesquiere *et al.* 2007; Higham *et al.* 2008; Higham *et*

al. 2009).   Males of multiple primate species, including olive baboons, have been shown to alter their mating behavior based on these sexual swellings (Deschner *et al.* 2004; Engelhardt *et al.* 2004; Brauch *et al.* 2007; Higham *et al.* 2009; Higham *et al.* 2012, but see Engelhardt *et al.* 2005). As a result, the number of available fertile females may vary significantly over a short period of time and males have access to cues regarding these reproductive opportunities. Since males may also be in groups of differing sizes, and therefore differing numbers of females, both OSR and the number of females may differ between groups and these differences potentially influence male behavior.

The "primary" mating strategy of male baboons (*P. h. anubis, P.h. cynocephalus, P.h. ursinus*) is solo competition for the well known "sexual consortship," a temporary relationship between a male and an estrous female characterized by close spatial proximity, male mate guarding, and relatively high rates of copulation (Hall and DeVore 1965; Small 1990; Bulger 1993; Bercovitch 1995). Consortships in olive baboons (*P. h. anubis*) typically last from a few hours to several days (Bercovitch 1985; Henzi *et al.* 1999; Danish pers. obs.), but what is less often appreciated about this system is that the consorting pair is typically accompanied by a retinue of "followers." Anywhere from one to eight adult males may maintain contact at variable distances with the consorting pair and with each other, while coordinating their movements with the consort pair for hours or even days (Hall and DeVore 1965; Hausfater 1975; Strum 1982, 1987, 1994; Bercovitch 1988; Sapolsky 1990; Forster and Strum 1994).

Following has been shown to be a means for males to gain access to consorting females by effecting consort takeovers (Chapter 1). Overall, 75% of consort takeovers were executed by males who were followers of the targeted consortships, with followers

accounting for up to 92% during the periods of likely ovulation. Followers relied on four tactics to achieve consort takeovers: 1) coalitionary challenge, whereby two or more males cooperated in aggressively ousting the consort male; 2) opportunistically using a distractions, such as the coalitionary challenge of a third party, to takeover the consortship; 3) taking over a consort female that has been abandoned by the previous consort male; and 4) individually challenging the consort male. Sneak copulations were rarely observed and only adolescent males were seen to utilize this tactic. As shown in Chapter 1, following in olive baboons is a flexible alternative mating strategy, and is suggested to be condition dependent since followers of differing dominance ranks were found to rely on different consort takeover tactics. Preliminary data also suggest that this behavior is costly (Danish unpublished data) and that followers likely face an increased risk of injury due to increased involvement in aggressive interactions (Chapter 1). While this phenomenon has been noted since early studies of baboons (Hall and DeVore 1965), the factors underlying the expression of this strategy have not been the focus of previous quantitative analyses.

The objective of this chapter was to examine the factors influencing the expression of following, by examining both intrinsic and extrinsic factors: dominance rank and the number of available females. I predicted that lower ranking males would spend more time following compared to higher ranking males, although I expected this difference to decrease during the period of likely ovulation since mating is more likely to result in conception during this time. Since the number of consorting females may influence male strategy, I also examined the percent of time spent following by relative dominance rank. I then examined whether dominance rank predicted male success in

taking over a consortship from a consorting male while using the alternative strategy following. I additionally examined the operational sex ratio in all groups and the proportion of observation days with multiple consorting females in each group. I had no a priori predictions regarding the influence of the available number of females, which was dependent on group size.

Methods

Study Site and Subjects

Subjects came from two habituated groups of olive baboons (*Papio hamadryas anubis*) that have been the focus of long-term study since 1999 in Laikipia District, Kenya (36°50'E, 0°15'N) (Lemasson et al. 2008; Shur et al. 2008a, 2008b). These subjects were studied from September 2009 to July 2010. During this period, these two groups underwent changes in dispersion, ranging, and social behavior suggestive of the onset of group fissioning, which ultimately generated four temporarily stable subgroups (see Introduction). Of these, I studied three subgroups (TDM, before and after fissioning, SUB, and WAZ), which differed in size: two small, averaging 5.3 and 5.5 males each and one larger, averaging 15.0 males (Table 3.1). In total, I observed 13 females for 17 cycles from all the three subgroups, seven of which were conceptive (see Table 3.1 for details and hours observed). These subgroups foraged separately from one another, such that if a male was with one subgroup, he could not interact with members of another subgroup until they aggregated at a common sleep site. With the exception of two males from the unstudied subgroup KAT who I observed entering their sister subgroup WAZ for several days at a time and only when that group had consorting females, male movement between the groups was long term (i.e., males remained after entering the new

group for at least several weeks). I therefore refer to these temporarily stable groups as groups. I classified the groups as small or large, instead of by number of males or females, since the size of all groups was stable and therefore group size did not vary significantly enough to make such an analysis informative.

<u>Consort and Follower Status</u>

All females that were not pregnant or lactating were considered cycling females, even when not displaying a sexual swelling. Cycling adult females of varying ages and dominance rank were selected; I particularly selected females of differing age and rank from the pool of cycling females, as opposed to selecting females randomly. Sexual swellings cues were used as an indication they would begin consorting soon; this also allowed us to plan my observations so that more than two selected females' consortship periods did not overlap. The selected females were followed daily from the onset of consortship formation with an adult male until the cessation of consortships. A consorting female was operationally defined as a cycling female with a sexual swelling with whom a particular male was maintaining close proximity to (often within 5 meters), preventing other males from interacting with the female (i.e., mate guarding), and copulating with her. Females typically consorted continuously, for six to 21 days (mean = 9.6, Danish unpublished data), particularly as the period of likely ovulation approached. I continued observing females who stopped consorting to ensure all consortships of a particular female were observed. If the female's sexual swelling started to deflate, indicating ovulation had likely occurred, and males stopped consorting with her mid-day, I continued to observe the female for the rest of the observation day and confirmed that she had ceased consorting the next day. All females' reproductive status, as well as the

identity of all their observed consort partners and followers, were recorded *ad libitum*, even if they were not the focus of detailed study.

For each consortship and day, males were classified as either "consort males," "followers," or "nonfollowers." Consort males were identified based on extended proximity maintenance with a cycling female with a sexual swelling as described above. I categorized all males not consorting using a male proximity score (MP-score) modified from Smut's (1985) composite proximity score (or "C-score"). I calculated the MP-scores from spatial data collected via 15 minute scan samples throughout the observation day, in which I collected distances of all visible adult males to the consort male using a Nikon Prostaff 550 rangefinder accurate to 0.5m within 100m. If a consort takeover, defined as a change of consort male, occurred I calculated the MP-scores separately for each consortship on an observation day. If a consortship continued the next observation day, I calculated the MP-score only using data from the current observation day since individual male behavior varied from day to day. The MP score is calculated as below for each consort male-male dyad, for n scan sample intervals:

$$MP = (1/distance_1) * ([1/number\ intervals]*100) + \dots (1/distance_n) * ([1/number\ intervals]*100)$$

The component parts of the MP-score were calculated from each scan sample interval by taking the product of the reciprocal of the distance between the males and the percentage of time at that distance (the product of the reciprocal of the number of scan sample intervals and 100). The MP-score is the sum of all such components, from the first scan sample to the nth scan sample. If a male was not visible during a particular scan sample, the component value for that sample was zero.

Based on preliminary research from a dataset not included in this analysis (Danish and Palombit 2008), I classified males that were seen during more than 25% of scan samples and with a MP-score of 1.9 or higher as "followers," while males with a MP-score less than 1.9 were classified as "nonfollowers." For this study, I recorded the distance of all males to the consort male as described here, and additionally recorded the identity of males I qualitatively identified as followers. I then examined the MP-scores of all males, and compared these scores to my qualitative assessment. I tested different values of the MP-score, until I determined the above criteria resulted in classification of males that matched my qualitative assessment of follower status from the preliminary dataset. I then used this measure for the current dataset, providing us with an objective measure of follower status for this study. I excluded any male consorting with another female as a follower, regardless of MP-score, since a consorting male is primarily responsible for proximity maintenance which precludes a consorting male from attending to more than one female concurrently.

Dominance Rank

I determined dominance rank from decided dyadic agonistic interactions; only supplants and submissive behaviors and vocalizations were used (e.g., bare-teeth display, fear bark) (see Hall and DeVore 1965). Data were collected both during focal animal samples of males and *ad libitum*, resulting in a dataset of 698 interactions (large group: 570, small group 1: 58, small group 2: 70). All males were observed during data collection for a similar amount of time, even considering *ad libitum* observations, since observers were moving throughout the group. Elo-ratings were determined for each male throughout the study period (starting value = 1000, k = 100 as described in Neumann *et*

al. 2011); the value of the Elo-rating increases with increasing dominance rank. The

rating process begins with all individuals at the same starting value, with the ratings

being updated after each successive interaction. The winner gains points and the loser

loses points; the number of points depends on the calculated probability of a particular

outcome between the two individuals, with the maximum value set as k. This method has

several advantages over the traditional dominance matrix based methods, including the

ability to handle sparse data sets and detect changes in dominance rank. Comparisons

have validated the robustness and reliability of this method, and even suggested that this

method may increase the power of analyses. These Elo-ratings can be used to derive a

linear hierarchy by listing males by their Elo-ratings in descending order, which I did for

a given observation day for most analyses. Further, Neumann *et al*. (2011) indicate that

the sequence of the interactions is particularly important, and that approximately nine

observations, including one with a dominant and one with a subordinate individual, are

needed to calculate an accurate initial Elo-rating. I used a male's mean Elo-rating for my

analysis of the proportion of successful male following events, which I calculated by

taking the average of a male's Elo-rating on each day of the observation period, for this

purpose.

 Response Variables

For all observed consortships, I recorded the duration of the consortship in

minutes, the identity of the consort male, and the follower status of all males present in

the group. Male Elo-ratings were later determined for the exact date of the observation.

The response variables were the lengthof time spent following an existing consort and the

length of time spent following an existing consort during the period of likely ovulation.

For one set of models, these response variables were calculated separately based on relative dominance rank as described below.

Length of time spent following an existing consort

I determined the length of time spent following for each male by determining the sum of the male's time spent following (in minutes). I also determined the total amount of time a male was present in the group and not himself involved in a consortship since consorting males cannot follow at the same time (hereafter "time available"). Therefore, this measure accounted for the presence of multiple cycling females since males consorting with females that were not the focus of this study were not considered available to follow the observed consortship. The sum of a male's time spent following was the sum of the duration of all consortships for which the male was classified as a follower based on MP-score; the duration of all observed consortships was recorded continuously. I determineded this separately for each female cycle for all males.

Length time spent following an existing consort during likely ovulation

The length of time spent following was calculated as described above, but only for the five days when conception was most likely. Ovulation occurs around the time when the sexual swelling undergoes rapid detumescence that is readily seen by visual assessment by human observers (Nunn 1999; Deschner *et al.* 2003; Gesquiere *et al.* 2007; Higham *et al.* 2008; Highham *et al.* 2009). Therefore, I operationally defined the period of likely ovulation as the day of detumescence and the four preceding days since Gesquire *et al.* (2007) suggest that both laboratory and field endocrinology data indicate that ovulation is most likely during this five day window. I included the day of detumescence since detumescence could occur at any time during the day.

Relative Dominance Rank

To examine influence of relative dominance rank, I recalculated the proportion of time spent following and the percent of time spent following during likely ovulation, splitting the data based on whether the particular male outranked the current consort male. I did this for each female cycle for all males, such that I calculated the proportion for each male when he outranked the consort male and did not outrank the consort male, which resulted in two values for the response variables for each male and female cycle; thus, all consortships were only included in calculating one of these two proportions. Thus, for these models, each male had two entries in the dataset for each female cycle, with the response variable calculated separately based on the relative dominance rank of the focus male and the consort male for each observed consortship. I then included whether the proportion was for a male who was outranked by the consort male or not outranked as a fixed effect in the relevant model (see below); the variable of interest here is whether the proportion of time an individual male spent consorting differed based on his relative rank compared to the consort male. Male identity was included as a random effect in these analyses.

Number of Successful Following Events

Each consortship a male followed was defined as a following event. For each male, I determined the number of successful following events, defined as following events that resulted in a consort takeover by the male. I analyzed all groups together due to the small sample size, particularly in the small groups.

Operational Sex Ratio (OSR)

I calculated the operational sex ratio (OSR) for the three groups as the number of consorting females (defined above) divided by the number of adult males present in the group. The number of consorting females, rather than cycling females, was used to determine the OSR since this more accurately represents female availability from a male view. I used this measure since cycling females are only receptive during the part of their cycle when they have a sexual swelling (Bercovitch 1995) and a female with a sexual swelling that was not yet consorting was of little interest to any adult male in the group and therefore most likely did not represent a meaningful reproductive opportunity. Since no adult males, even those without a consort female, are willing to invest in mate guarding a cycling female that is not consorting, I do not consider these females to represent biologically significant current reproductive opportunities.

Percent of Days with Multiple Cycling Females

For each group, I counted the number of consortships in the group on a given observation day. All observation days had at least one consortship that was the focus of study. I determined the percentage of days with multiple consorting female by dividing the number of days with more than one observed consorting female by the total number of observation days. I also determined the mean number of consorting females in each group from these data.

Data Analysis

I ran a generalized linear mixed model (hereafter GLMM) in the statistical software R v2.1.5.1 (R Development Core Team 2010) using Poisson distribution to assess each of the two response variables: 1) duration of time in minutes spent following

an existing consort and 2) duration of time in minutes spent following an existing consort during likely ovulation. Male identity was included in all models as a random effect. I ran two sets of models: A) actual dominance rank and B) relative dominance rank (see Table 3.2) using the glmmPQL function in R. This function accounts for overdispersion by using a Wald t test. Goodness-of-fit tests were run for all models to confirm that the standard errors of the data were Poisson distributed and therefore that Poisson distribution was appropriate. Since I ran four models on our dataset, I did a Bonferroni-Holm correction (Levin 1996; Wright 2012), which results in four different p values; both sets of p-values are ranked in ascending order and the calculated p-value must be less than its corresponding adjusted p-value to be considered significant. The four adjusted p-values were 0.050 (2B), 0.025 (1A), 0.017 (2A), and 0.013 (1B).

All models included the time available as a fixed effect, to account for differences in observation time, as well as male availability to consort. For models 1A and 2A, the fixed effects were male Elo-rating, group size, and the interaction of Elo-rating and group size. For models 1B and 2B, I split data used to derive the response variable based on whether the male outranked the current consort male or did not outrank the current consort male (relative rank), and recalculated the response variables. Thus, I obtained two values for the response variable and included whether the male outranked the current consort male as a fixed effect as described above. The other fixed effects for Models 1B and 2B were group size and the interaction between group size and relative rank.

Since the interaction fixed effects were significant in all models, I ran post hoc tests separately for small and large groups to determine how the influence of Elo-rating on the response variable differed in groups of differing sizes. For Models 1A and 2A, I

used a Spearman's rank correlation, since the variable Elo-rating is continuous, to examine the relationship between Elo-rating and the percent of time spent following (during likely ovulation). I used a Welch's Two Sample T-Test for Models 1B and 2B to test the difference of the mean of the percent of time spent following (during likely ovulation) when males were outranked by the consort male and not outranked by the consort male.

To examine the influence of dominance rank on the number of successful following events, I ran linear regressions and used the mean Elo-rating of each individual male for dominance rank, as opposed to categorizing males as high-, mid- or low-ranking. A linear regression model was performed to test the relationship between dominance rank, using the mean Elo-rating of the male, and the number of successful following episodes. I additionally included the number of following events, since male effort may also influence success.

Results

For Model 1A, the fixed effects Elo-rating (p = 0.017) and the interaction of Elo-rating and group size (p = 0.004) were significant (Table 3.2). Group size was not significant after Bonferroni-Holm adjustment (p = 0.038). Post hoc Spearman's correlations indicated that there was a negative correlation between Elo-rating and the percent of time spent following in the large group (p = 0.003), but not in the small groups (p = 0.163) (Table 3.3). Therefore, the percent of time spent following increases with decreasing dominance rank, as predicted, but only in large groups (Fig3.1).

For Model 1B, the fixed effect relative rank was significant (p < 0.001, Table 3.2). Thus, individuals followed more when not outranked by the consort male (Fig3.2).

Since the interation of relative rank and group size was slightly statistically significant (p = 0.035), although group size alone was slightly significant after Bonferroni-Holm correction (p = 0.035), we performed post hoc analyses for each group size. In large groups, but not small groups, males followed more when they were outranked by the consort male (p = 0.013, p = 0.970, Table 3.3).

For Model 2A, the fixed effect Elo-rating was significant (p = 0.016) (Table 3.2). Neither group size (p = 0.977) or the interaction of group size and Elo-rating (p = 0.381) were significant. Therefore, lower ranking males spend more time following during the likely period of ovulation than higher ranking males, contrary to my predictions, in large and small groups (Fig3.3).

For Model 2B, while the fixed effect group size (p<0.001) was significant, the relative rank was not significant (p=0.135) (Table 3.2). Therefore, males follow during likely ovulation regardless of their relative dominance rank to the consort male in small and large groups (Fig3.4).

Since it is clear that males of all dominance ranks exhibit following behavior, I examined the success rate of following episodes to determine if males of differing ranks obtain equal benefits from following. Both dominance rank and the number of following events explained 43% of the variance in success for males, with higher ranking males and males with more following events obtaining more consort takeovers than lower ranking males ($F_{2,21}$=9.8500, p=0.0010, see Table 3.4) (Fig3.5).

The OSRs of the groups were similar, indicating that per capita males have similar access to females in groups of differing sizes (Table 3.1). In large group, however, there is more than one consorting female on 84% of days (where there is at

least one consortship), with a mean of 2.8 consorting females. In comparison, in the small groups, such overlap is rare (8% and 16% of days). More than one female was in this more fertile time of her cycle on 74% of days in the large group, considering only days where at least one female was in the period of likely ovulation.

Discussion

Lower ranking males exhibited a higher proportion of time spent following as predicted, but only in the large group, suggesting that following functions as a means for lower ranking males to obtain access to females as theoretically predicted. No such pattern was observed in the small groups suggesting that the interaction of dominance rank and the number of reproductive opportunities is of importance. This pattern is not related to any pattern in consorting behavior, including differences due to dominance rank, since that was controlled for in the analysis by excluding time a male spent consorting from available time for following. My findings suggest that the decision rule involved in the expression of such strategies is not based on a simple relationship between male condition and strategy success. Gross (1996) suggested that multiple switchpoints (in male strategy) were possible, particularly when considering the influence of demography and the environment; my findings are consistent with the occurrence of multiple switchpoints in the decision rule of olive baboons or different fitness functions for males in groups of differing sizes.

Since all reproductive opportunities are not equal in terms of the likelihood of conception on a particular day of a female's cycle, and information regarding the potential benefit of mating with a particular female on a given day is available, male behavior is expected to be influenced by cues regarding the likelihood of ovulation. I

found that lower ranking males spent more time following during this period in both groups, with no effect of relative rank. Thus, male condition is the primary factor influencing following behavior during the most likely period of ovulation. Notably, the absolute percent of time spent following during the period of likely ovulation increased for most males, indicating males are modifying their behavior in response to this cue. These data are consistent with findings from other primates (Nunn 1999; Deschner *et al.* 2003; Ostner *et al.* 2006; Gesquiere *et al.* 2007; Heistermann *et al.* 2008; Higham *et al.* 2008; Higham *et al.* 2009) and from a variety of taxa beyond the primates (McLennan 1995; Poling *et al.* 2001; Tuttle 2003; Bercovitch *et al.* 2006; Foote *et al.* 2008), that demonstrate that males alter mating or mate guarding behavior based on cues regarding the likelihood of female ovulation. Tuttle's (2003) study of white throated sparrows (*Zonotrichia albicollis*), a species with fixed male polymorphism, found that while all males increased time spent mate guarding during the fertile period, the two male morphs did so to differing degrees. The influence of such cues on the expression of alternative mating strategies remains poorly understood; my findings show that males alter the expression of an alternative strategy differentially based on the same information, suggesting the importance of examining such interactions, as well as the importance of further studies focusing on the costs and benefits incurred by males of differing condition.

With relative dominance rank, as opposed to absolute dominance rank, I found that the expression of following differed amongst groups of differing sizes. In the large group, males followed more often when they were outranked by the consort male; in conjunction with the findings of the previous model, this suggests that following is

providing lower ranking males with an alternative means to compete with higher ranking males. In small groups, however, males did not follow based on their dominance rank relative to the consort male. In light of the previous model's results, this indicates that high ranking males are following the consortships of lower ranking males in small groups. The consistency of my two sets of models suggests that the differences in strategy expression I found are related to male decisions.

While males of all dominance rank were observed to follow, the effectiveness of this strategy was dominance rank dependent. High ranking males were more successful followers than lower ranking males; the cause of this differential success is uncertain, but most likely results from the superior fighting ability of higher ranking males, particularly since followers may be involved in aggressive interactions during consort takeovers. These findings suggest that high ranking males in small groups follow at similar rates as lower ranking males as a result of the potential benefit of following, as well as due to the number of reproductive opportunities they experience. Since male effort also increases the number of takeovers, high ranking males will particularly benefit from increasing their time spent following.

Since more than one female is likely to be mating concurrently in the large group, males may be limited in their ability to attempt to take advantage of all of these opportunities. While Cowlishaw and Dunbar (1991) suggest that the ability of high ranking males to monopolize access to females decreases with increasing group size as a result of increased female synchrony, males attempting to gain access to females will face similar constraints. While males in both group sizes have the same mean access to females, in terms of OSR, female cycles are not completely synchronous. Therefore,

males in large groups experience a greater absolute number of reproductive opportunities as a result of living in a group with more females, even once female synchrony was accounted for in the study groups (Table 3.1). I therefore propose that high ranking males in smaller groups follow a higher proportion of consortships than their counterparts in larger groups since they are less able to forego a particular reproductive opportunity since there are fewer such opportunities and they are less likely to encounter synchronous cycles.

Alberts *et al.* (2003) determined that as the number of males, but not females, increased, there was an increase the in the degree of deviation from the priority of access model. As the number of males increases, it will be more difficult for high ranking males to monitor the mating attempts of lower ranking males; thus, more rivals results in a reduction of mating skew (Cowlishaw and Dunbar 1991; Pawlowski et al. 1998; Alberts *et al.* 2003; van Noordwijk and van Schaik 2004; Kutsukake and Nunn 2006). Since the number of males in a group tends to be correlated with the number of females in the group (Andelman 1986; Mitani et al. 1996; Nunn 1999; Altmann 2000), separating the influences of male and female number is difficult. Regardless, I expect the largest deviation from this model in larger groups (Cowlishaw and Dunbar 2001; Alberts *et al.* 2003; reviewed in Alberts 2012), although the influence of alternative mating strategies on these differences in fit to the priority of access model between groups of different sizes is little studied.

The causes underlying variation in the degree of reproductive skew within and between species remains uncertain (Berard *et al.* 1993; Alberts *et al.* 2003; Bissonnette *et al.* 2011; Dubuc *et al.* 2011; Wroblewski *et al.* 2009; reviewed in Alberts 2012). While

alternative mating strategies have been implicated in reducing mating skew, I suggest that group size dependent differences in the expression of alterative mating strategies in a single species. Moreover, I suggest that these differences are due to the number of females, as well as males, in a group. Since the operational sex ratio was similar in all groups, males likely face a similar number of competitors for a single female. While the spatio-temporal distribution of reproductive opportunities has been implicated in the evolution of alternative mating strategies (Shuster and Wade 2003), my study suggests that the current spatio-temporal distribution of fertile females- and moreover, variation in that distribution- influences the condition dependent expression of alternative mating strategies. Density is expected to influence the switchpoint (Gross 1996); I suggest that the number of females, rather than the number of males, may be an influential attribute of density. The impact of such within species differential expression of an alternative mating strategy warrants further study, in more taxa.

Following is utilized to varying degrees by all individuals. The resuts of this study suggest that differences in strategy expression are determined by dominance rank based decisions regarding reproductive opportunities. Moreover, dominance rank influenced likelihood of success. Therefore, the expression of following results from dynamically flexible decision rules based on current reproductive opportunities, as well as male condition. Our results suggest, however, that during the period of likely ovulation, male condition is the primary determining factor underlying the expression of following. The spatio-temporal distribution of current reproductive opportunities is determined by group size, with individuals in larger groups experiencing more such opportunities. Thus, the spatio-temporal distribution of reproductive opportunities not

only influences the evolution of alternative strategies, but also the expression of these

same strategies.

Table 3.1 Summary of Study Groups

Group Size	Mean number of males (range)	Mean number of females (range)	Hours Observed	Number Females (Cycles, Conceptive Cycles) Observed	Mean OSR	Mean number consorting females	Percent of Days with Multiple Consorting Females
TDM	15.0 (11-19)	25.6 (22-30)	695	10 (13, 5)	0.19	2.8	84
SUB	5.3 (4-6)	6.2 (6-7)	188	2^1 (2, 0)	0.21	1.2	16
WAZ	5.5 (5-8)	8 (8)	96	2 (2, 1)	0.18	1.1	8

1- One female was also observed for one cycle in TDM prior to group fissioning

Mean OSR is calculated using the number of consorting females; mean number of consorting females is listed for each group. The percent of days with multiple consorting females includes data only from those days with at least one consortship.

Table 3.2 Summary of Model Statistics

Model	Estimate	Estimate and Standard Error	t-value	p-value
1A Percent of Time Spent Following	Fixed effects Elo-rating	$-1e^{-3} \pm 4e^{-4}$	-2.4	0.017
	Group Size (small)	-2.0 ± 0.9	-2.1	0.038
	Time Available	$4e^{-4} \pm 5e^{-5}$	7.0	<0.001
	Interaction	$3e^{-3} \pm 1e^{-3}$	2.9	0.004
1B Relative Rank Percent of Time Spent Following	Fixed effect Relative Rank (outrank)	-0.9 ± 0.2	-4.0	<0.001
	Group Size (small)	0.5 ± 0.2	2.4	0.019
	Time Available	$4e^{-4} \pm 4e^{-5}$	8.9	<0.001
	Interaction	0.8 ± 0.4	2.1	0.035
2A Percent of Time Spent Following (Period of Likely Ovulation)	Fixed effects Elo-rating	$-10e^{-4} \pm -6e^{-5}$	-2.4	0.016
	Group Size (small)	0.3 ± 1.2	$3e^{-2}$	0.977
	Time Available	$7e^{-4} \pm 1e^{-4}$	6.1	<0.001
	Interaction	$1e^{-3} \pm 1e^{-3}$	0.9	0.381
2B Relative Rank Percent of Time Spent Following (Period of Likely Ovulation)	Fixed effect Relative Rank (outrank)	-0.3 ± 0.2	-1.5	0.135
	Group Size (small)	0.9 ± 0.2	3.7	<0.001
	Time Available	$9e^{-4} \pm 8e^{-5}$	11.7	<0.001
	Interaction	-0.3 ± 0.5	-0.6	0.538

Table 3.3 Summary of Post hoc Tests

Model	Group Size	Expected	Test statistic	p-value
1A Percent of Time Spent Following	Large	Negative	$r = -0.22$	0.003
	Small	Negative	$r = 0.29$	0.163
1B Relative Rank Percent of Time Spent Following	Large	Higher when outranked	$t_{265} = 2.50$	0.013
	Small	Higher when outranked	$t_{39} = 0.04$	0.970

Table 3.4 Summary of Linear Regression

	Estimate	**Standard Error**	**T**	**p-value**
Intercept	-5.5660	2.4063	-2.3130	0.0309
Number of following events	0.1649	0.0381	4.3330	0.0003
Mean Elo-rating	0.0053	0.0020	2.6220	0.0159
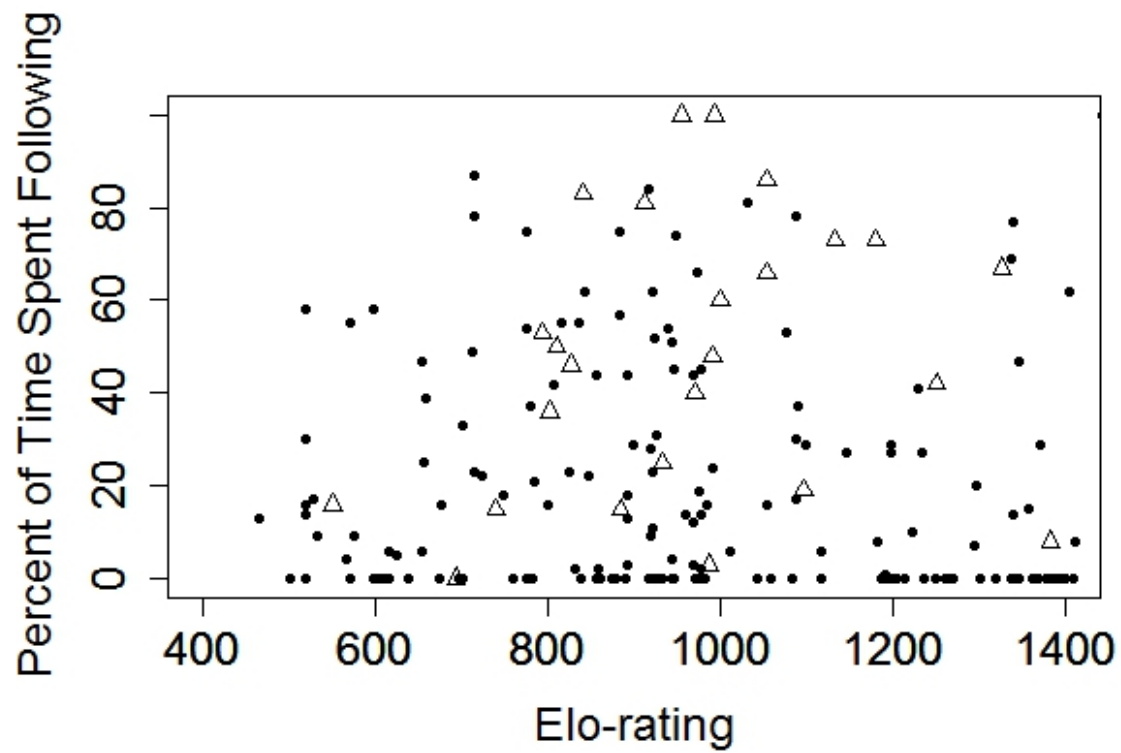
Fig3.1 Percent of time spent following by males of differing dominance ranks
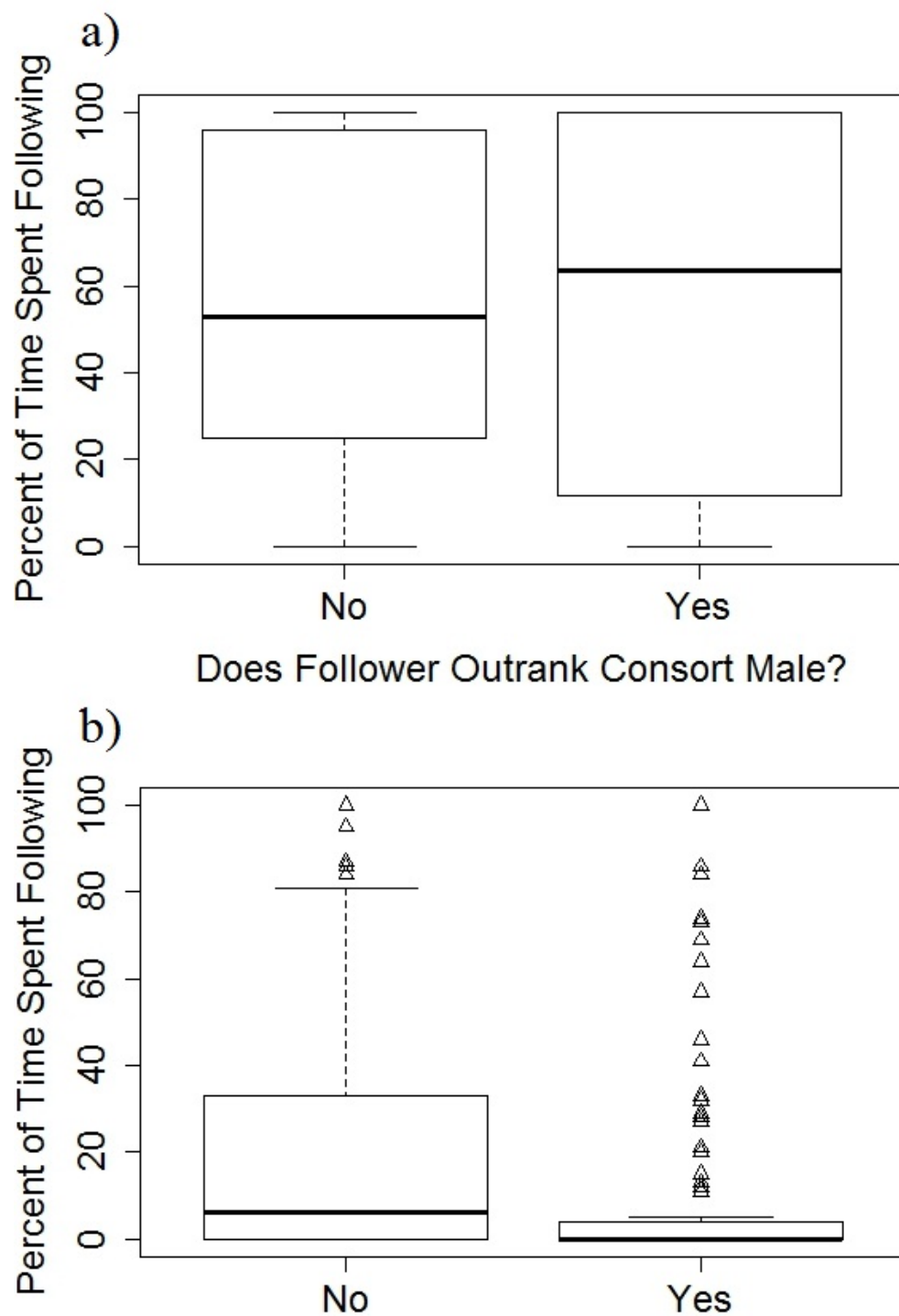
Fig3.2 Comparison of the percent of time spent following when outranking and not outranking the consort male

a) small and b) large groups
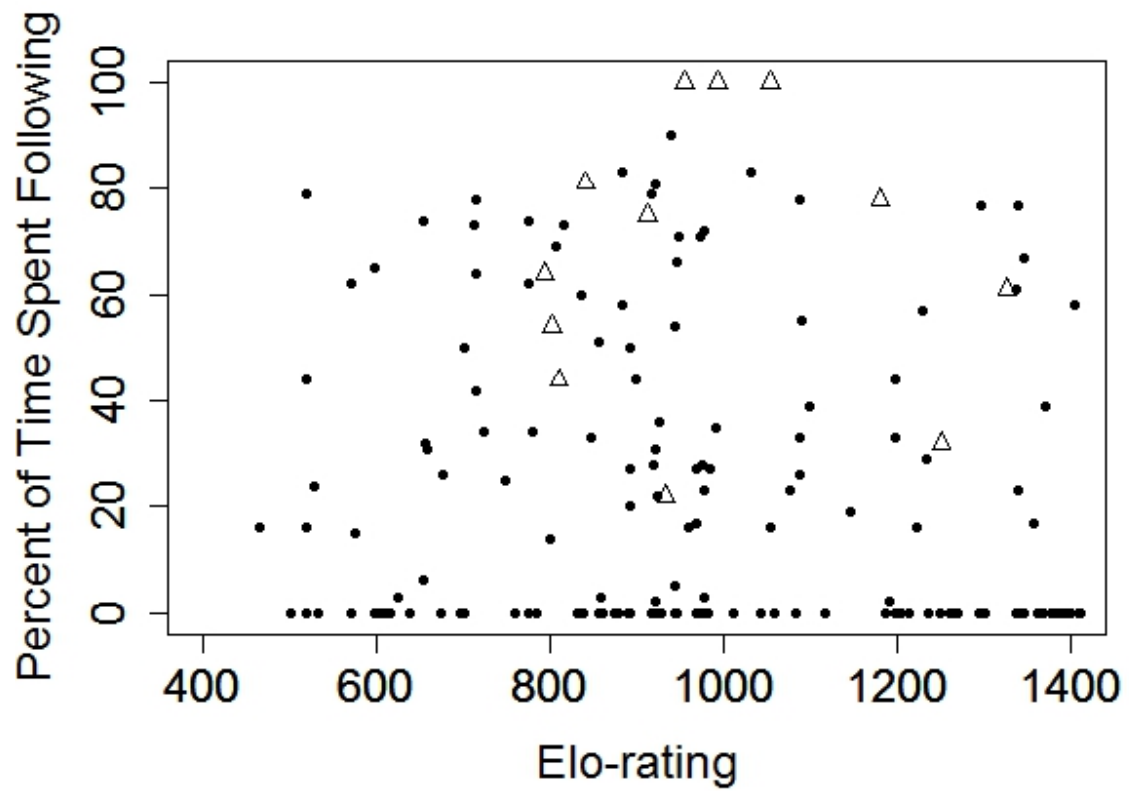
Fig3.3 Percent of time spent following during the period of likely ovulation by males of differing dominance ranks
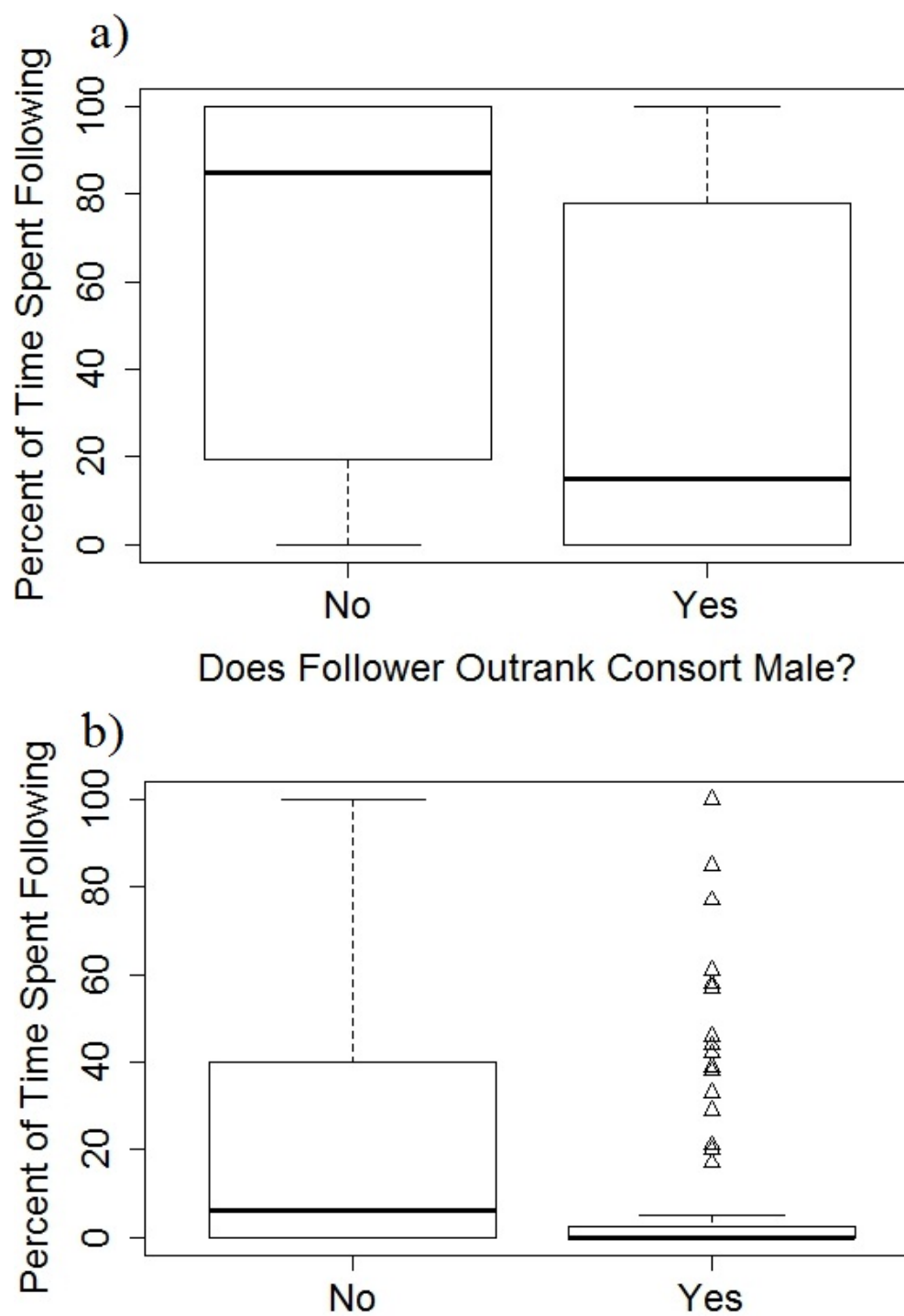
Fig3.4 Comparison of the percent of time spent following during the period of likely ovulation when outranking and not outranking the consort male

a) small and b) large groups
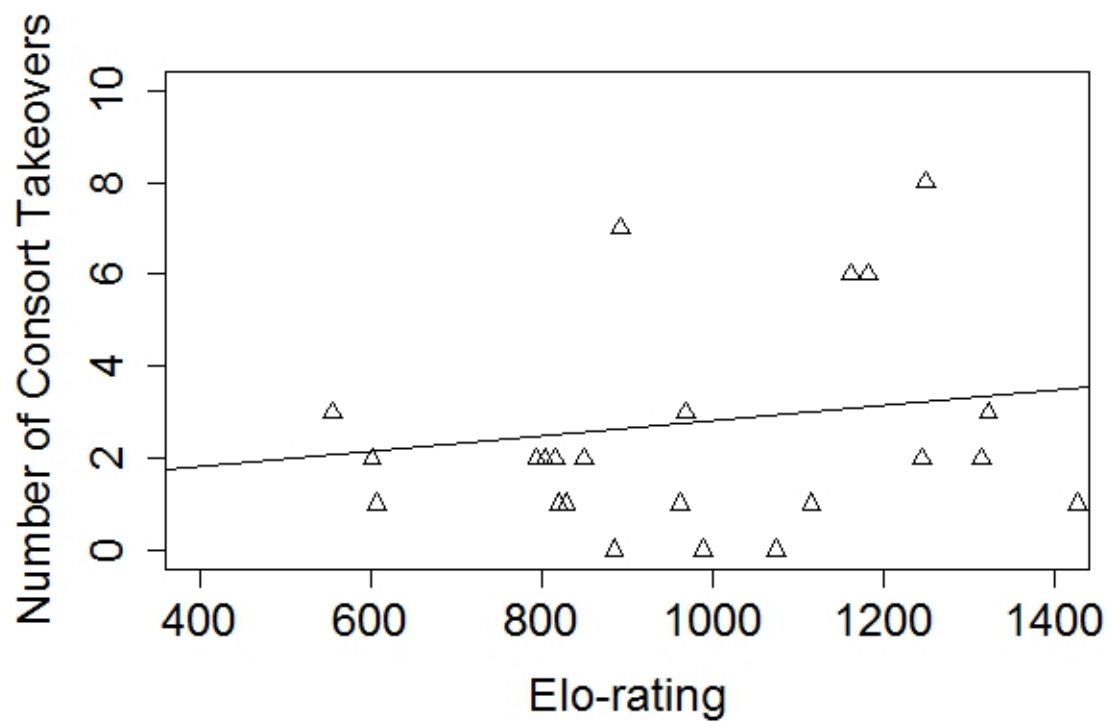
Fig3.5 Number of successful consort takeovers while following for males of differing dominance ranks

Each point represents an individual male, with regression line.
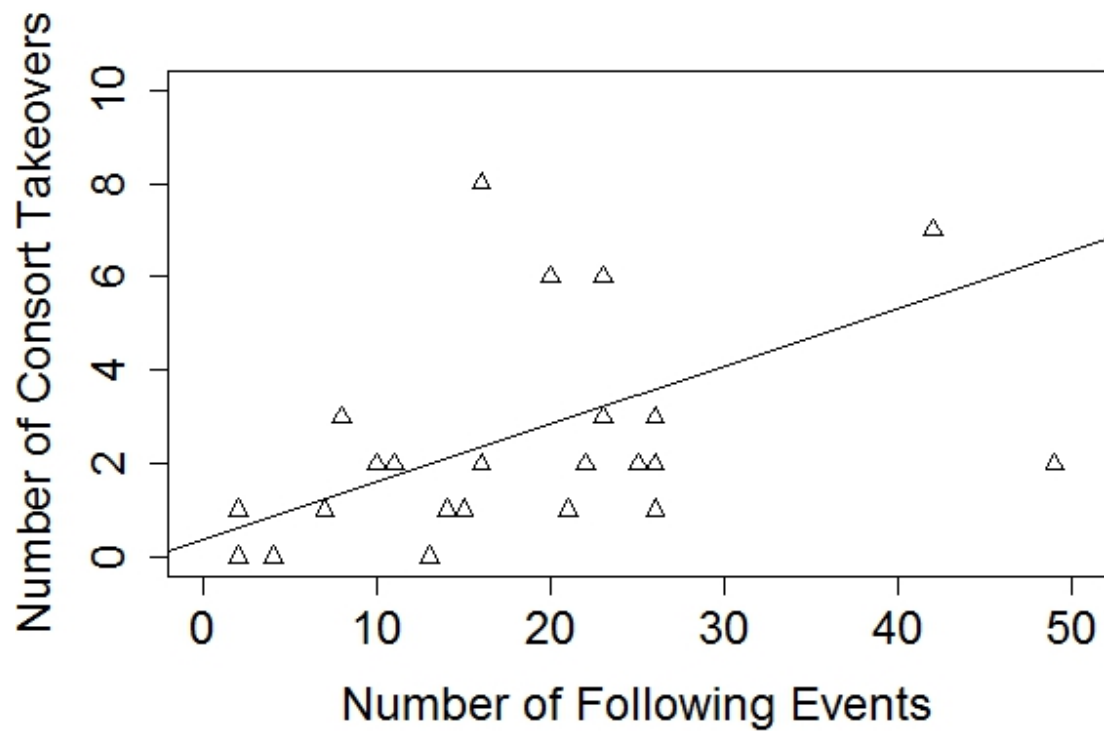
Fig3.6 The number of successful consort takeovers while following versus the total number of following events

Each point represents an individual male, with regression line.

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CHAPTER 4: FOLLOWERS INCUR TIME, BUT NOT DO NOT HAVE

SHORTER FEEDING BOUTS OR REDUCED TIME FEEDING

Introduction

Costs are critical in any functional analysis of behavior (Hinde 1975). Behavior involving a time investment, like mating, is expected to constrain other activities (Parker 1974). There are multiple potential costs, including energetic (Rasmussen 1985; Alberts *et al.* 1996; Komdeur 2001; Matsubara 2003; Prenter *et al.* 2003; Plaistow *et al.* 2003; Weingrill *et al.* 2003; Low 2005; Mass *et al.* 2009; Schubert *et al.* 2009; Pelletier *et al.* 2009; Higham *et al.* 2011), increased risk of predation (Howard 1978; McCauley and Lawson 1986; Ward 1986; Gwynne 1987; Sih *et al.*1990) injury from conspecifics (Alvarez 1993; Drews 1995), and decreased time spent on other activities. I focus on activity budget changes, feeding bout length and time costs since most studies that show that mating behavior increases the risk of predation, come from insects and anurans that call for mates and species with conspicuous ornamentation (e.g., guppies *Poecilia reticulata*, Endler 1987) and primate mating strategies do not involve such ornamentation. Notably, energetic constraints may represent a time constraint, if individuals spend less time feeding as a result of mating activity. The impact of mating beyond a loss of feeding time, such as constraining the number and quality of social interactions, remain poorly understood. I therefore focus on behavior which may result in either decreased energy consumption or increased energy expenditure (Alberts *et al.* 1996). Decreased energy consumption may result from either: 1) a decrease in food intake, either due to a decrease in time spent feeding or feeding bout length; and 2) a decrease in food quality (e.g., nutrition). The two potential causes of increased energy

expenditure are: 1) an increase in distance traveled due to either an increase in the amount of time spent moving or in the rate of movement; and 2) activity changes resulting from monitoring of the female or male competitors.

The energetic costs of mate guarding are of relevance here since many alternative strategies are an alternative to mate guarding. Energetic costs have been established in a wide range of taxa and include direct measures of energetic costs (e.g., weight loss) and indirect measures (e.g., reduced time feeding) (orb-web spiders *Metellina segmentata* Prenter *et al.* 2003; amphipod *Gammarus pulex*, Plaistow *et al.* 2003; New Zealand switchbird *Notiomystis cincta*, Low 2005; Seychelles warbler *Acrocephalus sechellensis*, Komdeur 2001; round-eared sengis *Macroscelides proboscideus*, Schubert *et al.* 2009; bighorn sheep rams *Ovis canadensis*, Pelletier *et al.* 2009; male mountain goats *Oreamnos americanus*, Pelletier *et al.* 2009; sifaka *Propithecus verreauxi*, Mass *et al.* 2009; rhesus macaques *Macaca mulatta*, Higham *et al.* 2011; Japanese macaques *Macaca fuscata yakui*, Matsubara 2003; chacma baboons *Papio hamadryas ursinus*, Weingrill *et al.* 2003; olive baboons *Papio hamadryas anubis*, Bercovitch 1983; yellow baboons *P. h. cynocephalus*, Rasmussen 1985 and Alberts *et al.* 1996). Mate guarding has not been found to have a consistent effect on the percent of time spent feeding; while rhesus and Japanese macaques experienced a reduction in time spent feeding (Matsubara 2003; Higham *et al.* 2011), results were inconsistent between study groups in yellow and chacma baboons, with only one of two social groups showing this reduction (Alberts *et al.* 1996; Weigrill *et al.* 2003). In addition, sifakas (*Propithecus verreauxi*) and olive baboons do not experience a reduction in time spent feeding (Mass *et al.* 2009). There are less data regarding feeding bout length: while yellow baboons experience shorter

feeding bouts (Alberts *et al*. 1996), sifakas do not (Mass *et al.* 2009). Alberts *et al.* (1996) additionally found that consorting male yellow baboons traveled shorter distances to match the typical female travel distance, which they propose may constrains males' usual foraging patterns. When the time spent traveling is used a proxy for distance, however, with mate guarding male rhesus macaques, Japanese macaques, and yellow baboons spending a similar amount of time traveling (Rasmussen 1985; Matsubara 2003; Higham *et al.* 2011), although there was a trend in the predicted direction for yellow baboons. While the data are inconsistent between primate species, these studies suggest that there is a potential for energetic costs related to feeding time, feeding bout length and travel distance or time spent traveling.

The energetic costs associated with alternative mating strategies are less studied, but also derive from a variety of taxa (field cricket *Acheta domesticus*, Hack *et al.* 1998; horseshoe crabs Limulus polyphemus, Smith *et al.* 2012; northern swordtail *Xiphophorus nigrensis*, Cummings *et al.* 2009; Atlantic salmon *Salmo salar*, Jonsson *et al.* 2012; southern elephant seals *Mirounga leonina,* Galimberti *et al.* 2007; grey seal *Halichoerus grypus*, Lidgard *et al*. 2005). Theoretical predictions indicate that the preferred or primary conditional strategy will be more costly than the alternative strategy (Bateson 1976; Dawkins 1980). For example, large dominant elephant seals that defend a territory on breeding grounds expend more energy than peripheral, nonterritorial males (Galimberti *et al*. 2007). Hack *et al.* (1998) found that the "primary" strategy of field crickets, stationary courtship involving calling, was less costly than the alternative strategy of quietly roaming.

Amongst the primates, few studies explicitly examine the energetic costs of alternative mating strategies; much of these data derive from general studies of mating behavior. Both mandrills (*Mandrillus sphinx*) and orangutans (*Pongo* sp.) exhibit pre-mating strategies associated with bimaturism (Schürmann and van Hooff 1986; Maggioncalda *et al.* 2000; Setchell and Dixson 2002; Setchell 2003; Utami Atmoko and van Hooff 2004). In orangutans, the day ranges of unflanged males, which are smaller and lack developed secondary sexual characteristics, are significantly longer than those of flanged, fully developed males when traveling alone due to their pursuit of a "go and search" strategy (Schürmann and van Hooff 1986; Setchell 2003). Males of both morphs adjusted their day ranges when consorting, however, with flanged males increasing and unflanged males decreasing their day ranges (Utami Atmoko and van Hooff 2004). Thus, unflanged males likely expend more energy daily, although both male morphs have similar day ranges while mating. Maggioncalda *et al.* (2000) additionally suggests that the endocrine profile differences associated with these male morphs allows unflanged males to avoid the metabolic and stress-related costs associated with secondary sexual characteristics while supporting spermatogenesis. Peripheral male mandrills, which lack secondary sexual characteristics of group associated males, exhibit higher body mass and rump fattedness associated with solitary feeding (Setchell and Dixson 2002; Setchell 2003). Peripheral males rely on sneak copulations, in contrast to the mate guarding of group-associated males. Matsubara (2003) also found that subordinate male Japanese macaques (*Macaca fuscata yakui*) relying on sneak copulations did not experience reduced time feeding on days when they mated, unlike the mate guarding alpha male.

These findings suggest that the sneak copulation strategy is less costly than mate guarding.

A commonality between these studies is that the behavior, particularly the time investment of the behavior, involved in the strategy will impact the energetic costs. Thus, I would expect that a more time consuming alternative mating strategy would also result in greater costs. The time investment of many primate alternative strategies is likely limited, based on behavioral descriptions of these strategies. For example, a coalitionary challenge may take only minutes and is not likely to involve significant energetic costs, although males involved in a coalition likely expose themselves to an increased risk of injury compared to not participating (Drews 1995). Even if they are less costly than the "primary" strategy, these alternative strategies are expected to be more costly than not attempting to mate. Therefore, a baseline cost needs to be established for the each species of interest; most studies compare two strategies, but not with a nonfollowing condition, as is typically done in studies on the cost of mate guarding.

The olive baboon (*Papio hamadryas anubis*) is a particularly interesting taxon to examine the costs of alternative mating strategies, because this species exhibits an alternative mating strategy that appears to involve a lengthier time investment and therefore has the potential to be energetically costly. The "primary" mating strategy of olive baboons is solo aggressive competition for the well known "sexual consortship" (Bercovitch 1995). These consortships are characterized by male mate guarding, with the consort male maintaining close spatial proximity and aggressively defending his access to the fertile female, and relatively high rates of copulation (Hall and DeVore 1965; Small 1990; Bulger 1993; Bercovitch 1995). I studied an often observed, but little studied

behavior called "following" (Hall and DeVore 1965; Hausfater 1975; Strum 1982, 1987, 1994; Bercovitch 1988; Sapolsky 1990; Forster and Strum 1994). Anywhere from one to eight adult male followers may maintain contact at variable distances with the consorting pair and with each other, coordinating their movements with the consort pair for hours or even days. These followers are responsible for a majority of consort takeovers, and my data support the conclusion that this behavior is an alternative mating strategy (Danish and Palombit submitted). Following, like consorting, involves the maintenance of proximity to target individuals for an extended period of time, as well as an increased likelihood of involvement in aggressive interactions (Danish and Palombit submitted). Therefore, I expect that followers will face similar constraints as consorting males-without necessarily obtaining any copulations.

In considering the costs faced by males, variation in how the potential benefits influence the costs males are willing to incur should also be considered. Olive baboon females, like many Cercopithecine primates, exhibit a distinctive sexual swelling during their fertile period (Nunn 1999; Deschner *et al*. 2003; Gesquiere *et al*. 2007; Higham *et al*. 2008; Highham *et al*. 2009). These swellings are reliable indicators of the timing of various stages of the ovulatory cycle. In many species, including the olive baboon, the swelling increases in size during the follicular stage and rapidly decreases in size following ovulation. Conception is most likely during the day of detumescence of the sexual swelling and the four preceding days in olive baboons (Higham *et al*. 2008). Males of multiple primate species have been shown to alter their mating behavior based on the likelihood of ovulation as indicated by these sexual swellings; in particular, male interest in females and to rate of copulation with females increases as the swelling size

increases (Deschner *et al.* 2004; Engelhardt *et al.* 2004; Brauch *et al.* 2007; Higham *et al.* 2009; Higham *et al.* 2012). Since male decisions are sensitive to variation in the potential reproductive benefit of females at different times, followers are also expected to attend to these cues, particularly since the expression of following is flexible (Danish and Palombit submitted). In addition, followers should be willing to incur higher costs during the likely period of ovulation.

My objectives were to examine the costs incurred by followers, examining energetic costs and social costs. For energetic costs, I examined the length of time spent feeding and traveling, as well as feeding bout duration since a reduction in either time spent feeding or feeding bout length is one potential cause of decreased energy consumption (Alberts *et al.* 1996). I hypothesized that followers would experience energetic constraints in the form of both a decrease in time spent feeding and a decrease in feeding bout length, since most previous studies found some reduction in feeding time and Alberts *et al.* (1996) found shorter feeding bouts for mate guarding males in the closely related yellow baboon. If followers experience a foraging cost, I expect this cost to be less than costs that incurred by consorting males since followers are less constrained in their movements. I predicted that followers would incur greater feeding costs on the most likely days of ovulation since I expect followers to increase their mating effort, further constraining normal activities, during the period of likely ovulation. Followers are involved in agonistic interactions with the consort male (Chapter 1), and I expect such interactions to be more frequent when the dyad is in closer proximity. As a result, I expect followers to spend more time involved in aggressive interactions or monitoring the consort male, and less time feeding, as proximity between the consort male and follower

decreases. I therefore predicted that proximity to the consort male would influenced the costs incurred by followers, particularly that the length of time spent feeding and feeding bout duration of followers would decrease with increasing proximity to the consort male. Finally, I hypothesized that following would constrain a male's ability to interact with other individuals, by constraining their ability to move around the group and interact with social partners; I predicted that followers would spend less time grooming compared to nonfollowing males.

Methods

Two habituated groups of olive baboons were studied from September 2009 to July 2010 in Laikipia District, Kenya (Segera/Mutara 36°50'E, 0°15'N) (Lemasson *et al*. 2008; Shur *et al*. 2008a, 2008b). During this period, these two groups underwent changes in dispersion, ranging, and social behavior suggestive of the onset of group fissioning, which ultimately generated four temporarily stable subgroups. Of these, I studied three; data derive from 79.6, 330.7, and 52.1 hours of focal data from 26 males from the three subgroups (Table 4.1).

I selected adult females, specifically selecting females of representative ages and dominance ranks, as opposed to random selection. I observed 14 females over 20 cycles. These females were observed throughout their entire estrous cycle and for consecutive cycles until conception. In this manner, I was able to observe male mating behavior for an entire female cycle, including all consort and follower males, and the onset of detumescence of the female's sexual swelling.

Consort and Follower Status

Males were classified as either "consort males," "followers," or "nonfollowers" with respect to the focal female's consortships. Consort males were identified based on extended proximity maintenance with a female with a sexual swelling; consort males stayed within sight of the female and followed her as she traveled. I categorized the remaining males in the group using a male proximity score (MP-score) modified from Smut's (1985) composite proximity score (or "C-score"), which was calculated for each male separately. I collected distances of all visible adult males to the consort male via scan samples at 15 minute intervals throughout the observation day. I used a Nikon Prostaff 550 rangefinder accurate to 0.5m within 100m. The MP score is calculated as below for each consort male-male dyad, for n scan sample intervals:

$$MP = (1/\text{distance}_1) * ([1/\text{number intervals}]*100) + \ldots (1/\text{distance}_n) * ([1/\text{number intervals}]*100)$$

The component parts of the MP-score were calculated from each scan sample interval by taking the product of the reciprocal of the distance between the males and the percentage of time at that distance (the product of the reciprocal of the number of scan sample intervals and 100). The MP-score is the sum of all such components, from the first scan sample to the nth scan sample. Based on previous studies (Danish and Palombit 2008; Danish and Palombit submitted, Danish and Palombit submitted), I classified males that were seen during more than 25% of scan samples and with a MP-score of 1.9 or higher as "followers," while males with a MP-score less than 1.9 were classified as "nonfollowers."

Behavioral Data

 I recorded ten-minute focal animal samples, rotating between all males either consorting with the focal female or following the female's consortships. Focal samples were extended if the focal animal was involved in grooming with another adult, in order to record the duration of grooming (Palombit unpublished protocol). I also recorded focal animal samples (Altmann 1974) on all adult males when not consorting or following (nonfollowing), when no focal female was consorting. Thus, all focal samples could be categorized as focals samples of following males, or nonfollowing male. The start time of each focal sample was recorded; all focals were labeled by the hour of the start time (i.e., 06:00-06:59, 07:00-07:59, etc).

Proximity Data During Focal Samples

 At the start of each focal sample and at two-minute intervals throughout the focal sample, I recorded the distance and identification of all individuals within six meters of the focal animal (Palombit unpublished protocol). I additionally recorded the distance to the nearest adult male and female, if there were no member of that age/sex class within six meters of the focal animal. For followers, I recorded the distance to both members of the consorting pair, even if they were not within six meters or the nearest adult animal. Distances were estimated to one meter increments up to six meters and at five meter increments up to 100 meters. This allowed us to determine the mean distance to the consort male for following focal samples.

Length of Time Spent Feeding and Traveling

 The activities of individuals were recorded continuously to the nearest second focal animal samples. The following activities were recorded: resting, traveling,

drinking, foraging for food (clearly searching), and eating (actively consuming food). I examined the length of time traveling, rather than recording paces (*sensu* Alberts *et al.* 1996) since it was not possible to record detailed social behavior along with paces. If the focal was not visible, activity was recorded as out of sight and this time was excluded from the analysis. If a focal animal was out of sight for more than 1 minute, that focal sample was not used in analysis. Thus, the length of time spent foraging and traveling was calculated for a particular focal sample, rather than a daily value.

Mean Feeding Bout Length

The mean feeding bout length was calculated for each focal sample. A feeding bout operationally began when the focal came into contact with a food item and ended when the focal was no longer in contact with the food source, either moving to a new site or ceasing food consumption for more than 10 seconds. If the focal moved from one clear food resource to another (e.g., different trees), these were treated as separate feeding bouts. For food resources on the ground, which are often less discrete than individual trees, a feeding bout was considered complete if the focal moved for more than 10 seconds. If the focal switched foods without switching sites (e.g., shifted from eating *Acacia drepanolobium* galls to grass seeds in the same area), this was treated as a single feeding bout since the animal was feeding without interruption. Since the hypothesis being tested involves the interruption of feeding, this was considered a more biologically accurate view of the feeding bout length experienced by the focal. If the focal rested and then began feeding from the same food site or area (without traveling to a new site), these two feeding periods were treated as a single bout, excluding the resting time. A focal was scored as resting if feeding stopped for more than 10 seconds. Bout length was

calculated by combining feeding and foraging into one measure, such that foraging time was included in feeding bout length.

Length of Time Spent Grooming

The occurrence of all grooming bouts was recorded continuously during focal sampling. Since grooming could only occur when an individual was resting, which was an activity I recorded continuously, the length of time resting was used in place of focal duration in analyses below.

Determining Days of Likely Ovulation

Cycling female baboons develop sexual swellings, which change in size throughout their cycle. Ovulation occurs around the time when the sexual swelling undergoes rapid detumescence that is readily seen by visual assessment by human observers (Nunn 1999; Deschner et al. 2003; Gesquiere et al. 2007; Higham et al. 2008; Highham et al. 2009). I recorded female reproductive status daily for all females, particularly noting the day of deflation for all females. Deflation is assessed based on both qualitative assessment of a decrease in swelling size from the previous day and the appearance of wrinkles in the swelling itself; deflation of the swelling is particularly conspicuous since deflation proceeds rapidly. Female cycle day can retroactively be determined using this deflation day (D-day), with preceding days denoted as D-1, D-2, etc. Following Higham *et al.* (2008), I assigned D-4 to D-0 (deflation day) as the most likely days of ovulation. I was thus able to label consorting and following focal data as during the period of likely ovulation or outside the period of likely ovulation.

Data Analysis

I ran six generalized linear mixed models (hereafter GLMM) in the statistical software R v2.1.5.1 (R Development Core Team 2010) using Poisson distribution to assess each of the predictions. Shapiro-Wilks tests confirmed that the data were not normally distributed and goodness-of-fit tests were run for all models to confirm Poisson distribution was appropriate. I used the glmmPQL function in R since this function account for overdispersion by using a Wald t test. The response variable and fixed effects for all models are summarized in Table 4.2. For any models incorporating the length of time of a particular activity (Models 1, 2, and 5), the duration of the focal sample was incorporated as an additional fixed effect, since the exact duration varied around ten minutes and some focals were extended to record the duration of a grooming event. The random effect was the same for all models: individual identity. Models 1, 3, and 5 used data from consorting, following, and nonfollowing males. Models 2 and 4 only used data from following males. Model 6 used data from following and nonfollowing males. Since models 1 and 2, and 3 and 4 test hypotheses using the same response variable, I did a Bonferroni-Holm correction (Levin 1996; Wright 2012), which resulted in two different p values; both sets of p-values are ranked in ascending order and the calculated p-value must be less than its corresponding adjusted p-value to be considered significant. The four adjusted p-values were 0.050 (Model 2 and 4), 0.025 (Model 1 and 3), 0. Summaries of all model parameters and estimates may be found in Table 4.3. Post hoc Tukey-Kramer HSD Tests were conducted as needed; summaries may be found in Table 4.4.

Results

Following, consorting and nonfollowing males spent a similar percent of time feeding contrary to predictions (p = 0.3992, Fig4.1) (see see Table 4.3 for summary of estimates from model). Female cycle period had no effect on feeding time of consorting (p = 0.8659) or following males (p = 0.1757). Group size was also not significant (p = 0.9061).

As the distance to the consort male increased, the length of time followers spent feeding increased (p = 0.0062, Fig4.2). The interaction of distance to the consort male and female cycle period was not significant (p = 0.0576), although there was a trend that followers are closer in proximity to the consort male on the likely days of ovulation (Fig4.3). Group size did not impact the length of time spent feeding in this model (p = 0.0715).

Followers had longer feeding bouts compared to consorting and nonfollowing males (p = 0.0033) contrary to my prediction, while consorting and nonfollowing males had feeding bouts of similar length, contrary to my prediction (Fig4.4). While followers have shorter feeding bouts during the period of likely ovulation compared to other periods (p = 0.0007), as predicted, post hoc tests indicated that followers had feeding bouts of a comparable length as nonfollowing males during the period of likely ovulation (p < 0.0500, Table 4.5) (Fig4.5). There was no significant effect of group size (p = 0.9917).

As the distance to the consort male increased, followers' feeding bouts increased in length (p = 0.0463, Fig4.6).. As with Model 2, followers were closer in proximity to

the consort male on the likely days of ovulation ($p < 0.0001$) (Fig4.3). There was no

effect of group size ($p = 0.5885$), consistent with Model 3.

Following, consorting and nonfollowing males spent a comparable percent of

time traveling, contrary to predictions ($p = 0.0650$) (Fig4.7). The percent of time spent

traveling did not differ between groups of differing size ($p = 0.4174$). There was no

significant effect for female cycle ($p = 0.2035$).

Nonfollowing males spending more time grooming compared to followers ($p = 0.0321$), Fig4.8). As time continued through the day, males spent less time grooming ($p < 0.0001$) (Table 4.4).

Discussion

Neither consorting males or followers experienced reduced time spent feeding;

this result was consistent across three study groups. While previous studies of consorting

males report inconsistent results for the percent of time spent feeding (Rasmussen 1985;

Alberts *et al.* 1996; Matsubara 2003; Weingrill *et al.* 2003; Mass et al. 2009; Higham *et al.* 2011), my findings are consistent with other studies in that consorting males do not

have shorter feeding bouts. I suggest that the unusually high rainfall during my study

(see Introduction) may have resulted in increased food abundance; I currently lack the

phenology data to test this hypothesis. Since both consorting and following males were

expected to spend less time feeding as a result of their proximity maintenance with

another individual, it is less surprising that followers also did not experience this cost.

Alberts *et al.* (1996) suggested that the reduced time spent traveling by consort males was

due to their proximity maintenance with the female and constrained their usual foraging

behavior. My findings do not support the hypothesis that restrictions of movement impact following or consorting males.

However, followers actually had longer feeding bouts in all groups, compared to nonfollowing males and consorting males, suggesting that followers may gain a feeding benefit. Other males tended to avoid a consorting male, unless interested in competing for the female (Packer 1989; Danish pers. obs.); I frequently observed other males avoiding the consort male, even if the consort male was lower ranking. Therefore, a consorting male may face less competition due to this reduced proximity by other males. I suggest that followers, due to their involvement with the consort male, may also encounter other males less frequently. As a result, followers would experience reduced feeding competition. Since followers are thought to invest less in proximity maintenance and monitoring compared to the consort male (Danish pers. obs.) followers may experience a slight increase in time spent feeding and feeding bout length.

The lack of influence of male behavior on activity budget and feeding bout length in my and other studies may be due to the limitations of the measures used. While a decrease in time spent traveling or feeding bout may result in decreased energy intake (Alberts *et al.* 1996), food choice and feeding rate may be more important in understanding energetic intake (Chivers 1998; Zinner 1999; Schuelke *et al.* 2006). In fact, Zinner (1999) found that time spent feeding explained only 30% of variation in food ingested, while there was no relationship between feeding bout length and food intake. Therefore, while I have excluded a decrease in energy intake due to time spent feeding and feeding bout length, consorting and following males may still experience decreased energy intake.

Followers vary in the degree of their proximity maintenance to the consorting pair (Danish unpublished data). Notably, followers are involved in a greater number of agonistic interactions with the consort male, compared to the number of agonistic interactions when not following or consorting (Chapter 1); such interactions are likely more common when a follower is closer to the consort male. Followers also spend less time feeding when closer to the consort male. Therefore, followers potentially increase the likelihood of being involved in an agonistic interaction and may additionally benefit from investing more time in social monitoring, and less time feeding, when they are in closer proximity to the consort male. Therefore, followers may have a means of mitigating multiple costs through their proximity to the consort male. Moreover, followers have shorter feeding bouts during the period of likely ovulation, when there is a greater potential benefit to mating with the female. Consort takeovers, and aggression related to such takeover attempts, are more frequent during the period of likely ovulation (Danish and Palombit submitted). Thus, males are able to invest in following differentially and respond to changes in potential benefits.

Most studies on the constraints imposed by mating behavior examine energetic costs or an increased rate of predation. Since mating behavior constrains the normal activities of individuals, I also expect the social interactions of these individuals to change. In a species like the olive baboon, which lives in semi-permanent social groups, interactions with other individuals influence the fitness of an individual. Thus, a reduction in time spent interacting with other individuals is an important- yet little studied- tradeoff. I found that followers spend less time engaged in grooming, a critical component of baboon sociality (Kummer 1968; Rowell 1972). This represents a loss of

time spent maintaining relationships such as friendships with adult females which are potentially relevant to both future reproductive success and to a male's investment with potential offspring (Smuts 1985; Palombit *et al.* 1997; Mènard *et al.* 2001; Huchard *et al.* 2009; Nguyen *et al.* 2009; Palombit 2009). In addition, grooming is also suggested to reduce somatic stress (Boccia *et al.* 1989; Gust *et al.* 1993; Aureli *et al.* 1999; Shutt *et al.* 2007). Followers are already predicted to experience increased stress due to their potential involvement in an increased number of agonistic interactions; further research on this potential cost is thus warranted. I establish that following constrains one of the usual social interactions of males, indicating that following has additional, more subtle costs.

My findings suggest that following does not impact males' foraging effort, of particular interest since following was expected to reduce feeding more than other alternative strategies reported in the primates (e.g, coalition formation, sneak copulation). While foraging effort is not impacted, there may still be an impact on energetic intake (Chivers 1998; Zinner 1999); future studies would benefit from including a more detailed analysis of caloric intake or the use of noninvasive endocrine data. Followers are also able to reduce their proximity to the consort male, particularly when the consorting female is not likely to conceive, reducing the foraging cost of following. Followers were limited, however, in their ability to invest in other social interactions while following and previous study suggests that followers are involved in more agonistic interactions (Danish and Palombit submitted). Such a reduction in positive social interactions like grooming and concomitant increase in agonistic interactions may produce somatic stress in followers, which warrants empirical examination. Therefore, I suggest that energetic

costs be examined further, using different measures, in addition to   other costs, which

warrant further study.

Table 4.1 Summary of Study Groups and Data

Group	Mean number of males (range)	Mean number of females (range)	Number of Females (Cycles) Observed	Number of Hours of Focal data:			Total Number of Hours of Focal Data
				Nonfollow	Consort	Follow	
Large	15.0 (11-19)	25.6 (22-30)	10 (14)	132.6	108.0	90.1	330.7
Small 1	5.3 (4-6)	6.2 (6-7)	2 (3)	17.6	25.2	36.8	79.6
Small 2	5.5 (5-8)	8 (8)	2 (3)	19.8	20.1	12.2	52.1

Table 4.2 Summary of Models

Model	Response Variable	Fixed Effects

1	Length of time spent feeding	(1) Time
		(2) Group size
		  - large
		  - small

3	Mean feeding bout length	(3) Male behavior
		  - consorting
		  - following
		  - nonfollowing

5	Length of time spent traveling	(4) Interaction of male behavior and female cycle period (likely or not likely ovulation)

2	Length of time spent feeding	(1) Mean distance to the consort male
		(2) Group size
		  - large
		  - small
		(3) Time
		(4) Female cycle period
		  - Likely ovulation
		  - Not likely ovulation

4	Mean feeding bout length	(5) Interaction between mean distance to the consort male and female cycle period

6	Length of time spent grooming	(1) Time
		(2) Male behavior
		  - Following
		  - Nonfollowing
		(3) Length of time resting

Table 4.3 Summary of Model Parameters

Model	Model/Effect	Estimate	Standard Deviation	P-value	Result as Predicted?
1	Fixed Effects: Male behavior - Following - Consorting	0.1	0.1	0.3992 NS	NO NO
	Group size (small)	$1e^{-2}$	0.1	0.9061	
	Time	0.1	$1e^{-2}$	<0.0001	
	Focal Duration	$-4e^{-3}$	$9e^{-4}$	<0.0001	
	Interaction of male behavior and female cycle period - consorting, likely ovulation - following, likely ovulation	$-2e^{-2}$ -0.2	0.1 0.1	0.8658 0.1757	NO NO
2	Fixed Effects: Distance to consort male	$9e^{-3}$	$3e^{-3}$	0.0062	
	Group size (small)	0.2	0.1	0.0715	YES
	Time	0.1	$1e^{-2}$	<0.0001	
	Focal Duration	$-2e^{-3}$	$1e^{-3}$	0.0522	
	Interaction between distance to the consort male and female cycle period (likely ovulation)	-0.0031	0.0006	0.0576	YES
3	Fixed Effects: Male behavior - Following - Consorting	0.6	0.2	0.0033 NS	NO NO
	Group size (small)	$-1e^{-3}$	0.1	0.9917	
	Time	0.1	$2e^{-2}$	<0.0001	
	Interaction of male				

	behavior and female cycle period				
	- consorting, likely ovulation	-0.1	0.2	<0.5092	NO
	- following, likely ovulation	-0.6	0.2	0.0007	YES
4	Fixed Effects: Distance to consort male	0.0067	0.0004	0.0463	YES
	Group size (small)	0.1	0.2	0.5885	
	Time	0.1	$3e^{-2}$	<0.0001	
	Interaction between distance to the consort male and female cycle period (likely ovulation)	$-2e^{-2}$	$5e^{-3}$	<0.0001	YES
5	Fixed Effects: Male behavior				
	- Following	-0.2	0.1	0.0650	NO
	- Consorting			NS	NO
	Group size (small)	$-5e^{-2}$	0.1	0.4174	
	Time	$4e^{-2}$	$8e^{-3}$	<0.0001	
	Focal Duration	$-8e^{-4}$	$5e^{-4}$	0.1230	
	Interaction of male behavior and female cycle period				
	- consorting, likely ovulation			NS	NO
	- following, likely ovulation	0.1	0.1	0.2035	NO
6	Fixed Effects: Male behavior (Nonfollowing)	0.3	0.1	0.0321	YES
	Time	$6e^{-2}$	$2e^{-2}$	0.0074	
	Time Resting	$5e^{-3}$	$2e^{-4}$	<0.0001	

Table 4.4 Summary of Time Effects

Time	Number of Focal Samples	Percent of Time Spent Feeding (Model 1)	Mean Feeding Bout Length (Model 2)	Percent of Time Spent Feeding (Model 3)	Mean Feeding Bout Length (Model 4)	Percent of Time Spent Traveling (Model 5)	Percent of Time Spent Grooming (Model 6)
06:00-06:59	100	2.4 ± 6.0	23.2 ± 28.8	4.9 ± 9.4	9.4 ± 2.3	10.6 ± 19.7	19.4 ± 34.6
07:00-07:59	342	6.7 ± 11.1	38.3 ± 76.2	5.9 ± 8.0	24.8 ± 21.1	14.8 ± 12.8	9.8 ± 11.8
08:00-08:59	373	14.3 ± 14.0	33.3 ± 34.5	14.6 ± 13.3	43.1 ± 43.6	25.9 ± 19.2	8.0 ± 14.6
09:00-09:59	368	17.9 ± 16.0	32.4 ± 40.3	18.1 ± 13.4	28.8 ± 26.0	35.5 ± 20.0	5.1 ± 13.0
10:00-10:59	344	20.8 ± 17.1	50.9 ± 84.0	19.5 ± 14.1	40.2 ± 48.6	35.0 ± 18.2	4.9 ± 9.1
11:00-11:59	327	24.6 ± 16.0	37.4 ± 33.1	25.3 ± 16.8	42.4 ± 35.8	37.3 ± 14.1	8.2 ± 14.1
12:00-12:59	273	24.3 ± 17.6	45.2 ± 56.7	26.6 ± 19.2	58.7 ± 80.4	32.3 ± 18.9	4.0 ± 10.4
13:00-13:59	153	27.2 ± 23.1	63.6 ± 91.8	22.6 ± 15.3	52.2 ± 42.1	24.5 ± 17.9	7.8 ± 16.1
14:00-14:59	124	32.7 ± 22.6	72.2 ± 72.3	31.6 ± 22.4	90.8 ± 86.1	23.1 ± 16.1	7.2 ± 21.9
15:00-15:59	97	33.2 ± 27.9	82.5 ± 125.7	33.3 ± 23.3	89.5 ± 95.6	29.4 ± 19.4	7.0 ± 16.4
16:00-16:59	87	49.0 ± 25.9	95.3 ± 114.8	44.1 ± 23.2	96.6 ± 155.7	36.0 ± 21.4	4.8 ± 14.4
17:00-17:59	58	41.7 ± 28.4	71.2 ± 105.4	41.0 ± 28.5	59.9 ± 71.9	35.9 ± 21.0	8.2 ± 22.2
18:00-18:59	6	15.1 ± 14.0	16.3 ± 10.3	1.5 ± 2.1	3.0	57.3 ± 19.6	0.0 ± 0.0

Table 4.5 Summary of Tukey-Kramer HSD Post hoc Tests

Model	Result		P-value	Result as Predicted?
3	Male Behavior Following (likely ovulation) (48.6) Nonfollowing (45.2) Consorting (likely ovulation) (40.8)	Group A A A	$p < 0.0500$	NO
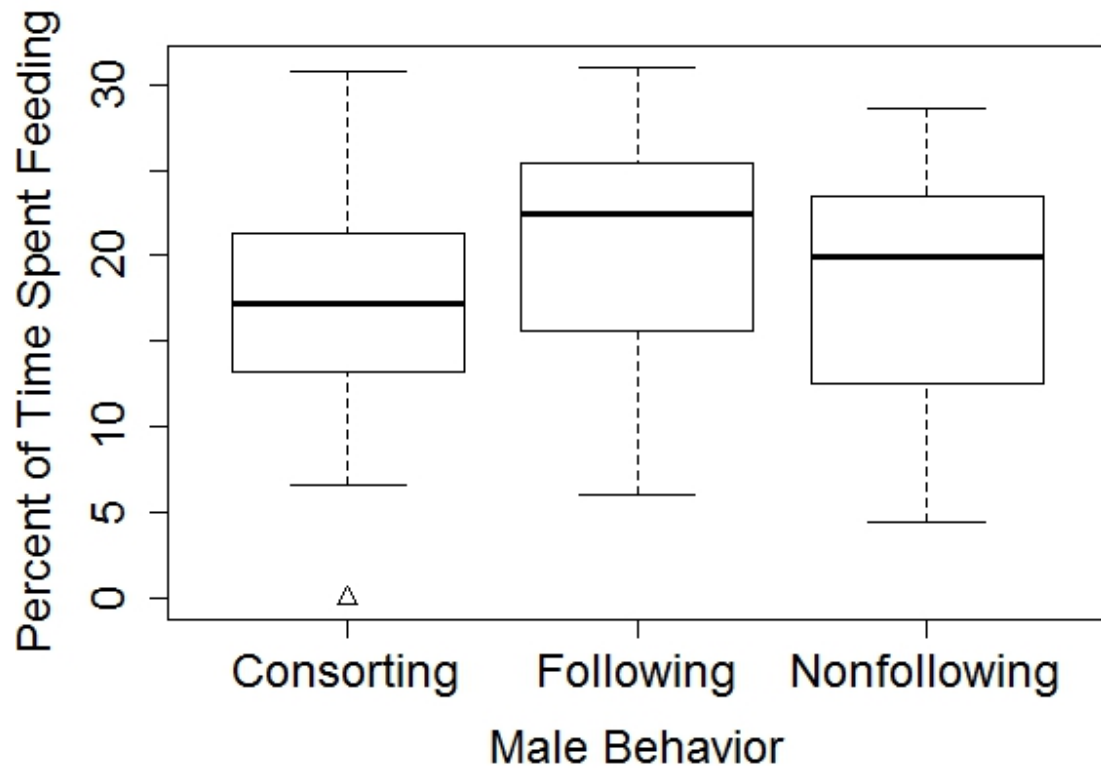
Fig4.1 No Difference in the percent of time spent feeding for consorting, following, and nonfollowing males
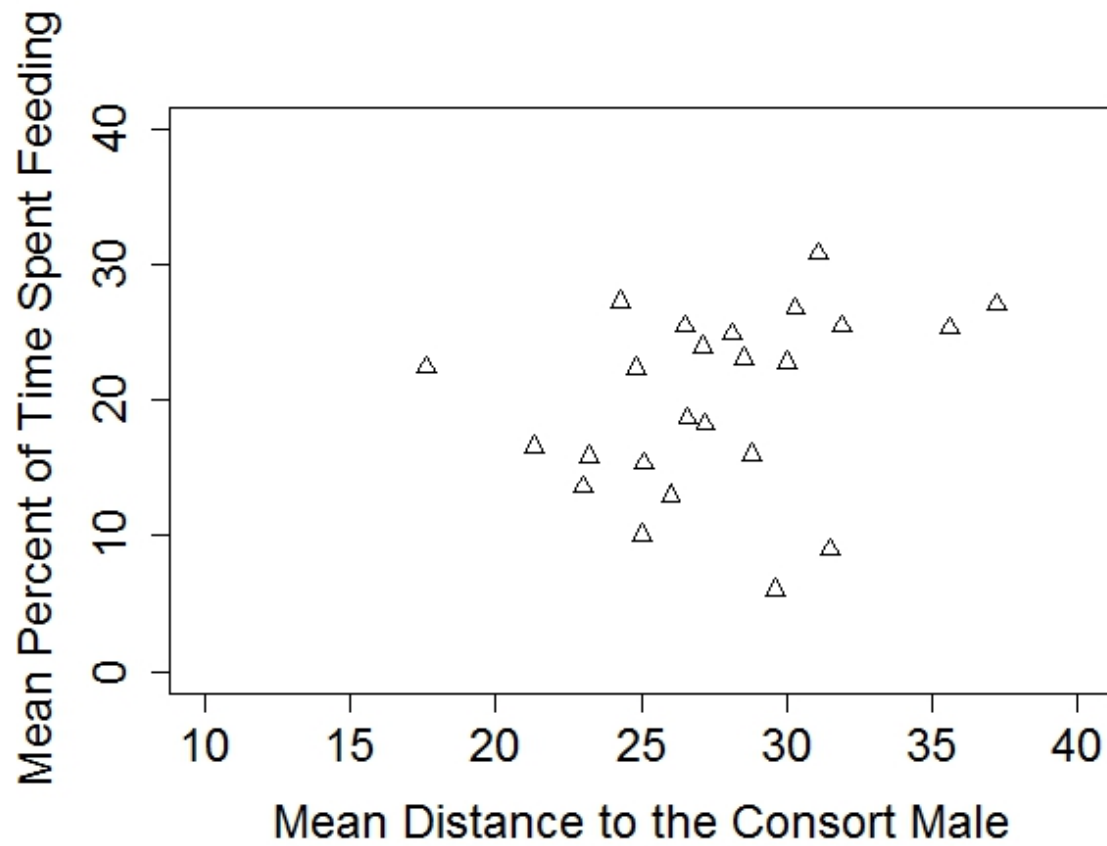
Fig4.2- Variation of percent of time spent feeding with variation in follower distance to consort male

Fig4.3- Comparison of the mean distance of followers to the consort male during the period of likely and unlikely ovulation

Fig4.4- Comparison of feeding bout length for consorting, following, and nonfollowing males

Fig4.5- Variation in feeding bout length with variation in follower distance to consort male

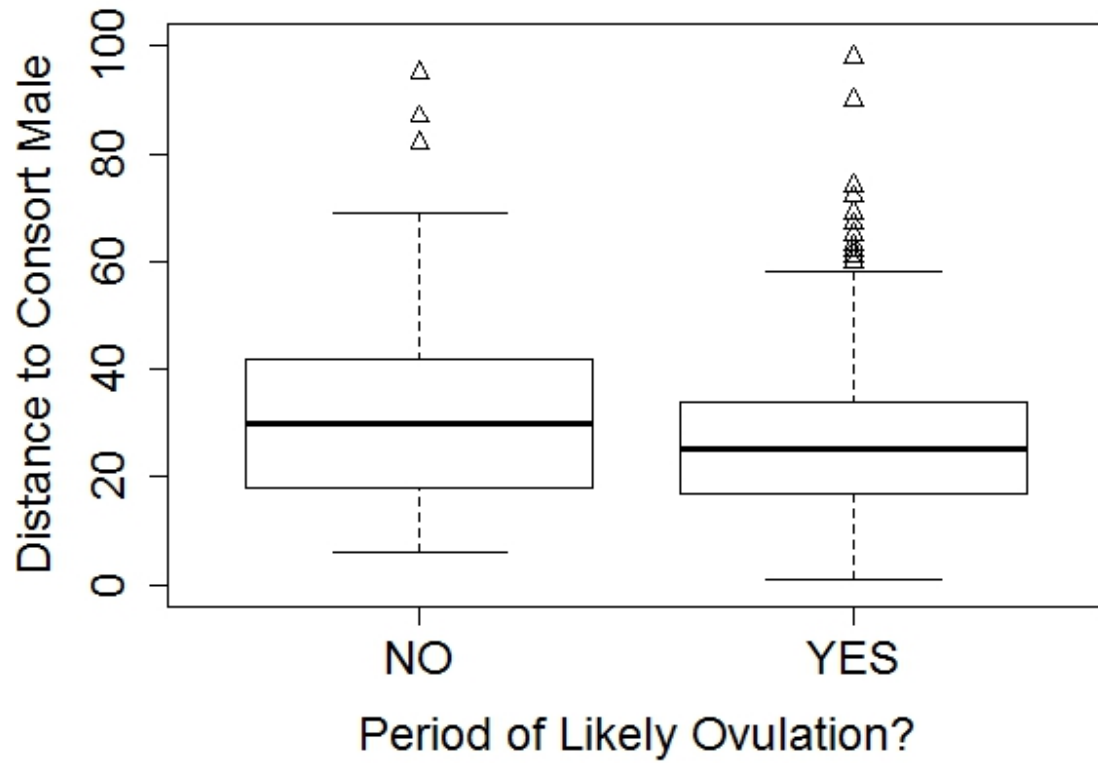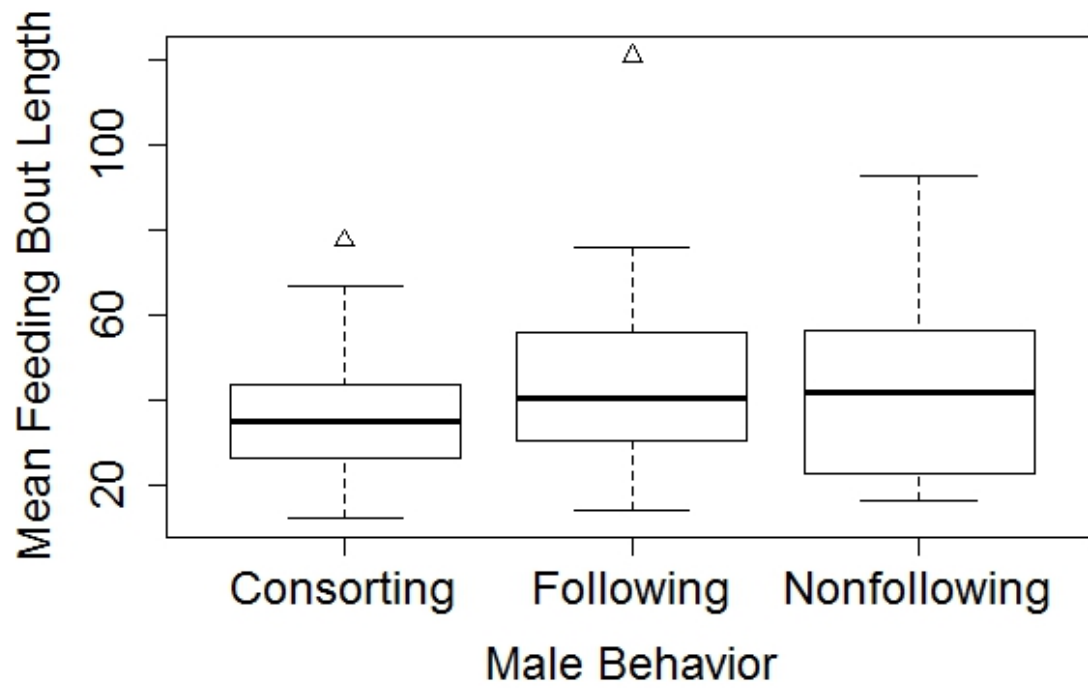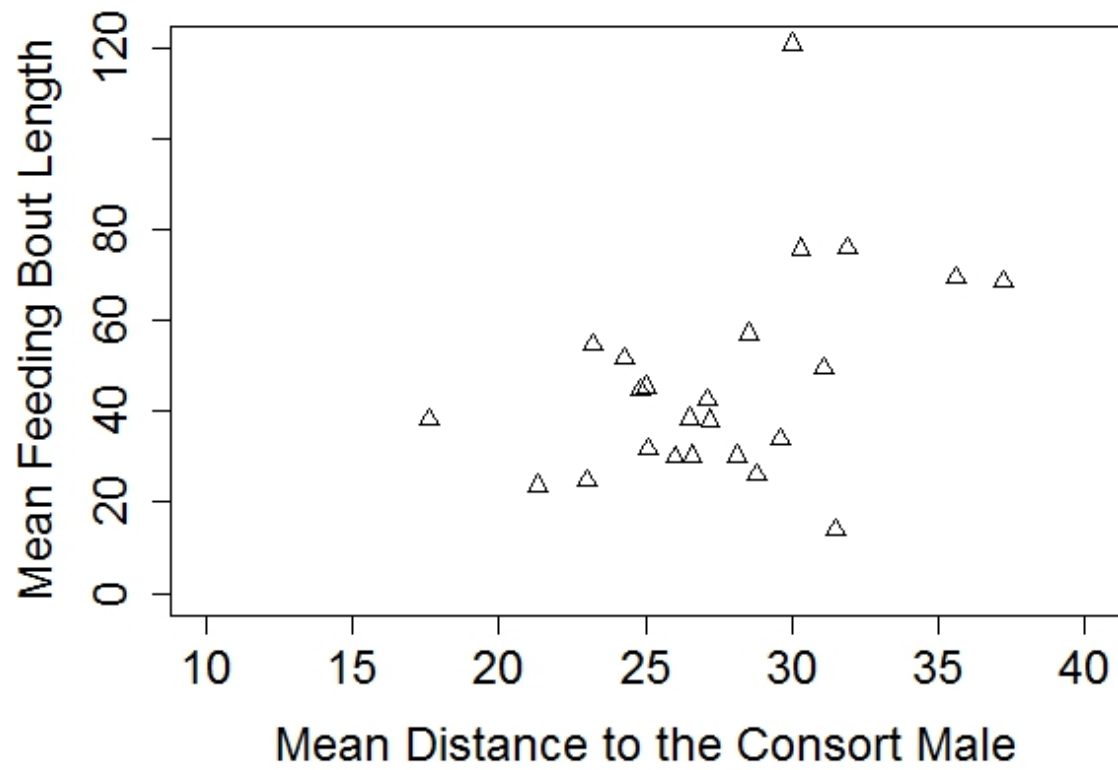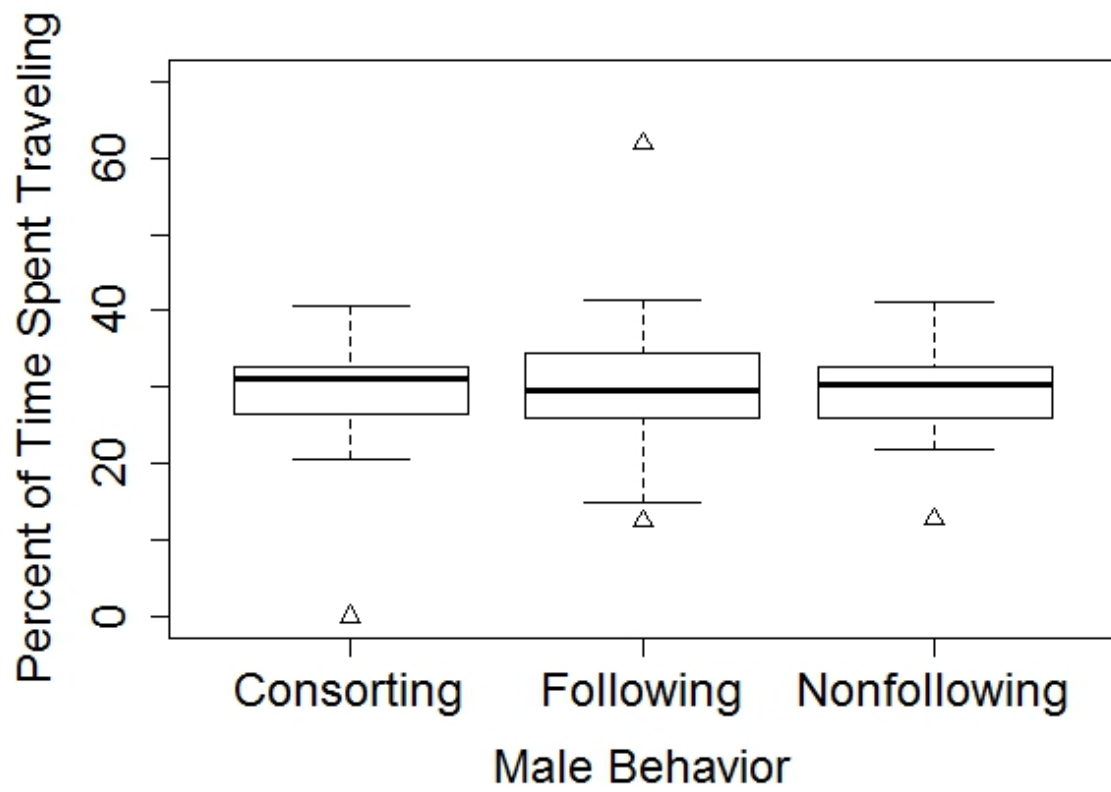**Fig4.6- Comparison of the percent of time spent traveling for consorting, following, and nonfollowing males**
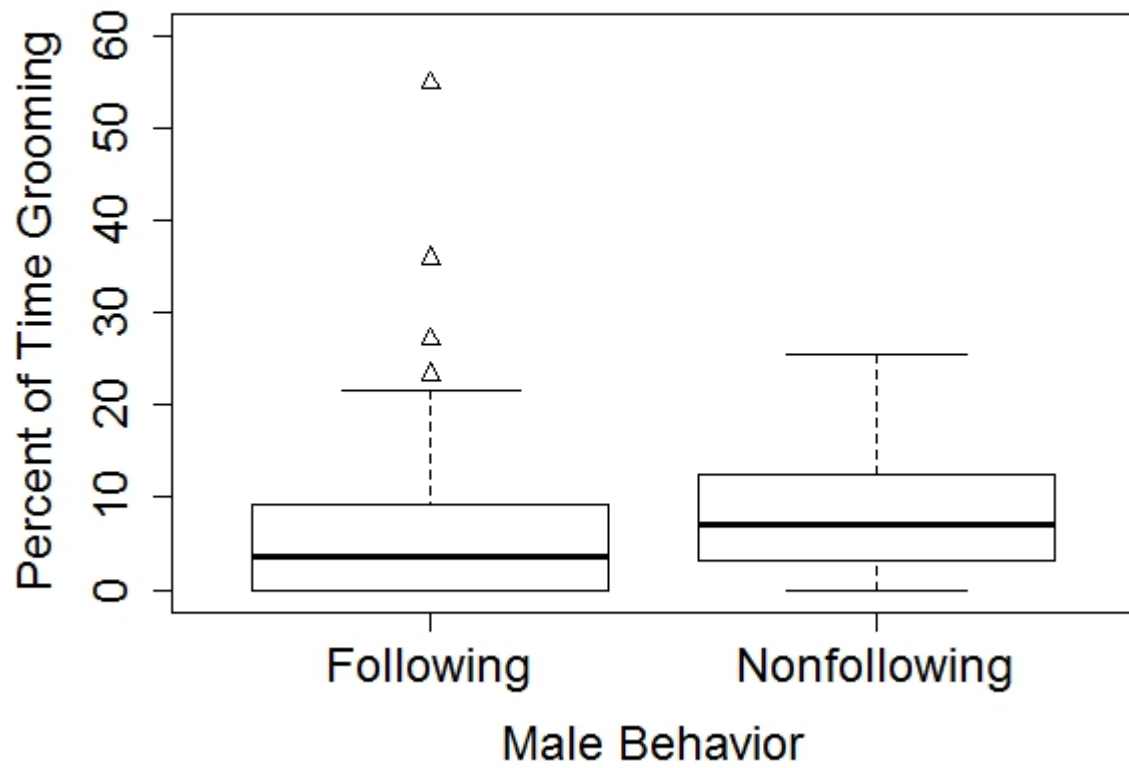
Fig4.7- Comparison of the percent of time (while resting) spent grooming when following and not mating

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CHAPTER FIVE: INFLUENCE OF INTERSEXUAL INTERACTIONS ON

FOLLOWING

Introduction

Recent evidence regarding the high degree of conflict between the sexes (Smuts

and Smuts 1993; Alonzo and Warner 2000; Luttberg 2004; Arnqvist and Rowe 2005;

Alonzo 2008, Muller et al. 2011) underscores the importance of examining the behavior

of both sexes and particularly the interaction between the sexes. Alonzo (2008) suggests

that this is particularly critical for understanding the evolution of alternative mating

strategies since both these strategies and intersexual interactions are dynamically related.

Models indicate that female preferences can eliminate or maintain the occurrence of

alternative mating strategies in a population, as can male coercion (Henson and Warner

1997; Alonzo and Warner 2000; Rios-Cardenas 2007). Variation in female preference

has even been suggested as an alternative to frequency dependent selection maintenance

of alternative strategies (Rios-Cardenas 2007). We know little regarding the influence of

intersexual interactions on alternative strategy choice, when strategies are flexible, or on

the outcome of individuals pursuing alternative mating strategies.

The influence of intersexual interactions is well studied in the context of mating

success. Female preferences influenced which male consorts and the likelihood of an

escalated challenge for females in yellow baboons (*Papio hamadryas cynocephalus*)

(Bercovitch 1995). Female preference, but not female resistance, influences male mating

success in chimpanzees (*Pan troglodytes verus*) (Stumpf and Boesch 2006). Stumpf and

Boesch (2010) additionally indicate that male coercion did not influence mating success,

contrary to Muller et al.'s (2007) findings in another population of chimpanzees (*Pan*

troglodytes schweinfuthii). Recent evidence indicates that copulatory approaches,

typically considered indicative of female preference, are correlated with male aggression

(Muller et al. 2011). Thus, Muller et al.'s (2011) finding underscores the importance of

testing for a correlation in measures of female preference and the difficulties in

distinguishing between female preference and male coercion.

Olive baboons (*Papio hamadryas anubis*) are an ideal species in which to

examine the influence of intersexual interactions on alternative mating strategies since

they are known to exhibit a little studied alternative mating strategy, "following"

(Chapter 1, 2). In addition, as with chimpanzees (Muller et al. 2007), cycling female

olive baboons are more likely to be wounded than noncycing females (MacCormick et al.

2012). Smuts (1985) found that female olive baboons were the target of male aggression

approximately once every 17 hours and that an individual female is likely to receive a

serious wound from a male once a year. Coupled with the notable size and canine

dimorphism of olive baboons, there is clearly a potential for sexual coercion in this

species. The "primary" mating strategy of male olive baboons is solo competition for the

well known "sexual consortship," a temporary relationship between a male and an estrous

female characterized by close spatial proximity, male mate guarding, and relatively high

rates of copulation (Hall and DeVore 1965; Small 1990; Bulger 1993; Bercovitch 1995).

Consortships in olive baboons (*P. h. anubis*) typically last from a few hours to several

days (Bercovitch 1995; Danish pers. obs.), but what is less often appreciated about this

system is that the consorting pair is typically accompanied by a retinue of "followers."

Anywhere from one to eight adult males may maintain contact at variable distances with

the consorting pair and with each other, while coordinating their movements with the

consort pair for hours or even days (Hall and DeVore 1965; Hausfater 1975; Strum 1982, 1994; Bercovitch 1988; Sapolsky 1990; Forster and Strum 1994). Following is an alternative mating strategy, providing males with access to fertile females (Chapter 1, 2).

Since Muller et al. (2011) suggested that measures of female preference are correlated to male aggression directed at females, I tested this prediction using baboons as a model species. While both female preferences and male coercion are thought to influence the evolution of alternative mating strategies, the influence of these selective forces on the expression of alternative mating strategies remains unknown. I therefore predicted that the proportion of time a male spent following a particular female's consortships would increase with increasing female proceptivity and male aggression towards that female. I additionally predicted that follower success would increase with increasing female proceptivity and male aggression.

Methods

Study Site and Subjects

Subjects came from two habituated groups of olive baboons (*Papio hamadryas anubis*) that have been the focus of long-term study since 1999 in Laikipia District, Kenya (36°50'E, 0°15'N) (Lemasson et al. 2008; Shur et al. 2008a, 2008b). Subjects were studied from September 2009 to July 2010.

Data Collection on Cycling and Consorting Females

All females that were not pregnant or lactating were considered cycling females, even when not displaying a sexual swelling. Cycling adult females of varying ages and dominance rank were selected, particularly selecting females of differing age and rank from the pool of cycling females, as opposed to selecting females randomly. A

consorting female was operationally defined as a cycling female with a sexual swelling

with whom a particular male was maintaining close proximity (often within 5 meters),

preventing other males from interacting with the female (i.e., mate guarding), and

copulating with her. Females typically consorted continuously, for six to 21 days (mean

= 9.6, Danish unpublished data), particularly as the period of likely ovulation approached.

The selected cycling females were followed during two periods, during which ten minute

focal samples were collected: 1) while not consorting; and 2) while consorting.

Dyadic Association Time

Following Stumpf and Boesch (2010) and Muller et al.'s (2011) studies on

chimpanzees we controlled for dyadic association time. When the focal female was

cycling, but not consorting we used observation time or duration of all focal samples

(depending on the measure, see below) as the dyadic association time since all males

were able to associate with the female during this period. When the female was

consorting, we used the duration of time of the focal samples collected for a dyad as its

dyadic association time.

Female proceptive measures

Following Bercovitch (1995), I used female presentation and grooming of males

as measure of female proceptivity. I recorded all occurrences of female presentations to

all males when observing a female prior to the onset of consorting. I therefore used the

total time of the observation days, rather than the duration of all focal samples, to

calculate the rate of this behavior. Since I was unable to observe consorting females if I

was not conducting a focal sample, I used the duration of all focal samples on a member

of the consorting pair as the dyadic association time. I recorded the duration of all

grooming bouts during focal samples to determine the proportion of the dyadic association time the female groomed a particular male (hereafter referred to as female grooming). Since duration of grooming was only recorded during focal samples, I used the duration of time we observed a female as the dyadic association time prior to the onset of consorting.

Mount and copulation resistance

I operationally defined mount resistance as female movement away from the male while the male was attempting to mount or copulate. I defined mounting as follows: a male grasp the female's hindquarters with his hands, while placing his feet on the female's legs. Pelvic thrusting by the male may occur. A copulation was defined as a mount with intromission. Thus, if the female moves, the mount attempt ceases or the copulation is interrupted. I calculated the proportion of mount and copulation attempts that were resisted for each male-female dyad by dividing the number of mount and copulations that were resisted by the total number of mounts and copulations by dyad. Since mounting and copulation behavior was rare when a female was not consorting, I only analyzed this measure during the period when a female was consorting.

Copulatory Darts

I defined a copulatory dart as the rapid movement by the female away from a copulating male during or immediately following a copulation; this behavior could occur before ejaculation, effectively interrupting the copulation, or after ejaculation. I recorded all occurrences of this behavior during focal sampling. I determined the proportion of a female's copulation with a particular male including a copulatory dart by dividing the number of copulations with a copulatory dart by the total number of copulations. As

above, this measure was only used in analyses of the consorting period. The role of copulatory darts is debated, as copulatory darts have been hypothesized to either increase male intrasexual competition or to increase the likelihood of future mating with the same male (O'Connell and Cowlishaw 1995). Thus, it is uncertain if this behavior is a measure of female preference or resistance.

Measure of Male Coercion

I recorded all occurrences of male aggression directed at the cycling female throughout the observation day when observing a female prior to the onset of consorting. I included threats (vocal, ground slap), chases, bites, pushing, and hitting as measure of male aggression (Hall and DeVore 1965). I did not use supplants in this measure, since this is a common and not overtly threatening event that commonly occurs between males and females since adult males dominate all females. I therefore used the total observation day time, rather than the duration of all focal samples, to calculate the rate of this behavior. Since I was not able to observe consorting females when not conducting a focal sample, I used the duration of all focal samples on a member of the consorting pair.

Hinde's index

I calculated Hinde's Index to obtain a score of relative female proximity to all males. I calculated this measure for each male-female dyad as described in Hinde and Atkinson (1970), by subtracting the proportion of withdrawals by the female from the proportion of approaches by the female. Thus, negative values of Hinde's Index indicate that the male is primarily responsible for proximity. During focal sampling, the direction of approaches and withdrawals between males and females were collected. An approach

was defined as entering the two meter radius of the other individual and a withdrawal was defined as leaving that two meter radius.

Consort and Follower Status

For each consortship and day, males were classified as either "consort males," "followers," or "nonfollowers." Consort males were identified based on extended proximity maintenance with a cycling female with a sexual swelling as described above. We categorized all males not consorting using a male proximity score (MP-score) modified from Smut's (1985) composite proximity score (or "C-score") (as in Chapters 1-4). We calculated the MP-scores from spatial data collected via 15 minute scan samples throughout the observation day, in which we collected distances of all visible adult males to the consort male using a Nikon Prostaff 550 rangefinder accurate to 0.5m within 100m. If a consort takeover, defined as a change of consort male, occurred we calculated the MP-scores separately for each consortship on an observation day. If a consortship continued the next observation day, we calculated the MP-score only using data from the current observation day since individual male behavior varied from day to day. We classified males that were seen during more than 25% of scan samples and with a MP-score of 1.9 or higher as "followers," while males with a MP-score less than 1.9 were classified as "nonfollowers."

Length of time spent following an existing consortships

We calculated the length of time spent following for each male by determining the sum of the male's time spent following (in minutes). We also determined the total amount of time a male was present in the group and not himself involved in a consortship

since consorting males cannot follow at the same time (hereafter "time available") (see Chapter 3). We calculated this separately for each female for all males.

Proportion of successful following events

Each consortship a male followed was defined as a following event. For each male, we determined the number of successful following events, defined as following events that resulted in a consort takeover by the male. We then calculated the proportion of successful following events by the male.

Data Analysis

I analyzed data from the two time periods separately. To examine if female preference or male aggression prior to the formation of consortships influenced following behavior, I ran a Generalized Linear Mixed Model (GLMM) with the length of time spent following as the response variable. Shapiro-Wilks tests confirmed that the data were not normally distributed and goodness-of-fit tests were run for all models to confirm Poisson distribution was appropriate. I used the glmmPQL function in the statistical software R v2.1.5.1 (R Development Core Team 2010) since this function account for overdispersion by using a Wald t test. I first determined if any of our fixed effects were correlated using Spearman's rank correlations. This also allowed me to determine if measures of female preference were correlated to male aggression as in Muller et al.'s (20111) study. I used a Bonferroni-Holm correction to account for multiple testing. Since there were correlations between the rate of male aggression, female presentations, and female grooming I used a Principal Components Analysis (PCA) to create new variables from these three variables. Principle component loadings greater than 0.30 or less than -0.30 were considered significant, while principal component loadings greater than 0.40 or less

than -0.40 were considered significant and more important and principal component loadings greater than 0.50 or less than -0.50 were considered very significant (Hair et al. 1987; McGarigal et al. 2000). Since the principal components are orthogonal, they can be used as fixed effects in a GLMM. My fixed effects were Principal Component 1 (PC1), PC2, PC3, Hinde's Index and time available. The random effect was male identity.

To examine if female preference, female resistance, and male aggression while consorting influenced following behavior, I ran a Generalized Linear Mixed Model (GLMM) with the length of time spent following as the response variable as above. I first determined if any of the fixed effects were correlated using Spearman's rank correlations. This also allowed me to determine if measures of female preference were correlated to male aggression as in Muller et al.'s (2011) study. I used a Bonferroni-Holm correction to account for multiple testing. Since there the correlation between the rate of male aggression and female presentations was a trend, though not statistically significant, I used a Principal Components Analysis (PCA) to create new variables from these two variables. Principal component loadings were evaluated as above. My fixed effects were Principal Component 1 (PC1), PC2, female grooming, Hinde's Index, the proportion of mounts and copulations that were resisted, and the proportion of copulations with a copulatory dart. The random effect was male identity.

I then determined if my behavioral measures predicted follower success by running a linear regression with all variables that were significant in the GLMM. I ran two linear regressions, one for each observation period.

Results

The rate of female presentation and grooming while not consorting was positively correlated (r=0.43, p=0.0005, Table 1). In addition, both female presentation and grooming were correlated with the rate of male aggression directed at the same female (presentation: r=0.31, p=0.0011; grooming: r=0.44, p=0.0004, Table 1). Only the rate of female presentation and the rate of male aggression while consorting were correlated, although this was only a trend after the Bonferroni-Holm correction (r=0.35, p=0.0045, Table 2).

The PCA for the not consorting period generated three principal components (Table 3). Values of PC1 increased with increasing rates for female presentation, female grooming, and male aggression. Thus, PC1 includes information linked to all three variables, fitting with Muller et al.'s (2011) finding that measures of female preference and male aggression are correlated. Increasing values of PC2 were associated with increasing female time grooming and male aggression rates, and decreasing rates of female presentation; the primary loading for this principal component was female grooming. Increasing values of PC3 were associated with increasing rates of female presentations and decreasing male aggression rates. Thus, PC3 represents apparent female preference not associated with male aggression.

For the cycling period, the length of time spent following increased with increasing values of PC1 (p = 0.0040, Table 4) (Fig1). The percent of time spent following was not influenced by PC2 (p = 0.8062), PC3 (p = 0.9207), or Hinde's Index (p = 0.6247).

The PCA for the consorting period generated two principal components (Table 5). Values of PC1 increased with increasing rates of both female presentations and male aggression. Thus, PC1 includes information linked to both variables, fitting with Muller et al.'s (2011) finding that ratees of female preference and male aggression are correlated. Increasing values of PC2 were associated with increasing rates of female presentations and decreasing rates of male aggression. Thus, PC2 represents apparent female preference not associated with male aggression.

For the consorting period, the length of time spent following increased with increasing values of PC1 ($p = 0.0040$), increasing female grooming ($p = 0.0466$), and decreasing proportion of resisted mounts and copulations ($p = 0.0382$) (Table 4) (Figs2-4). PC2 ($p = 0.1167$), Hinde's Index ($p = 0.1296$), and the proportion of copulations with a copulatory dart ($p = 0.1384$) did not influence time spent following.

For the cycling but not consorting period, PC1 and PC2 explained 30% of the variance in success ($F_{4,36} = 3.9$, $p = 0.0097$), although PC3 and Hinde's Index were not significant ($p = 0.6680$, $p = 0.9031$). Individuals with higher PC1 values and lower PC2 values were therefore more successful followers (Figs5-6). For the consorting period, none of the variables of interest explained variation in follower success ($F_{6,32} = 1.0$, $p = 0.4142$).

Discussion

Consistent with Muller et al.'s (2011) study, female preference measures were correlated with male aggression rates; such measures therefore most likely do not measure female preference independent of male aggression. My qualitative observations support this conclusion; females often presented to a male that had threatened them

within several minutes or even seconds. Sexual conflict can impose selective pressures on female preferences (Anderrson and Simmons 2006); thus, male coercion may alter female preferences resulting in female preferences that are related to avoiding aggression.

While intersexual interactions between males and cycling females influenced male following behavior, the role of female preferences remains unclear since my measure of female preference was correlated with male aggression. Thus, male coercion influences male following behavior, but further measures of female preference are needed to determine the influence of female choice. One notable exception was grooming by the female while consorting, which was not correlated with male aggression. This suggests that female grooming may be a more useful measure of female preference than female presentations, although only when consorting. Since I found that increasing female grooming and male aggression (and associated female presentation) both independently influenced male following behavior, this suggests that both female preferences and male aggression independently influence male behavior.

Since female resistance was not correlated to male aggression, measures of resistance may provide insight into female preference; although female resistance did not influence male behavior in some studies (Bercovitch 1995; Stumpf and Boesch 2006), my findings suggest that female resistance influences male following behavior. While Muller et al. (2011) suggest that female resistance may be problematic if females resist a copulation with one male to avoid coercion from a second male, such male aggression from a third party is unlikely when a female is consorting. The efficacy of such a measure will be dependent on the particular species, but is a potential measure of female preference that my findings indicate is not correlated to male aggression.

Interestingly, success in following was only predicted by measures of male aggression and correlated with female presentation and grooming during the cycling period. Since increased time following a female increases follower success (Chapter 3), and these same measures predict time spent following, the influence of intersexual interactions on follower success is likely via increased time spent following. This finding suggests that males benefit from allocating mating effort to females based on their previous interactions with those females. Since males spend less time following the consortships of female that resist their mount and copulation attempts, female cooperation while consorting should influence male mating success as suggested in previous studies (Bercovitch 1995; Stumpf and Boesch 2006, 2010). Thus, male choice is also potentially relevant in understanding following behavior.

Typically, the influence of female preference or male coercion on male alternative mating strategies considers only female preference for males pursuing a particular strategy or male coercion by males pursuing a particular strategy. There is considerable potential, however, for female preference and male coercion to be independent of male strategy when these strategies are flexible or if female benefits are not dependent on male strategy. Following is flexible, and while lower ranking males follow more often than higher ranking males (Chapter 3), all males exhibit following. In addition, males are likely to rise and fall in dominance rank, and therefore their reliance on following, throughout their lifetime. Moreover, olive baboons have been suggested to chose mates based on male's ability to provide paternal care via "friendships" (Smuts 1985) and these male friends have been shown to shield females from harassment from other females (Lemasson et al. 2007; Palombit 2009). There is no evidence to support the proposition

that males provide indirect benefits to females based on the mating strategy utilized. Female preference for multiple mates as an infanticide avoidance strategy (reviewed in Setchell and Kappeler 2006) may also result in female preferences that are not tied to male strategy choice.

This study indicates that following, an alternative mating strategy, is influenced by intersexual interactions in olive baboons. Although distinguishing between female preference and male coercion is difficult, my findings suggest that both female preference and male coercion influence male behavior. I propose that female resistance and grooming in the context of consortships are potentially useful measures of female preference independent of male aggression, although such behaviors will likely be taxon specific and require confirmation. My findings additionally indicate that such intersexual interactions should be considered more broadly than as definitive based on alternative strategy choice. Thus, males face selective pressure to preferentially invest mating effort in individuals based on intersexual interactions, since these interactions influence mating success. Further studies focusing on other species, as well as experimental study to better distinguish between female preference and male coercion, would further our understanding of the influence of intersexual interactions on alternative mating strategies.

Table 5.1- Correlations of Variables, measured prior to consorting

Variable 1	Variable 2	Spearman's rho	P-value	Adjusted p-value for significance
Male Aggression	**Groom**	**0.44**	**0.0004**	**0.0085**
Present	**Groom**	**0.43**	**0.0005**	**0.0102**
Male Aggression	**Present**	**0.31**	**0.0011**	**0.0127**
Present	Hinde index	-0.26	0.0473	0.0170
Male Aggression	Hinde index	-0.20	0.1263	0.0253
Groom	Hinde index	-0.19	0.1520	0.0500

Table 5.2- Correlations of Variables, measured when consorting

Variable 1	Variable 2	Spearman's rho	P-value	Adjusted p-value for significance
Male Aggression	***Present***	***0.35***	***0.0045***	***0.0034***
Groom	Hinde Index	0.23	0.0759	0.0037
Male Aggression	Resistance	0.26	0.0888	0.0039
Hinde Index	Dart	-0.24	0.1092	0.0043
Present	Dart	-0.17	0.2675	0.0047
Male Aggression	Hinde Index	-0.14	0.2777	0.0051
Present	Groom	0.12	0.3499	0.0057
Groom	Resistance	0.13	0.3776	0.0064
Groom	Dart	-0.11	0.4573	0.0073
Present	Resistance	0.11	0.4689	0.0085
Male Aggression	Dart	-0.09	0.5585	0.0102
Male Aggression	Groom	0.06	0.6252	0.0127
Present	Hinde Index	-0.06	0.6404	0.0170
Hinde Index	Resistance	0.04	0.8062	0.0253
Dart	Resistance	0.12	0.4601	0.0500

Table 5.3- Summary of PCA for cycling, but not consorting period

	PC1	PC2	PC3
Standard Deviation	1.54	0.61	0.50
Proportion of Variance	0.80	0.12	0.08
Cumulative Proportion	0.80	0.92	1.00
Loadings	**Present 0.59** **Groom 0.58** **Aggression 0.56**	**Present -0.38** **Groom 0.83** **Aggression 0.41**	**Present 0.72** Groom -0.02 **Aggression -0.70**

Significant loadings are in bold font.

Table 5.4- Summary of GLMM Parameters

Model	Model/Effect	Estimate and standard deviation	P-value
Cycling, not consorting	Fixed Effects		
	PC1	0.28 ± 0.09	0.0040
	PC2	-0.05 ± 0.21	0.8062
	PC3	-0.03 ± 0.26	0.9207
	Hinde's Index	-0.19 ± 0.33	0.5776
	Time available to follow	$7e^{-4} \pm 1e^{-4}$	<0.0001
Consorting	Fixed Effects		
	PC1	0.51 ± 0.15	0.0040
	PC2	0.29 ± 0.18	0.1167
	Groom	3.90 ± 1.77	0.0466
	Hinde's Index	0.68 ± 0.42	0.1296
	Resistance	-1.92 ± 0.84	0.0382
	Copulatory Dart	-0.28 ± 0.18	0.1384
	Time available to follow	$3e^{-4} \pm 8e^{-5}$	0.0049

Table5. 5- Summary of PCA for consorting period

	PC1	PC2
Standard Deviation	1.21	0.74
Proportion of Variance	0.73	0.27
Cumulative Proportion	0.73	1.00
Loadings	**Present 0.71** **Aggression 0.71**	**Present 0.71** **Aggression -0.71**

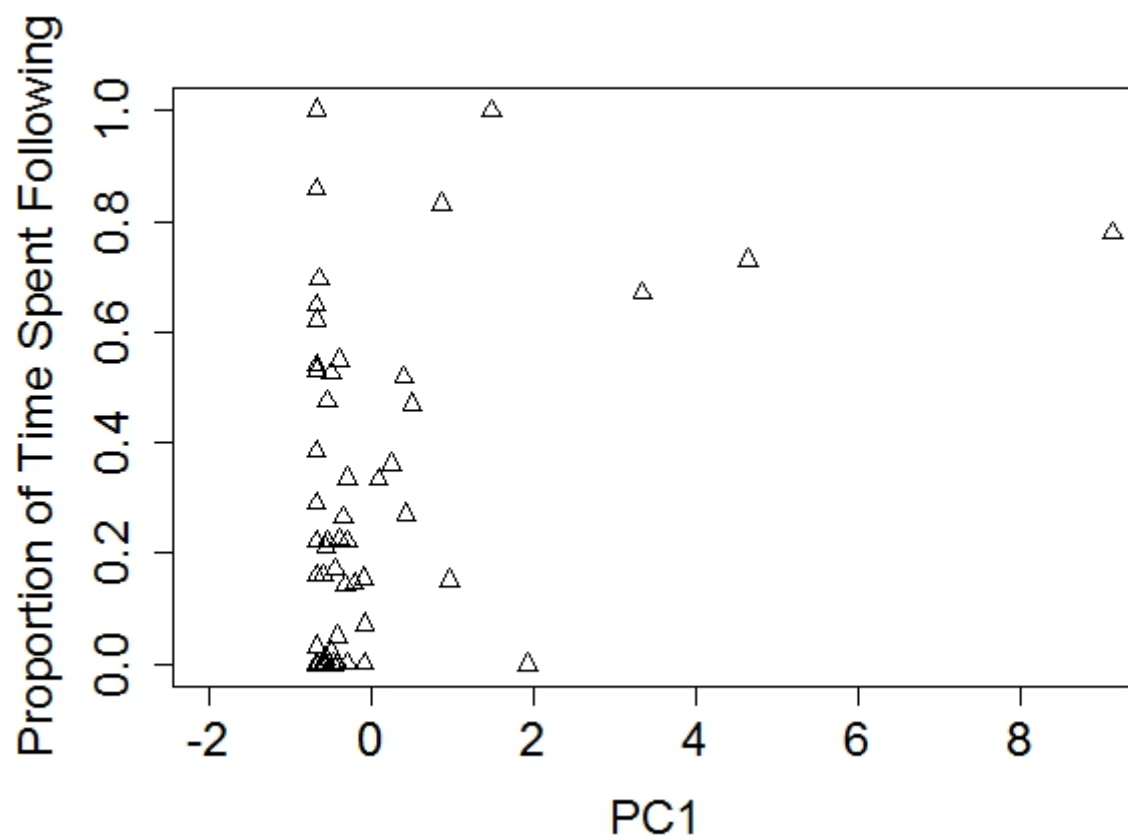Significant loadings are in bold font.

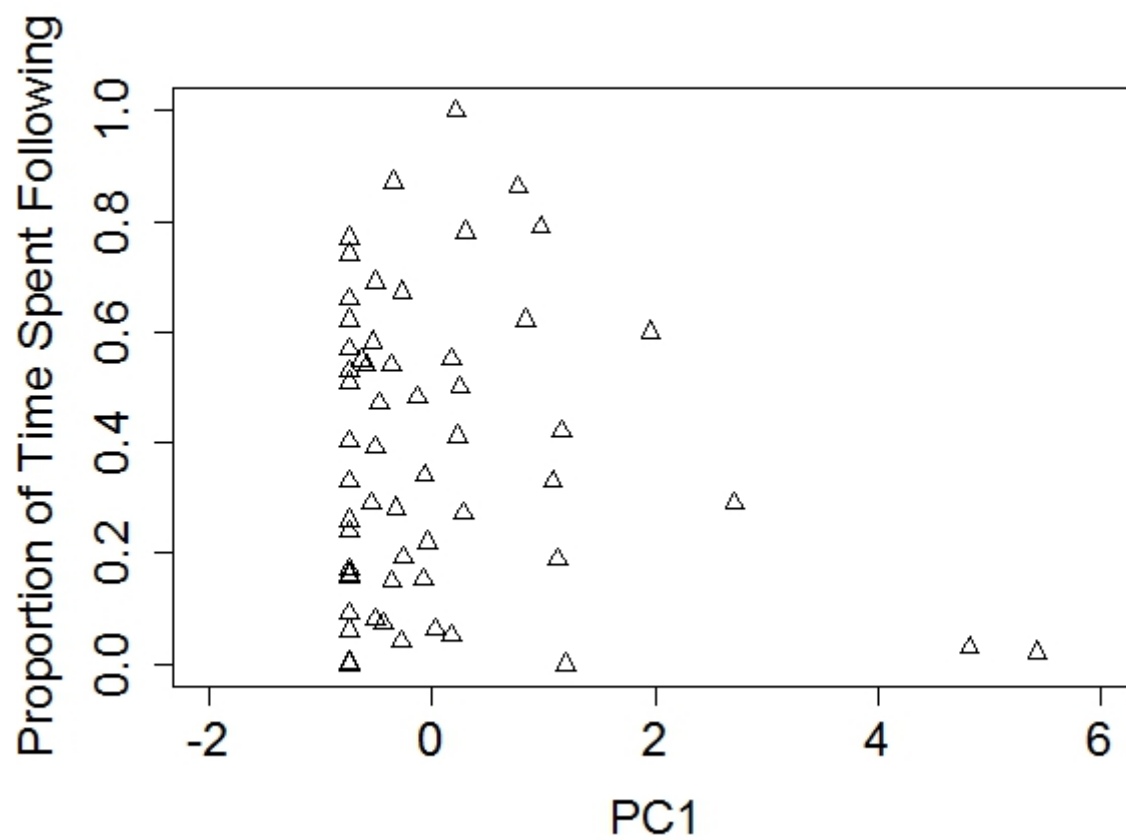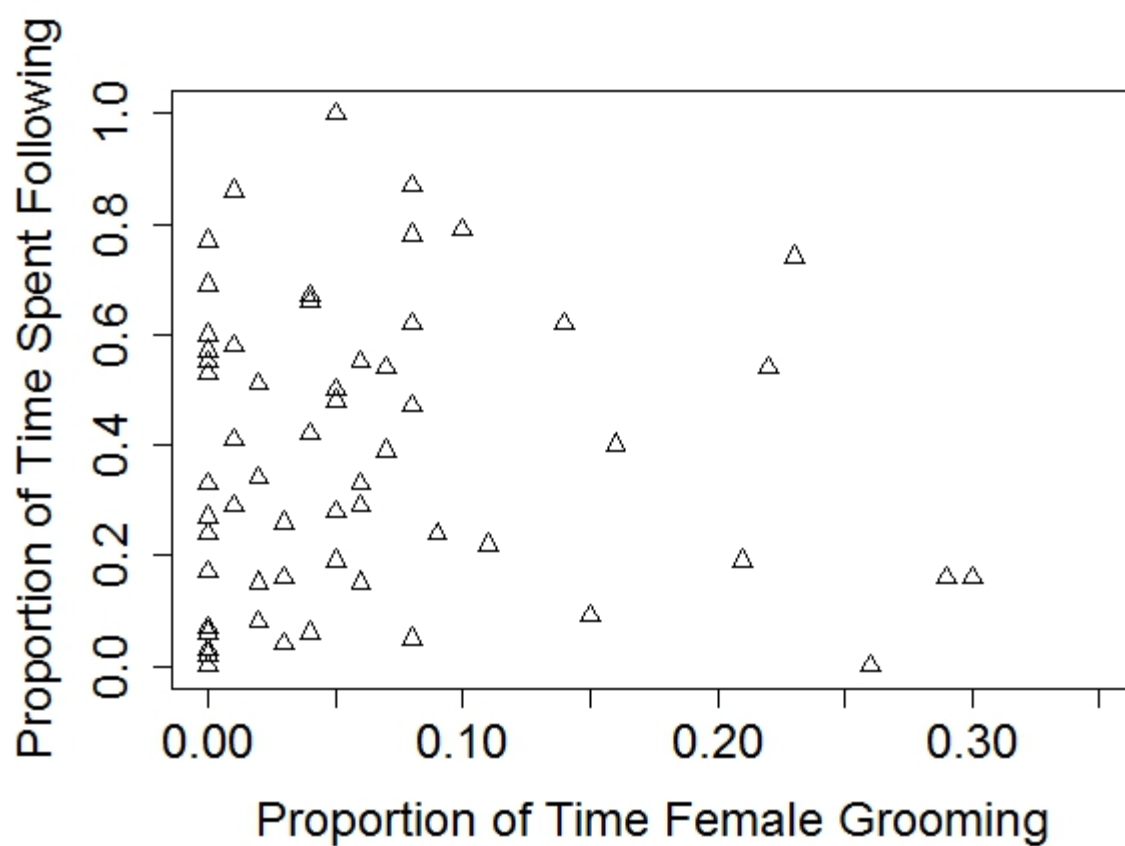**Fig5.1 Influence of PC1 on the Proportion of Time Spent Following**

Fig5.2 Influence of PC1 on the Proportion of Time Spent Following

Fig5.3 Influence of the Proportion of Time Female Grooming on the Proportion of Time Spent Following
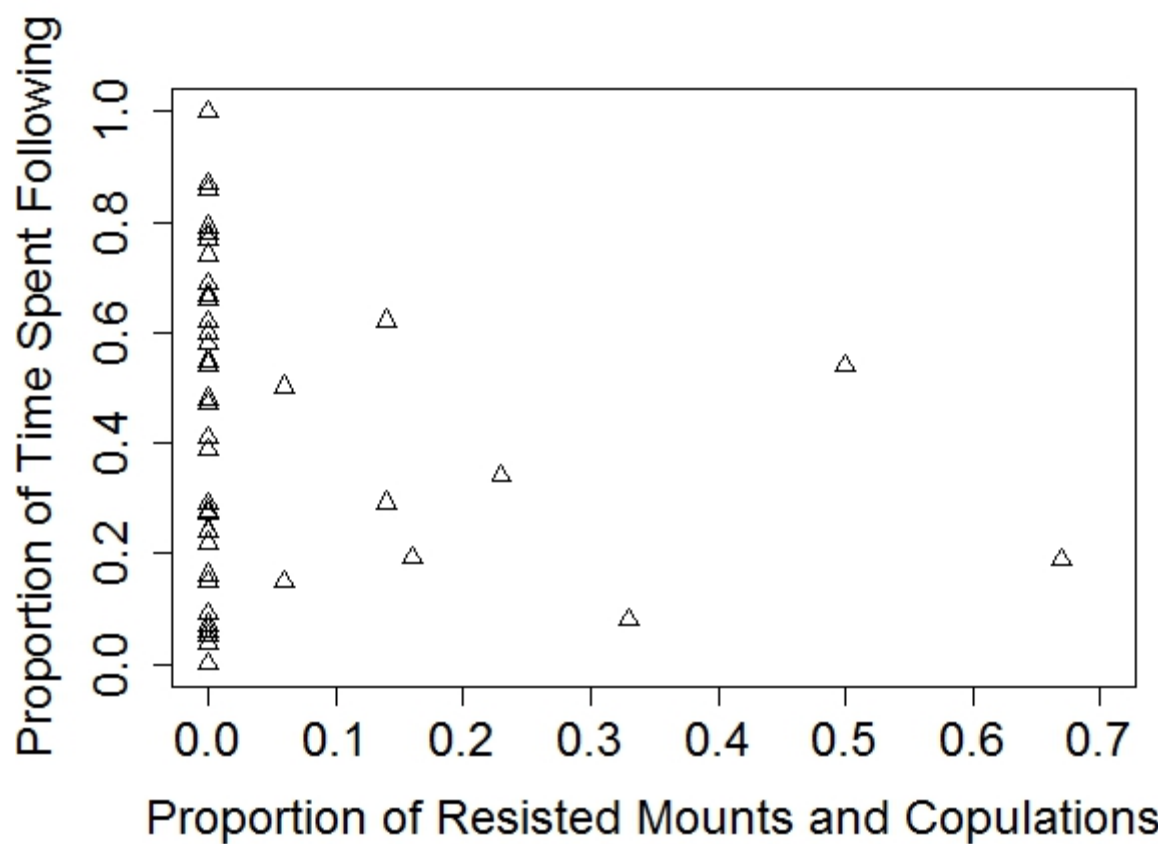
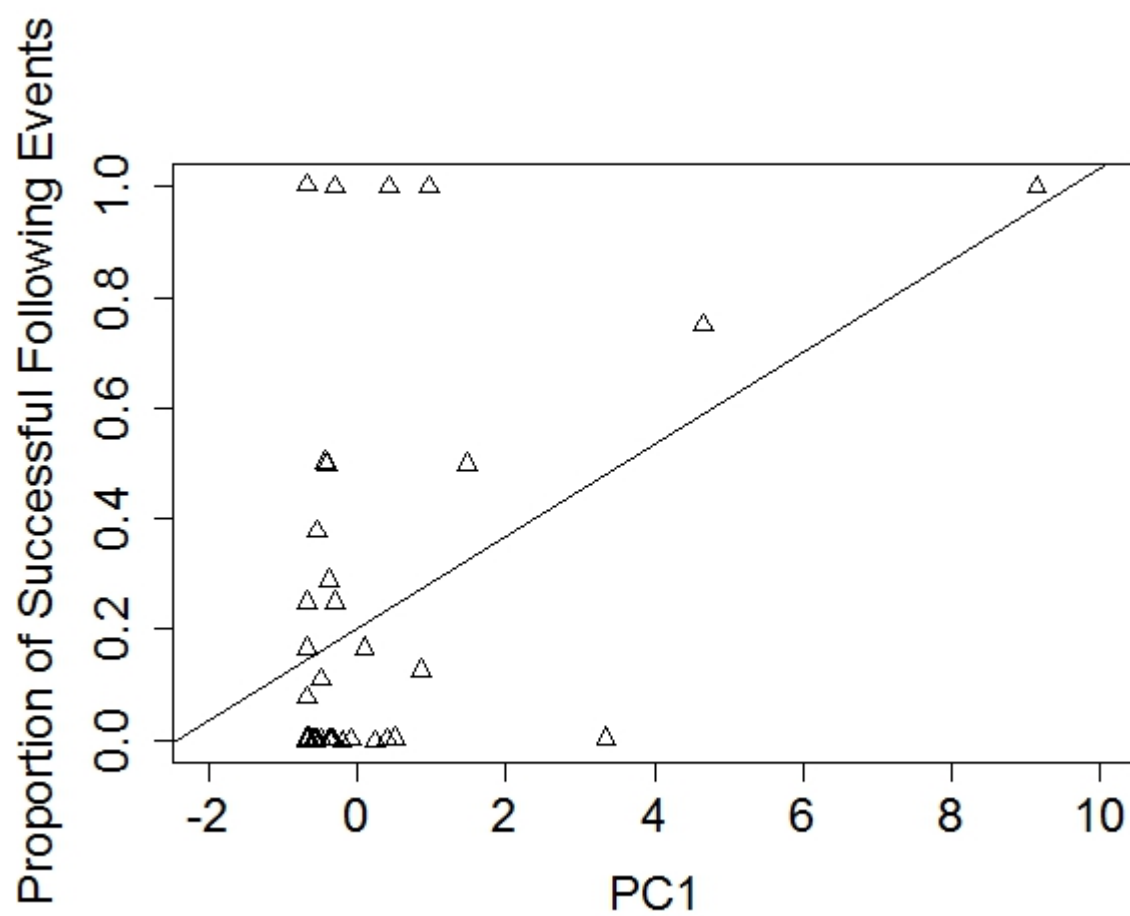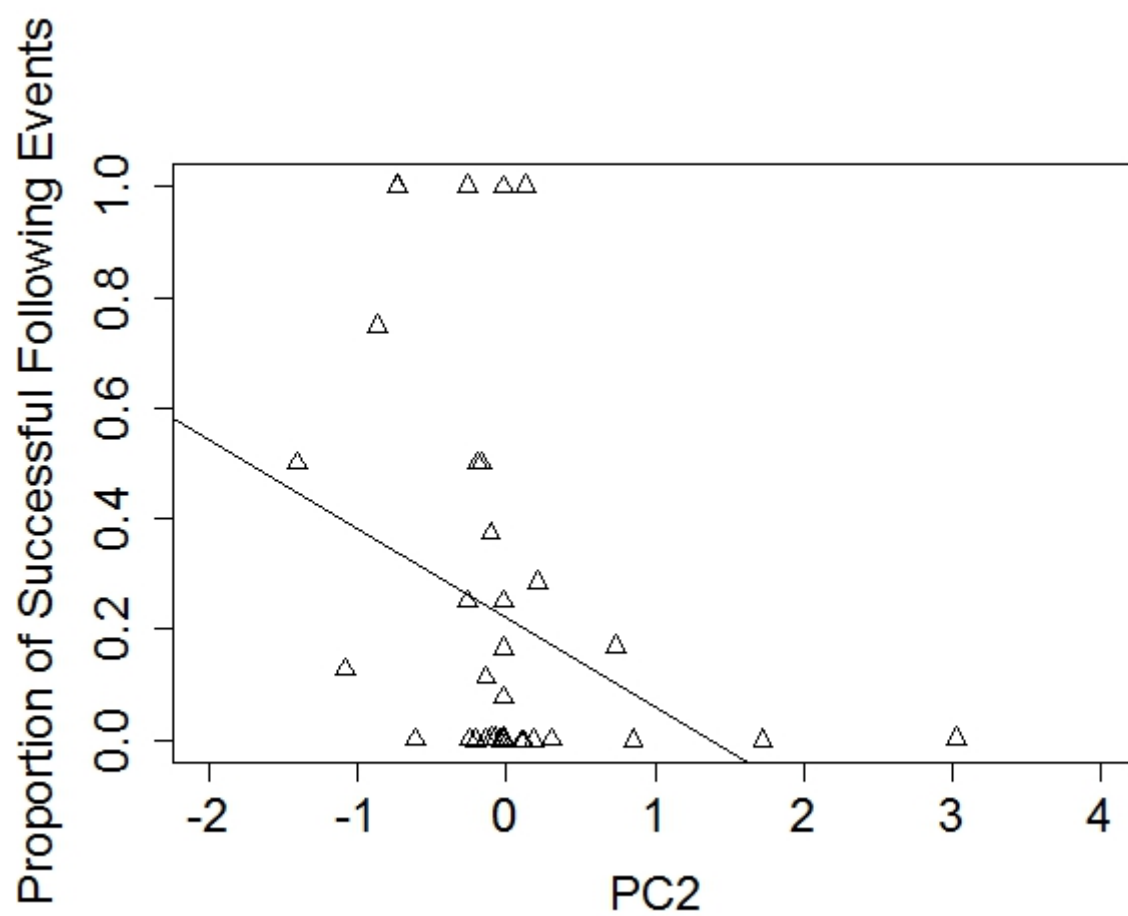**Fig5.4 Influence of the Proportion of Resisted Mounts and Copulations on the Proportion of Time Spent Following**

Fig5.5 Influence of PC1 on the Proportion of Successful Following Events

Fig5.6 Influence of PC2 on the Proportion of Successful Following Events

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CONCLUSION

This study contributes to our understanding of alternative mating strategies by examining a little studied alternative mating strategy in primates. In this section, I summarize the major findings of my dissertation, and discuss general conclusions and future directions.

Chapters 1 and 2 provide the first quantitative data demonstrating that following is an alternative mating strategy. This finding is supported by behavioral data regarding consortships and consort takeovers, as well as paternity data. My finding that followers, rather than nonfollowers, typically pursue individual aggressive challenges and coalitionary challenges forces us to reexamine the historical view of mate competition and mating strategies in male olive baboons. That following is an important part of the overall system of competition and challenge has important implications when considering the benefits and costs of mating strategies, particularly since following involves a greater time investment than the time involved in the takeover attempt itself. Moreover, my findings directly link following to deviation from the Priority of Access (PoA) Model and a reduction in reproductive skew. Alternative mating strategies have been proposed as a cause of such deviation, but few studies have empirically demonstrated that the expression of an alternative mating strategy results in deviation from the PoA Model (Alberts et al. 2003; Wroblewski et al. 2009; Bissonnette et al. 2011; Dubuc et al. 2011). This study suggests a different model for paternal relatedness within social groups with implications for social evolution models; since paternity is less skewed, age cohorts will not be more likely to be paternal kin as has been previously proposed (Altmann et al.

1996; Widdig et al. 2001). Thus, species that exhibit alternative mating strategies are not likely to be characterized by paternally related age cohorts.

Chapter 3 suggests that the expression of following is influenced by male condition as theoretically expected (Gross 1996). Following provides lower ranking males with mating opportunities, although males of all dominance rank follow. In addition, higher ranking males in smaller groups, with fewer reproductive opportunities, follow more often than both lower ranking males in small groups and high ranking males in large groups. Thus, the expression of following results from dynamically flexible decision rules based on current reproductive opportunities, as well as male condition. This finding suggests that a life history perspective, including the incorporation of male emigration and immigration, is critical to understanding following. I propose that differences in the expression of following by males of differing dominance rank may be responsible for the observed variation in within species deviation from the PoA Model (reviewed in Alberts 2012).

Chapter 4 indicates that followers do not experience costs related to activity budget or feeding bout lngth. Proximity to the consort male influences the potential costs, and followers maintain closer proximity during the period of likely ovulation; this finding suggests that males are sensitive to the potential costs and benefits, and are able to mitigate the costs incurred. My findings suggest that energetic costs should be further examined, prefereably using physiological markers of energetic status to ascertain whether followers do in fact incur energetic costs. Followers experience time costs, however, resulting in a restriction in their ability to interact with other individuals, while

also being involved in more agonistic interactions. My work suggests that more subtle aspects of cost, including physiological stress should be examined in future work.

Chapter 5 provides evidence that intersexual interactions influence the expression and success of following. My findings also suggest that behaviors typically used as measures of female preference are correlated with male aggression. Although distinguishing between female preference and male coercion is difficult, my findings suggest that both female preference and male coercion influence male behavior. I also propose that future work examining the influence of female preference or male coercion on male alternative mating strategies consider these behaviors from a dyadic perspective rather than assuming intersexual interactions are determined by strategy choice.

Following has been observed in several (sub)species of baboons and macaques. I suggest that following or similar behaviors are potential alternative strategies in any species in which consortships are a usual aspect of mating behavior; the taxonomic distribution of this behavior therefore may be broader than is currently appreciated. Further study, incorporating additional species that exhibit following, will allow us to understand better the patterns of this strategy and the conditions under which it evolves. The macaques are a particularly interesting taxon for comparison since there is evidence that macaques rely more on sneak copulations and less on coalitions than baboons (Noë 1989; Berard et al. 1994). Variation in reproductive seasonality would also be interesting to incorporate into a comparative analysis.

Most research on alternative male mating strategies has been on insects, fish, birds, and non-primate mammals, while very few studies have focused on primates; our existing models derive primarily from nonmammalian taxa (reviewed in Andersson

1994). The paucity of primate data represents an empirical and phylogenetic gap, of particular significance to models of alternative strategies since primates are noteworthy for a high degree of behavioral flexibility (Setchell 2008). Many recent studies of humans emphasize this noteworthy flexibility in reproductive behaviors, and explain this variation as alternative mating strategies dynamically adopted and abandoned by individuals (Gangestad and Simpson 2000). Much of the variation exhibited in human reproductive and mating strategies today is consistent with this theory. Indeed, Gangestad and Simpson (2000) have suggested that precisely this kind of "strategic pluralism" is a defining feature of human reproductive behavior throughout human evolution and helps explain variation in mating behavior in contemporary human populations. Thus, my findings contribute to our existing models of alternative mating strategies and reproductive behavior, and to our understanding of human evolution.

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