

**HORMONES ASSOCIATED WITH FRIENDSHIP BETWEEN
ADULT MALE AND LACTATING FEMALE OLIVE BABOONS,**

Papio hamadryas anubis

by

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ABSTRACT OF THE DISSERTATION

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Adult male and lactating female olive baboons (*Papio hamadryas anubis*) form non-sexual attachments described by researchers as “friendships.” Explanations for the evolutionary function of baboon friendship for males and females have been debated by many primatologists, but have yet to be determined conclusively. I tested hypotheses concerning the adaptive significance of friendship for each sex with analyses of fecal hormones. For males, I examined the association between testosterone and glucocorticoids, and friendship formation and maintenance. For lactating females, I investigated the association between glucocorticoid concentrations and friendship. Fecal samples and data on social behavior and spatial relations were collected from 26 adult male and 22 lactating female baboons in two study groups located in Laikipia, Kenya. Hormone concentrations were assessed by radioimmunoassay. Friendships were

determined from composite proximity scores (C-scores) calculated for each male-female dyad in the groups.

In male friends, profiles for testosterone, but not glucocorticoids, were consistent with a “paternal care” hormonal profile found in pair bonded primates and rodents. I argue that testosterone concentrations in male baboons suggest a hormonal mechanism underlying friendship and paternal solicitude similar to that in other mammals. The glucocorticoid profile of male friends led me to an alternative conclusion: periparturition and chronic elevation of glucocorticoids in male baboons during the lactation phase of their female friends functions to decrease testosterone and thereby divert male behavioral strategies from male-male competition and mating effort toward friendship with lactating females (and their infants).

In lactating females, glucocorticoid levels were consistent with the hypothesis that male friends buffer lactating females from harassment induced stress. More particularly, my data suggest that lactating females are susceptible to stress from harassment by adult males rather than higher-ranking females, and that male friends may serve a protective function.

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For showing me the truest meaning of that word.

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INTRODUCTION

Why do we form social relationships? What purposes do they serve? Obviously these are very broad questions but they are a useful starting point when I try to explain my research to others. Everyone has relationships and those simple questions can help frame my response. Usually the next step is to decide what kind of relationships I am referring to, and then try to agree how to define a particular type of relationship. Is it romantic? Sexual? Platonic? Professional? Familial? Relationships are rarely simple enough to define with a single term, but they usually have a particular focus. Sometimes the focus can help define the relationship. We are students to learn, teachers to teach. We are co-workers to work together, or parents to raise children. Sometimes the definition is less clear, such as when we form intimate relationships over time with one particular person. These bonds might simply be about companionship or sex, but often they are more complex and serve a number of different functions all at once. If we can begin to understand the functions of even these complex relationships, perhaps that will help tell us why we form them.

So then, what is my research? I investigate the purposes of relationships, but the “we” is a bit broader in this case, and the type of relationship is more specific. I address the question “Why do olive baboons form *friendships* and what functions do they serve for each participant”? Another way to phrase the question is from an evolutionary perspective. “What is the adaptive value of friendship for olive baboons”? I begin this dissertation with a general discussion of the evolution of sociality and then more specifically address baboon friendship. Next, I outline the various hypotheses that have been suggested to explain friendships for both males and females. Finally, I introduce the

topic of socioendocrinology and discuss the rationale for using hormones to complement behavioral observations to test each hypothesis. Each subsequent chapter focuses on a series of independent tests of hypotheses. Chapter 1 tests the Parental Care hypothesis for friendship in adult males with an analysis of testosterone in male friends coinciding with lactation in females. Similarly, Chapter 2 tests the Parental Care hypothesis with an analysis of male friend glucocorticoid concentrations. Finally, Chapter 3 turns to lactating female friends and an analysis of their glucocorticoid profiles to test the alternate hypotheses that male friends help mitigate harassment from either adult males or higher-ranking females.

Mason (1976) points out that regardless of the particular dynamics of primate groups, the analysis of sociality at any level must begin with a consideration of the individual's choice of social strategy options that optimizes reproductive success. Rather than just focus on the bonds themselves, Mason argues that we should explore how bonds serve the interests of each participant, male versus female, and how each participant has been influenced by common ecology to arrive at its social strategies.

Primate Sociality and Attachment

According to Eisenberg *et al.* (1972), sociality in the basal ancestral primate was likely limited to brief periods of contact between males and females for the purpose of mating. Ecological influences on sociality and incentive for association (let alone attachment) were minimal. Each sex remained solitary throughout most of its life, with the exception of females with dependent offspring. The first step in this scheme of social evolution was increased tolerance by individual females for either individual males,

which led to monogamy, or for other females, which led to cohesive female groups. The path leading to gregarious polygyny began with tolerance by these grouped females for individual adult males, resulting in an incipient unimale social pattern. In turn, increased tolerance among males and diminished costs of male-male associations, relative to the benefits of increased mate access, led to multi-male patterns. These social structures initially may have included only simple age-graded male assemblages, but eventually they led to increasingly stable and complex bisexual social groupings.

Other authors have offered variations on the trajectory of primate social evolution from solitary individuals to heterosexually bonded pairs and large mixed-sex groups (see Kummer, 1978; Clutton-Brock and Harvey, 1977; Wrangham, 1986; Lee, 1994), but there is little consensus. What these authors share is the conviction that relationships between males and females (and in societies in general) have evolved in response to both ecological and social pressures, and that in each species, individuals' social strategies must be understood as the result of costs and benefits of grouping (Wrangham, 1987; Lee, 1994).

Lee (1994) summarizes the functional categories influencing group formation, size, composition and stability, along with the costs and benefits associated with each factor (Table 1). It should be noted that in addition to explicating costs and benefits to individuals as participants in large, complex social systems, these functional categories, and their implications, can also be considered at the level of dyadic relationships, *e.g.*, adult male-female associations or pair bonds. Lee (1994) affirms this point, presenting a system of social categories from *solitary* to *gregarious* to *social* species based upon the aggregation propensity of individuals. Here aggregation is defined as “an association

Table 1. Summary of Costs and Benefits of Associations Between Individuals (reprinted from Lee, 1994)

Functional Category	Benefits	Costs
Predation	Dilution, defense, swamping; exchange of information; reduced time spent vigilant	Conspicuousness; larger area, higher area, higher contact probability
Foraging	Food defense; efficient food location; shared information as to quality, abundance and renewal; co-operative hunting	Reduction of individual intake on shared resources (competition); increased energy costs of foraging to cover a larger area or maintain a group
Information Exchange	Opportunities for easy, quick and energetically inexpensive exchange of signals; enhanced assessment of status of signaler	Parasitism of signal producer by non-producer; increase in competition between signalers
Access to Mates	Opportunities to gain access to mates, to assess mate quality, to complete mating; reduced search costs for mates	Competition for access to mates (direct or indirect through sperm competition); status differentiation in mating success; choice of mates leading to high variance in reproductive success; potential for infanticide to increase access to reproductive females
Access to helpers for rearing infants	Enhanced protection of vulnerable infants; reduced maternal energy costs and thus shorter intervals between reproduction; provisioning of infants with food	Potential for infanticide by non-parent helpers; delayed dispersal and reproduction by helpers
Disease transmission		Increased probability of morbidity through disease; higher parasite loads
Thermoregulation	Reduced costs of heat production when exposed to energetically costly cold stresses	

between two or more individuals which is unlikely to be repeated through time” (Lee, 1994:278). In contrast, *associations* are more stable and are characterized by repeated interactions. Although in this framework, an aggregation or association may include two same-sex individuals as well as pairs in a mating context, it is clear that an analysis of the

formation, maintenance, and characteristics of male-female relationships and interactions may be an important starting point for understanding the broader social framework.

Restating the economic perspective on social evolution, Lee (1994:281) asserts, “The reconciliation of individual needs in relation to competition and cooperation is the principle factor underlying the maintenance of sociality.” A social system may be described in terms of the nature of interactions between individuals, and the characteristics and behaviors expressed as a function of their relationships (Hinde, 1976). Thus, by focusing on interactions and relationships, rather than gross mating strategy definitions of species, social analysis can move from broad generalizations of species' social patterns to understanding the underlying ecological systems that influence individual social strategies.

Wrangham (1987) takes up this task, subsuming factors influencing the evolution of sociality into ecological and social categories from each sex-biased perspective. He maintains that ecological and social pressures act in concert to influence sociality, and that models based strictly on ecological pressure may fail to account for differential effects of ecology on each sex. While a species' environment may influence its group size, Wrangham (1987) points out that female social behavior and spatio-temporal distribution are influenced primarily by ecological conditions and constraints. Male interactions with conspecifics are then influenced by the distribution of females in time and space. The resulting social environment feeds back into female choice, providing the second set of factors, social pressures, *e.g.*, threat of sexually selected infanticide (Hrdy, 1974; Hausfater and Hrdy, 1984; van Schaik, 1996), which yield the social pattern expressed by the species.

Even given the diversity of ecological variables influencing female primates, several authors have formulated models predicting individual responses to particular ecological challenges (Emlen and Oring, 1977; Lee, 1994). According to Lee (1994), there are a maximum number of 17 modes that sociality can take, based on two sexes and three distribution states: *solitary*, *with-non-kin*, and *with-kin*. As already noted, distribution state decisions begin with female access to resources and male access to females. A number of additional factors, including body size, mortality, metabolic rate, and reproductive rate constrain social options.

In Lee's (1994) model, shifts from state to state among the 17 options can only occur along a limited number of pathways, with phylogenetic constraints providing the impetus or barrier to state-shifts. The prediction of her model is that any given social state may be reached through more than one pathway. For example, male-female associations could be reached by: 1) combining a solitary male with a solitary female, 2) eliminating extra males from a polyandrous group, 3) eliminating extra females from a polygynous group, or 4) eliminating both extra males and extra females from a polygynandrous group. Moreover, the final form of the association could also be a function of whether extra-group eliminations involved kin or non-kin. As long as logical state shift pathways exist for a species, populations should vary socially. Specific conditions, and both temporal and spatial variations in ecology, should yield predictable social variations along logical pathways of the option network. In turn, vastly different forms of adult male-female dyads (*e.g.*, sexual versus nonsexual associations) may share important similarities that reflect shared ecological challenges.

An analysis evaluating the adaptive causes of monogamy demonstrates that correlations among traditional variables remain equivocal; the efficacy of predictive models may be limited for many primate taxa (van Schaik and van Hooff, 1983; van Schaik and Paul, 1996; Komers and Brotherton, 1997). For example, parental care does not explain the distribution of obligate monogamy; in primates, and across mammalian taxa, monogamy evolved less often in conjunction with paternal care than without it (Wright, 1990; Komers and Brotherton, 1997). In species where fathers and offspring were already in regular association, paternal care may have evolved simply as an outcome of these connections (Dunbar, 1995; Komers and Brotherton, 1997), or alternatively as a form of mating effort (*sensu* Smuts and Gubernick, 1992) in which males indicate their superior quality by attending the offspring of potential mates.

The term monogamy has been used variably to describe a number of different social strategies in primates including obligate monogamy, facultative monogamy, reproductive monogamy, and social monogamy (see Kleiman, 1977; van Schaik and van Hooff, 1983; Komers and Brotherton, 1997). In humans, monogamy has become synonymous with heterosexual pair bonding within a larger framework of social affiliations (Alexander and Noonan, 1979; Fisher, 1992). On a physiological level, social monogamy as heterosexual attachment may be recognized by predictable hormonal profiles expressed normatively as well as following separation-induced stress (Mendoza *et al.*, 2002). An important foundation of my research is that both sexual and nonsexual male-female attachments may share a common evolutionary trajectory (see Lee, 1994) and that a wide variety of attachments (including parent to infant, infant to parent, adult male to female, and adult female to male) share a common psychoneuroendocrine

foundation (Mason and Mendoza, 1998). If ostensibly different forms of adult male-female attachments (*e.g.*, sexual versus nonsexual associations) manifest in similar hormone profiles, they may share common adaptive functions for each participant.

Definition of *Bond* and *Attachment*

Consistent definitions of *attachment* and *bond* are difficult to distill from literature on primate sociality; authors use these terms in many different ways. Bowlby (1969, 1973, 1991:304) suggests a series of attachment features (in humans, but applicable to other species) based on the hypothesis that all forms of attachment are ontogenic extensions of the child/mother-figure affectional bond:

1. *Attachment behaviour is conceived as any form of behaviour that results in a person attaining or retaining proximity to some other preferred individual. So long as the attachment figure remains accessible and responsive the behaviour may consist of little more than checking by eye or ear on the whereabouts of the figure and exchanging glances and greetings. In certain circumstances, however, following or clinging to the attachment figure may occur and also calling or crying, which are likely to elicit his or her care giving.*
2. *As a class of behaviour with its own dynamic, attachment behaviour is conceived as distinct from feeding behaviour and sexual behaviour.*
3. *During the course of healthy development attachment behaviour leads to the development of affectional bonds or attachments, initially between child and parent and later between adult and adult.*
4. *Attachment behaviour, like other forms of instinctive behaviour, is mediated by behavioural systems which early in development become goal-corrected.*
5. *Whereas an attachment bond endures, the various forms of attachment behaviour that contribute to it are active only when required.*
6. *Many of the most intense emotions arise during the formation, the maintenance, the disruption and renewal of attachment relationships*
7. *Attachment behaviour has become a characteristic of many species during the course of their evolution because it contributes to the individual's survival by keeping him or her in touch with one or more caregivers, thereby reducing the risk of harm.*

8. *Behaviour complementary to attachment behaviour and serving a complementary function, that of protecting the attached individual, is caregiving.*
9. *In view of attachment behaviour being potentially active throughout life and also of its having the vital biological function proposed, it is a grave error to suppose that when active in an adult, attachment behaviour is indicative either of pathology or of regression to immature behaviour.*
10. *Disturbed patterns of attachment behaviour can be present at any age due to development having followed a deviant pathway.*
11. *Principal determinants of the pathway along which an individual's attachment behaviour develops, and the pattern in which it becomes organized, are experiences with attachment figures during the years of immaturity—infancy, childhood and adolescence.*
12. *On the way in which an individual's attachment behaviour becomes organized within his or her personality turns the pattern of affectional bonds made during later life.*

Insel (1997:726, citing Harlow and Mears, 1979) notes that the idea of attachment "includes several quite different processes depending on the social context: parent-infant, filial, and pair (male-female) bond formation are all forms of attachment. All of these forms involve seeking proximity and all involve a response to separation, but the strategy for and the consequences of achieving proximity vary depending on the relationship."

For the purposes of this dissertation, I use a simple, multi-purpose definition of attachment, "one individual striving to maintain proximity with a specific other individual, displaying distress upon separation from or loss of the other, and attempting to restore proximity following separation-" (Mendoza and Mason 1997:203). They elaborate: "Some of the clearest indices of attachment are spatial. Attachment is expressed in propinquity: approaching, following, seeking to be close to and in contact with the object of attachment, choosing to be near it rather than another. Other important operational criteria are behavioral and physiological signs of agitation and distress when

the attached individual is forcibly separated from the object of its attachment, reduction of these signs by reunion with the attachment figure..." (Mason and Mendoza, 1998:766).

Friendship

Trivers (1972) proposed dissimilar expectations for male and female reproductive strategies and since then, the idea of systematic variation in female reproductive success has become a paradigm in studies of wild primates (Silk, 2002a). Wrangham (1980) first suggested that females were the driving force of primate social evolution and anthropologists have come to realize that female behavioral strategies, particularly those relating to social relationships and affiliation preferences, may in fact underscore the expression of sociality across numerous dimensions in many primate species (Wrangham, 1980; van Schaik, 1989).

One of the most widespread and earliest recognized patterns of female primate behavior with conspicuous adaptive consequences concerned female hierarchy formation and, particularly in the Old World monkeys, female kin-bonded groups (Wrangham, 1980). Olive baboons (*Papio hamadryas anubis*), yellow baboons (*P.h.cynocephalus*) and chacma baboons (*P.h. griseipes*) provide an excellent example of how a suite of social patterns, including female dominance hierarchies, durable matriline, and female philopatry/male dispersal, is expressed in conjunction with strong *intragroup* contest competition and weak *intergroup* contest competition (Silk, 2002a). In baboons, nonsexual male-female associations coincide with this social dynamic.

Friendship in nonhuman primates has been defined with a number of different emphases in relation to the participants or behaviors observed. Broadly, friendship has

been used synonymously with *affiliative bond* by Tomasello and Call (1997) and characterized by Silk (2002b:425) as “close and affiliative social relationships which may include same-sex partners.” In baboons, friendship was first described by Strum (1974) and Smuts (1985) as long-term bonds between adult males and anoestrous females, which are found among nearly all populations. Friendship is defined here as, “Particularly high rates of association between anoestrous females and certain adult males. These male companions are typically unrelated to the females and may hold any rank in the male dominance hierarchy.” (Palombit *et al.*, 1997:599).

Although Alexander and Noonan (1979) maintains that human friendship evolved as an outgrowth of kin selection, proposing that throughout most of our evolutionary history, humans lived in small interdependent male-dominated kin groups, this scenario certainly does not apply to all primates. The female philopatry/male dispersing dynamics of sociality in most cercopithecine primates, including baboons, belies a similar explanation for friendship in these taxa (Terbourgh and Janson, 1986). Upon reaching adolescence, male Old World monkeys typically emigrate from the natal group and eventually transfer into a group of unrelated females (Terbourgh and Janson, 1986). In contrast, females remain in the natal troop and form long-lasting affiliative and supportive relationships with female kin (Strum, 1987). Silk (2002b) notes that from one perspective, if friendship is defined as a relationship between nonkin, then it might be understood as the evolutionary product of reciprocal altruism (*sensu* Trivers, 1971). According to this premise, friendship relies on a contingency of benefit exchanges between friends. One friend provides benefits to the other only as long as it has received benefits in the past or *expects* benefits in the future.

Barrett and Henzi (2002) have contradicted a simplistic reciprocal altruism explanation for friendship in baboons, arguing that individuals in this species do not possess the cognitive ability to maintain long-term accounts of reciprocal exchanges. They point out that data on dyadic grooming bouts observed over one-year and two-year studies of two separate populations of baboons indicate that individuals closely monitor and maintain a short-term exchange balance. Roles change frequently in the course of short time frames and grooming frequencies are well-matched for each partner. The grooming rate imbalance between friends in Smuts' (1985) and Palombit *et al.*'s (2001) studies affirms Bendor's (1993) contention that short-term imbalances may be temporarily overlooked in order to preserve highly valued relationships. Several authors argue that in the course of long term reciprocal relationships in non-kin, the commodities exchanged by individuals do not necessarily have to be identical and point to exchanges of food, grooming, and support in agonistic encounters which depend on context and complex variables particular to each exchange partner (in wild chimpanzees, *Pan troglodytes*, Mitani *et al.*, 2000; in captive chimpanzees, de Waal, 1994; in vervets, *Cercopithecus aethiops*, Seyfarth and Cheney, 1984).

Palombit *et al.* (1997:599-600) review several hypotheses for the adaptive value of friendships to female baboons. First, males may protect lactating females' infants from sexually selected infanticide (Busse and Hamilton, 1981), which is of purported widespread significance across primates (Palombit, 2000). Second, friends may shield females and/or their infants from non-lethal harassment from males and higher-ranking female rivals (Altmann, 1980; Wasser, 1983; Rhine *et al.*, 1988; Wasser and Starling, 1988). Third, a friendship may confer no immediate protection benefits to a female, but

promote an attachment between the male friend and her infant (Ransom and Ransom, 1971; Smuts, 1985; Strum, 1987; Smuts and Gubernick, 1992). The value of friendship comes later, *e.g.*, when the male supports the juvenile in non-lethal agonistic interactions with others (Buchan *et al.*, 2003).

The adaptive significance of friendships for males is more unclear and debated. The potential survival benefits to infants raise the obvious possibility that male friendship behavior constitutes *parental effort* (Hamilton, 1984). Smuts (1985), however, proposed a *mating effort* hypothesis: males may care for unrelated infants in order to obtain future mating access to their female friends when estrous cycles resume. Tests of these hypotheses have yielded equivocal results. In support of the Paternal Care hypothesis, Palombit *et al.* (1997) report that at least 70% of female chacma baboon friendships were with a male who had consorted with the female friend in the (previous) conceptive cycle. Bercovitch (1995) argues similarly for friendships among olive baboons. Moreover, the strength of a male chacma baboon's responses to playback of his female friend's scream was positively correlated with his dominance rank at the time of the infant conception many months before, but not correlated with his rank at the time of the friendship (Palombit *et al.*, 2001). This suggests an effect of paternity probability contrary to the Smuts (1985) Mating Effort hypothesis. Subsequent mating success for (former) male friends was not obviously enhanced in chacma baboons (Weingrill, 2000) or in olive baboons (Bercovitch, 1991, 1995). Nevertheless, the potential mating effort benefits of male-infant association have been strongly argued for primates generally (Smuts and Gubernick, 1992; van Schaik and Paul, 1996), and genetic paternity data are needed to test the hypothesis more rigorously.

Originally outlined by Hinde (1976, 1977, 1983) to describe relationships between two individuals, Silk (2002b:427-433) discusses four elements of social behavior to identify friendships in nonhuman primates. First, *content* includes the behaviors that distinguish friendships from all other male-female dyads possible in a group. Grooming and proximity maintenance are two consistent factors used to recognize friendship or other dyadic relationships (Cords, 1997; Palombit *et al.*, 1997; Smuts, 1995; Dunbar, 1991). Second, *frequency* indicates how often predetermined behaviors occur and measures the strength of social bonds with a preferred partner index or composite proximity measure (see Smuts, 1985). Third, *quality* depends on an observer's ability to interpret and subjectively rank the nature of social interactions between individuals. Friendships are characterized as distinct from other relationships based on those interpretations. Finally, *patterning* describes the objective assessment of predetermined configurations of social affiliation such as behavior reciprocities, kin networks and hierarchy relationships, and identifies friendships potentially embedded within the larger social structures.

Smuts' (1985) composite proximity score (or "C-score") has become a standard method for initially identifying baboon friendship (Bentley-Condit and Smith, 1999; Palombit *et al.*, 1997, 2001; Silk, 2002b). The percentage of time spent within distance categories is multiplied by a constant representing the reciprocal of the mid-point of the inner and outer limits of the category. These weighted proximity times are then summed to arrive at the composite score (Palombit *et al.*, 1997; modified from Smuts, 1985):

$$C = 1(\%Time_{0-2m}) + 0.25(\%Time_{2-6m})$$

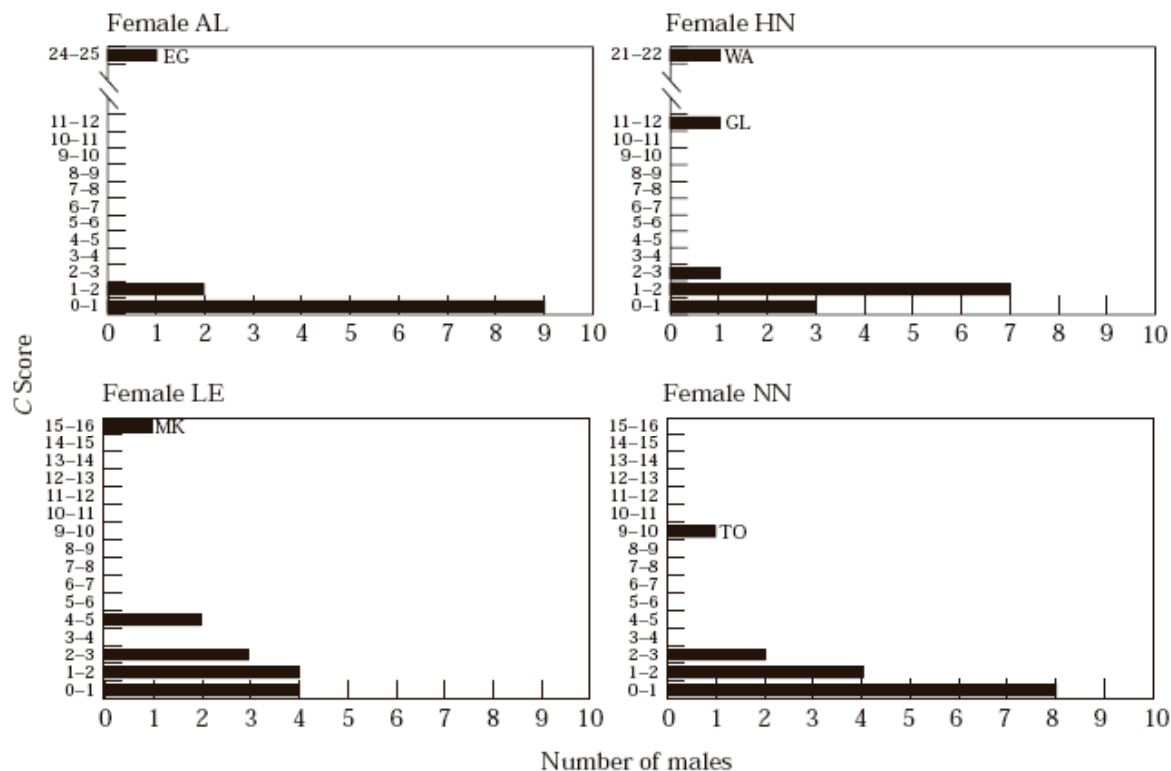


Figure 1. *The distribution of composite proximity scores (C-scores) for four representative lactating females. The number of males in the group (X-axis) with a C-score falling within the range given (Y-axis) is shown for each female. Males “EG”, “WA”, “GL”, “MK” and “TO” are defined as “friends” of the respective females (reprinted from Palombit *et al.*, 1997:603).*

For each female, a discontinuous distribution of C-scores indicates a friendship with one or more males (Figure 1). According to Silk (2002b:434), “The method that Smuts (1985) developed for identifying male-female friendships among baboons has the great virtue of being precise and unambiguous. It also has the virtue of being empirically grounded, as it reflects the underlying distribution of the data.”

Socioendocrinology

The early science of endocrinology was heavily influenced by comparative psychology. Hormone profiles of individual animals, at first rodents and livestock and

later primates such as rhesus macaques, (*Macaca mulatta*), were originally studied in laboratories without regard to their natural social context (Worthman, 1990).

Reproduction or aggression was studied in pairs of subjects. Behavioral endocrinologists adapted tools from experimental psychologists, such as operant conditioning and stimulus reinforcement training. They discovered that varying hormonal replacement regimes had observable and often predictable effects on subjects' Skinnerian-task performances.

Adults' sexual behaviors could be manipulated with selective hormone exposure during ontogeny. All too often, behavioral endocrinologists failed to consider the adaptive significance and ultimate explanations for the behaviors they observed (Whitten, 2000).

On the opposite end of the spectrum, socioecologists studied behavior as a function of group dynamics and in relation to the larger environmental context, often ignoring proximate and phylogenetic mechanisms (Richard, 1981; Whitten, 2000). As each of these sciences matured and expanded independently, their questions becoming ever broader and more comprehensive, their overlap inevitably grew as well (Bercovitch and Ziegler, 1990; Whitten, 2000). The emerging discipline of socioendocrinology is one beneficiary of this synthesis.

Bercovitch and Ziegler (1990:1) argue that evolutionary principles can not be separated from the study of hormones and their interactions with behavior. They describe the role of socioendocrinology in animal research:

Socioendocrinology is the study of the effects of the social environment on the interactions between hormones and behavior. A primary goal of socioendocrinology is to understand the links between the social reproductive success of individuals. This perspective provides a framework for connecting evolutionary biology with reproductive endocrinology. Evolutionary biologists focus on explaining the adaptive significance of social behavior, or its ultimate causes, whereas endocrinologists concentrate on explaining how physiology affects social

behavior or its proximate causes. Socioendocrinology will bridge these avenues of inquiry by providing a framework for understanding the adaptive flexibility in both hormones and behavior that accompanies the lability in social systems characteristic of primates.

Baboon Hormones and Friendship

Recent studies of primate social relationships highlight how analysis of testosterone and the glucocorticoid hormones complement behavioral data. Hormones allow for independent tests of hypotheses based on behavioral observations. Numerous studies of mammals including rodents, nonhuman primates and humans, suggest a general mammalian trend: fatherhood and active paternal care are correlated with lowered testosterone and glucocorticoids as well as greater hormonal situation reactivity to infant-related stimuli (in *Saguinus oedipus*, Ziegler *et al.*, 1996; in *Callithrix kuhlii*, Nunes *et al.*, 2001, 2002; in human males Fleming *et al.*, 1997a, 1997b; Storey *et al.*, 2000; Berg and Wynn-Edwards, 2001; Wynne-Edwards, 2001; Gray *et al.* 2002, 2006, 2007). These data have important implications for the study of friendships in baboons. Evidence for similar hormonal mechanisms in male baboons participating in friendships would be consistent with the functional hypothesis that friendship behavior in males constitutes paternal care of offspring.

Glucocorticoids have long been useful assays of stress-response activation (Mason and Mendoza, 1998; Sapolsky, 1993a, 2002). These hormones play an autoregulatory role, keeping the body from reacting to short-term stress with immune-response hyperactivity. Many studies demonstrate that social stress elevates glucocorticoid levels. Abbott *et al.*'s (2003) meta-analysis of rank-related differences in physiology in seven primate species reveals that subordinate individuals have higher

cortisol levels than dominants, but only when they experience relatively higher rates of social stressors, or when they experience decreased opportunity for social support. Such stress-related hormonal profiles are likely to be costly to female fitness. Sustained glucocorticoid levels resulting from chronic stress suppress fecundity and increase susceptibility to disease and infections (McEwen, 1998; Sapolsky, 1999, 2002; Sapolsky *et al.*, 2000).

Social relationships may mitigate the (negative) effects of stress hormones (Sapolsky, 1993b, 2005; Abbott *et al.*, 2003). By focusing on dominance status, many studies implicate *intrasexual* harassment. Observations of rough handling and potentially lethal infant “kidnapping” by higher-ranking females (Smuts, 1985) indicate the relevance of female harassment for olive baboon mothers. Smuts and Smuts (1993) also argue the significance of male coercion, for example, by reporting that, on average, a lactating female olive baboon falls victim to (nonlethal) male aggression five times per week, and is seriously wounded by a male once a year. Thus, protection from harassment from males may be an important selective force driving friendships between anestrus females and adult males (Strum and Western, 1982; Stein, 1984; Smuts, 1985; Palombit *et al.*, 1997).

In summary, primate relationships have evolved in response to a vast array of socioecological demands. They reflect individuals’ behavioral choices to maximize reproductive fitness. Like monogamous pair bonds, friendships have emerged in some species as an important element of the overall reproductive strategy for both males and females. Socioendocrinology synthesizes proximate explanations for friendship with an understanding of their adaptive significance for each partner. Hormonal profiles of

baboons provide independent tests of conclusions based on behavioral data. To that end, this research investigates the association between hormones and friendship formation and maintenance in both adult males and lactating female olive baboons.

CHAPTER ONE

ASSOCIATION BETWEEN MALE TESTOSTERONE CONCENTRATIONS AND FORMATION AND MAINTENANCE OF FRIENDSHIP WITH LACTATING FEMALES IN WILD OLIVE BABOONS (*Papio hamadryas anubis*)

INTRODUCTION

Hormones provide behavior researchers with an opportunity to independently test hypotheses concerning social relationships. Extreme testosterone fluctuations in adult male vertebrates may represent facultative shifts among alternative reproductive strategies (Wingfield *et al.*, 1990). For example, concentrations may remain at basal levels during non-breeding periods and rise moderately during typical breeding activities; however, throughout periods of intense competition for access to mates, testosterone can elevate dramatically to levels approaching an individuals' physiological maximum (Wingfield *et al.*, 1990; Cavigelli and Pereira, 2000, Muller and Wrangham, 2003; Archer, 2006). Numerous studies of mammals including rodents, nonhuman primates and humans suggest an additional trend: fatherhood and active paternal care are correlated with suppressed testosterone levels and periparturition reduction of testosterone concentrations (Reburn and Wynne-Edwards, 1999; Ziegler, 2000; Nunes *et al.*, 2001, 2002; Fleming *et al.*, 2002; Wynne-Edwards, 2001; Wynne-Edwards and Timonin, 2007; Gray *et al.*, 2007). Adult male and lactating female olive baboons (*Papio hamadryas anubis*) along with yellow baboons (*P. h. cynocephalus*) and chacma baboons (*P. h. griseipes*), form non-sexual attachments that Strum (1974) and Smuts (1985) first described as "friendships." These males often maintain supportive relationships with their friends' infants that last for years (Smuts, 1985). Evidence for similar hormonal mechanisms underlying paternal care and male baboon friendship formation and attention

to infants would be consistent with the functional hypothesis that friendship behavior in males constitutes paternal care of offspring.

Friendships typically commence at the birth of a female's infant and are expressed most conspicuously during her six to eighteen-month lactation phase. In this paper, we define friendship as "high rates of association between anoestrous females and certain adult males. These male companions are typically unrelated to females and may hold any rank in the male dominance hierarchy" (Palombit *et al.*, 1997:599).

The question of adaptive significance of baboon friendship for each sex has been raised by many primatologists but has yet to be answered conclusively (Smuts, 1985; Strum, 1987; Bercovitch, 1995; Palombit *et al.*, 1997). Palombit *et al.* (1997:599-600) reviewed several hypotheses for the adaptive value of friendships to female baboons. First, males may protect lactating females' infants from sexually selected infanticide (Busse and Hamilton, 1981). This hypothesis has gained support for a number of primate species including chacma baboons (Palombit *et al.*, 1997, van Schaik, 1996; Weingrill, 2000; Beehner *et al.*, 2006), but is not strongly supported for olive baboons (Palombit, 2003b; Henzi and Barrett, 2003). Second, friends may protect females and/or their infants from non-lethal harassment from other adult males as well as subadult males and higher-ranking females (Altmann, 1980; Wasser, 1983; Rhine *et al.*, 1988; Wasser and Starling, 1988). Third, a female may develop a friendship with a male to promote a long-term attachment between the male and her infant. This attachment may not serve an immediate benefit to either the female or her infant at the time of the friendship, but may facilitate future male support of the infant in agonistic interactions with other group members (Ransom and Ransom, 1971; Smuts, 1985; Strum, 1987, Buchan *et al.*, 2003).

The adaptive significance of friendships for males is even more empirically unclear. Smuts (1985) suggested that friendship may constitute *mating effort* (see Low, 1978). Males may enhance their own long-term mating access to female friends by demonstrating protective or care-taking qualities (Smuts and Gubernick, 1992). Ray and Sapolsky (1992) did not test this hypothesis directly, but found that as a category “highly affiliative males” (those with a high frequency of reciprocal grooming and other positive social interactions with non-estrous females and their infants) did not consort with estrous females at rates higher than other males. In olive baboons (Bercovitch, 1991, 1995) as well as chacma baboons (Weingrill, 2000) there was no obvious association between a male’s friendship status and the frequency of his copulations with his friend, compared to other males’, in subsequent estrous periods. Nevertheless, the potential mating effort benefit of male-infant association continues to be strongly argued for primates generally (Smuts and Gubernick, 1992; van Schaik and Paul, 1996). As genetic paternity data become available on study populations, this hypothesis can be tested more explicitly.

Several researchers suggest an offspring-care explanation for male friendship (Bercovitch, 1995; Palombit, 2003a, 2003b). While infant paternity in studies of olive baboons remains largely uncertain, if males prove to be the fathers of friends’ infants then male friendship would clearly constitute parental effort (Hamilton, 1984). Although they did not investigate friendship empirically, Buchan *et al.* (2003) report that male yellow baboons are more likely to support genetic offspring than unrelated individuals in agonistic disputes. Paternal support can result in clear, long term fitness benefits for offspring in the form of rank and resource acquisition (Borries *et al.*, 1999). In chacma baboons, Palombit *et al.* (1997) found a positive correlation between a male’s response to

playbacks of his friend's scream and his dominance rank at the time of the infant conception. Males may be capable of assessing paternity of a friend's infant and react to the friend's distress accordingly. Moreover, nearly 70% of females' friendships were with males with whom they had consorted during previous conceptive cycles (Palombit *et al.*, 1997). Bercovitch (1995) reported similar findings in olive baboons.

We tested the offspring care hypothesis in a 12-month study of wild olive baboons. Based on previous research we made four predictions. First, we predicted that testosterone levels will be lower in males involved in friendships with females than in controls (see Methods below). Second, we predicted that periparturition testosterone levels will decrease in males with female friends but not in controls matched for the time period.

Third, we predicted that among males in friendships, testosterone will be associated negatively with a male's relative contribution to maintaining the friendship. Baboon friendships vary considerably regarding the relative investment of partners in maintaining the relationship (Smuts, 1985; Palombit *et al.*, 1997). The adaptive significance of this variation remains unclear, but evidence that lactating female baboons compete for social access to male friends suggests that the nature or "quality" of a friendship influences a female's accrual of the benefits offered by these bonds (Palombit *et al.*, 2001). While the benefits for males are clearly different than those for females, the degree to which males benefit from friendships should be reflected in their effort at maintaining them (Trivers, 1971). If the primary benefit is enhanced fitness as a result of parental effort, male responsibility for maintaining a friendship should co-vary with hormone profile.

Finally, we considered the effect of timing of infant development on testosterone profiles in male friends. For infant baboons, risk from both lethal and nonlethal harassment by other group members is greatest early in the lactation phase and declines as they become more independent (Smuts, 1985, Palombit *et al.*, 1997, 2001). In humans, new fathers may experience a temporary situational increase in testosterone in response to infant distress while otherwise maintaining low testosterone (Storey *et al.*, 2000). Later, testosterone increases significantly in the months after birth. Although their research does not address variation in male testosterone levels changes during female friend lactation, Bergman *et al.* (2006) suggest that during the course of male chacma baboon reproductive careers, long-term variations in testosterone profiles reflect a situational response to alternating mating versus parenting strategies. The same patterns may be observed if olive baboons shift from a parenting strategy early in lactation to a mating strategy late in lactation as the harassment threat to infants decreases. Thus, we predicted that testosterone levels in males with female friends will correspond with the timing of infant development; late in the lactation phase, levels of testosterone will be significantly higher than those experienced shortly after parturition.

METHODS

Study Site and Subjects

Research was conducted at Segera Ranch and adjacent area located on the Laikipia plateau (36°50'E, 0°15'N), Central, Kenya. The site lies at an altitude of 1,700m; mean annual temperature range is 10-22 degrees Celsius, and annual rainfall averages approximately 500mm (Palombit, unpublished data). The semi-arid habitat is

mixed grassland interspersed with patchy *Acacia drepanolobium* scrub away from waterways dominated by *Acacia xanthophloea*.

Olive baboon groups live in multi-male, multi-female groups in which females remain in the natal group and form linear dominance hierarchies (Hall and Devore, 1965, Altmann, 1980). Female ranks remain stable for long periods of time; a daughter typically assumes the rank adjacent to her mother (Smuts, 1985). Males typically emigrate to other groups as young adults and often rise rapidly in the male hierarchy of the new group (Smuts, 1985).

Quantitative behavior sampling and fecal sampling for hormone analysis were conducted on two habituated baboon groups studied since 2000 by Palombit and colleagues. The first group, KAT, comprised 37-42 individuals including 9-11 adult males, 18-20 adult (cycling) females, and immature offspring. The second group, TDM, comprised 89-95 individuals including 19-21 adult males, 26-30 adult females, and immature offspring. Dominance interactions had been scored by direction of supplants and aggressive interactions for KAT for the previous five years and for TDM for the previous four years.

Twenty-six adult males at the beginning of the study and twenty-two lactating females were selected as subjects. One primiparous KAT female whose infant disappeared six weeks post-parturition and who subsequently resumed cycling six weeks later was eliminated as a subject. No adult males permanently transferred out of either group during the study. One adult male, who immigrated into TDM late in the study, and who did not appear to form a friendship, was not added as a subject. Male-controls were resident adult males of all ranks who were not involved in friendships with lactating

females (based on C-score, see below) and who were not observed consorting with any estrous females within two days prior to fecal sample collection. Male Friends and Controls were matched for time period by analyzing glucocorticoid concentrations of each group in relation to the parturition and lactation periods of female friends.

Behavioral Observations and Analysis

We observed the study groups from September 2004 to August 2005. Data were collected from 7:00h to 14:00h for an approximate total of 900 contact hours. All behavioral data were collected on a hand-held Psion Workabout MX Basic data recorder (Raco Industries, Cincinnati, Ohio) and downloaded into a base-camp computer at the end of the day. A total of 1,966 focal samples as well as *ad libitum* observations (Altmann, 1974) were collected on 22 females and 26 males. A focal behavior sample consisted of a 10-minute observation period during which 57 predetermined relevant behaviors were recorded continuously, and nearest neighbor spatial relations at 2-minute intervals. Nearest neighbor data listed all individuals within 6m of the subject and their distances from the subject. *Ad libitum* observations included data on consortships, female reproductive states, diet, dominance, and demography.

We calculated dominance ranks for males and females in each of the two groups based on the direction of decided dyadic interactions including supplants, bare-teeth displays, and aggressive chases (Hall, 1962). Dyadic interactions were plotted on a dominance matrix to determine hierarchy (Martin and Bateson, 1993). Individuals were categorized as either “high-rank” (top half of all ranks) or “low-rank” (bottom half of all ranks) for our analyses since linear placement of closely ranked individuals, particularly

males, was sometimes ambiguous in these study groups (Bergman *et al.*, 2005). *Ad libitum* data indicated no evidence that an individual changed the assigned dominance category during this study.

Measures used to quantify variations in male-female social relationships and identify friendships followed Smuts (1985) and Palombit *et al.* (1997). First, we measured the duration of time that subjects were in *close proximity* as the proportion of time that two individuals spent within 2m of one another, beginning when one individual approached the other within 2m and ending when either individual withdrew further than 2m away. Second, the proportion of time subjects spent within 2-6m of others was calculated from instantaneous sampling of nearest neighbors.

These spatial data were used to calculate Smuts's (1985) composite proximity score (or "C-score") which has become a standard method for identifying baboon friendships (Bentley-Condit and Smith, 1999; Palombit *et al.*, 1997, 2001; Silk, 2002). The percentage of time spent within each distance category was multiplied by a constant (the reciprocal of the mid-point of the inner and outer limits of that category). These weighted proximity times were then summed to arrive at the composite score (Palombit *et al.*, 1997; modified from Smuts, 1985):

$$C = 1(\%Time_{0-2m}) + 0.25(\%Time_{2-6m})$$

Since the average length of the lactation phase in female subjects was 32.5 weeks (s=8.1, n=16), C-scores were calculated based on the time period from parturition to 32-weeks post-parturition (or until cycling actually resumed). For each female, a discontinuous distribution of C-scores indicated a friendship with one or more males (Palombit *et al.*,

1997). We identified 30 friendships involving 17 males and the 16 lactating females who gave birth during the first 10 months of the study.

Once a friendship was identified by C-score, we used “Hinde’s Index” (Hinde and Atkinson, 1970) to assess the relative contribution of each partner towards maintaining proximity. The difference between the percentage of approaches within 2m (A) by the female and the percentage of withdrawals (W) by the female was calculated according to the following equation:

$$A_F/(A_F+A_M)-W_F/(W_F+W_M)$$

A positive Hinde’s Index score in the range 0 to 100 indicated that the female was responsible (Female-Responsible) for close proximity maintenance while a negative score (-100 to 0) indicated that the male was responsible (Male-Responsible). We set the timeframe for Hinde’s Index score calculations from parturition to 32 weeks post-parturition. This corresponded to the time period used to calculate C-Scores and maximized the number of friendships analyzed while still meeting the minimum data requirements for Hinde’s Index calculations.

Hormone Sampling and Analysis

We collected 674 fecal samples from 26 males. Fecal sampling was evenly distributed across all subjects during the study. We employed a combination of opportunistic and targeted sampling (*sensu* Bergman *et al.*, 2005), which allowed for one sample to be collected per individual approximately every eight days. All samples were collected 6:00h-12:00h in order to reduce sampling error from fluctuation of hormone concentrations in feces excreted throughout the day (Whitten *et al.*, 1998). Feces from

positively identified individuals was gathered and homogenized with a wooden spatula. Approximately 0.5g was placed in 10ml of methanol:acetone (4:1) and mixed into solution with a combination of shaking and chopping with the spatula.

Hormones were extracted from feces and assayed using the methods described in detail by Beehner and Whitten (2004). Within 10 hours of collection, 4ml of the homogenate was separated from fecal material and filtered using a 0.2- μ m polytetrafluoroethylene (PTFE) syringe filter. This solution was diluted 1:2 with filtered water, loaded onto solid-phase extraction cartridges (Sep-Pak Plus C18 cartridge, Waters Associates, Milford, Massachusetts, U.S.A.), primed according to the manufacturer's instructions, and washed with 0.1% sodium azide solution. Cartridges were placed in individual Whirl-Pak bags with silica gel beads to absorb moisture and stored in a standard freezer (-10° C) until transport to the laboratory.

At Emory university, cartridges were stored at subzero temperature (-80° C) until hormones were eluted with 3ml of methanol. Duplicate aliquots of samples to be analyzed were evaporated under nitrogen and reconstituted in phosphosaline gelatin working buffer. Samples were radioimmunoassayed (RIA) for testosterone using a testosterone RIA kit (DSL-4100, Webster, Texas). Although testosterone is metabolized in the liver and excreted in feces in several conjugated androgen forms, we had previously validated this kit for reactivity with baboon fecal testosterone. Unless otherwise noted, testosterone concentration results are expressed as ng/g fecal dry weight \pm SEM). Interassay coefficients of variation were $9.88 \pm 0.11\%$ (high control, n=28), $5.77 \pm 1.73\%$ (low control, n=28), $6.39 \pm 0.53\%$ (fecal extract pool, n=25). Intra-assay coefficient of variation was $4.68 \pm 1.03\%$ (fecal extract pool, n=8).

We determined mean testosterone concentrations for each male from all samples obtained throughout the study. The difference in mean concentrations between males in the two groups was not significant (Mann-Whitney U test: $U=83$, $n_1=17$, $n_2=9$, $p=0.75$); data on both groups were pooled for all subsequent analyses. Testosterone concentration was unrelated to dominance rank in all males combined (Mann-Whitney U test: $U=106$, $n_1=16$, $n_2=10$, $p=0.18$) and in the subset of Male Friend subjects (Mann-Whitney U test: $U=26$, $n_1=7$, $n_2=5$, $p=0.20$).

In order to reduce effects not related to parturition while maintaining sufficient behavior and hormonal data for analysis, the periparturition period was defined as the 2-week period before (Before) and the 2-week period after (After) the birth of a female friend's infant. Testosterone concentrations from multiple fecal samples (minimum-two, maximum-four) collected during each two-week period from any male were averaged for each time period. We collected minimum combined periparturition behavioral and hormonal data to include 20 friendships in this set of analyses. Among these friendships five males had multiple (either two or three) friendships during the study. Although there were no overlaps in any individual male's friends' periparturition periods, friendships were analyzed in two ways. First, to ensure the independent contribution of data from each male, Before-mean and After-mean testosterone concentrations for any males' multiple friendships were calculated. Second, in particular analyses (see Figures 2-4) any males' multiple friendships were considered independent to allow for comparison between friendships in which males versus females maintained responsibility for proximity maintenance. There was no significant difference between the two methods for

calculating the sample Before and After means (Mann-Whitney U test: $U=120$, $n_1=20$, $n_2=12$, $p=0.98$).

To evaluate temporal variations in testosterone concentration during lactation, the 32-week period of lactation was divided into four 8-week intervals (Figure 6). In order to assess a change in testosterone level from early post-parturition to late-lactation, the two-week After period (rather than Interval 1) was compared to Interval 4 (Figure 7). The shorter After period better represents testosterone levels immediately after parturition than the 8-week Interval 1.

Statistical Analysis

We used two-tailed nonparametric tests for all analyses with α set at 0.05. Wilcoxon Paired-Sample Tests were used to compare periparturition testosterone in Male Friends versus Controls and among Male Friends only, to compare periparturition testosterone in Male-Responsible versus Female-Responsible friends. To analyze temporal variation in testosterone levels in Controls and Male Friends, the 32-week period of lactation was divided into four 8-week intervals. The Kruskal-Wallis test was used to compare data sets for each interval. The Mann-Whitney U Test was used to compare testosterone levels in Male Friends versus Controls during the 32-week lactation phase. Spearman's Rank Correlation Test was used to analyze the association between periparturition testosterone change and Hinde's Index. All statistics were performed with StatistiXL (version 1.7) statistical software for Microsoft Windows.

RESULTS

Male Testosterone Concentrations Before and After Parturition

Results were consistent with our prediction that periparturition testosterone levels will decrease in males with female friends but not in controls matched for the time period. Testosterone levels in future Male Friends and Controls were similar in the two weeks prior to parturition (Before: Mann-Whitney U test: $U=32$, $n_1=12$, $n_2=5$, $p=0.88$). However, testosterone concentration significantly decreased following parturition in Male Friends (Before: 34.17 ± 3.20 ; After: 27.23 ± 2.16 ; Wilcoxon Paired-Sample Test, $T=10$, $n=12$, $p<0.05$) but not in Controls (Before: 36.60 ± 2.88 ; After: 37.29 ± 2.27 ; Wilcoxon Paired-Sample Test, $T=5$, $n=5$, $p=0.63$). (Figure 1)

We also predicted that among males in friendships, testosterone will be associated negatively with a male's relative contribution to maintaining the friendship and our results were consistent with this prediction. Of 19 friendships for which data are available, proximity was maintained primarily by the female in 4 cases (21.1%) and by the male in 15 cases (78.9%) (Table1). Males in Male-Responsible friendships experienced a significant decline in periparturition testosterone concentration (Before: 36.09 ± 2.67 ; After: 26.70 ± 2.20 ; Wilcoxon Paired-Sample Test, $T=14$, $n=15$, $p<0.005$) (Figure 2). There was no significant periparturition change in testosterone concentration among males in Female-Responsible friendships (Before: 28.30 ± 5.38 ; After: 23.08 ± 3.54 ; Wilcoxon Paired-Sample Test, $T=4$, $n=4$, $p=0.88$). Although a periparturition increase in Female-Responsible friendships would also be consistent with the above prediction, the lack of a significant periparturition testosterone change may be an artifact of the small sample size of Female-Responsible friendships (4). Males involved in Female-

Responsible friendships had significantly lower testosterone levels than males in Male-Responsible friendships but only during the Before period (Mann-Whitney U test Before: $U=41.00$, $n_1=4$, $n_2=15$, $p<0.05$; After: $U=36.50$, $n_1=4$, $n_2=15$, $p=0.53$) (figure 3). The average percent decrease was greater in Male-Responsible friends (26.01%) than Female-Responsible friends (18.45%). Thus, the periparturition testosterone decrease in male friends overall (noted above) is primarily due to Male-Responsible friends. These data support the paternal care hypothesis for baboon friendship; upon the birth of their friends' infants, male olive baboons exhibit a testosterone profile commonly associated with fathers in pair-bonded primates. The association between testosterone and parturition is even more pronounced in males who invest more in maintaining proximity in friendships.

However, the association between Hinde's Index score and the magnitude of the periparturition testosterone change was not significant either for Male-Responsible and Female-Responsible friends combined ($r_s = -0.04$, $DF=19$, $p=0.86$) or for Male-Responsible friends alone ($r_s=0.16$, $DF=15$, $p=0.56$) (Figure 4). Although Male-Responsible friends as a group experienced a highly significant periparturition decrease in testosterone (see above), there was a great deal of individual variability in periparturition change. Testosterone increased in 32% of Male Friends overall. The role of competing reproductive strategies during the course of friendships, *e.g.* short-term consortships with estrous females, may heavily influence individual testosterone profiles during the course of friendships.

Male Testosterone Concentrations During First 32 Weeks of Lactation

We predicted that during the lactation phase overall, testosterone levels will be lower in males involved in friendships than in control males. Male Friends (29.05 ± 1.06) did have significantly lower 32-week mean testosterone concentration than Controls (34.59 ± 0.55) (Mann-Whitney U Test: $U=24$, $n_1=4$, $n_2=4$, $p<0.05$) (Figure 5). When comparing 8-week periods, testosterone concentration did not differ significantly across the four lactation intervals in Male Friends (Kruskal-Wallis Test: $F=0.06$, $DF_1=3$, $DF_2=48$, $p=0.98$) or in Controls (Kruskal-Wallis Test: $F=0.32$, $DF_1=3$, $DF_2=13$, $p=0.82$). Male Friends exhibited significantly lower testosterone levels than Controls in Interval 1 (Mann-Whitney U test: $U=52$, $n_1=15$, $n_2=5$, $p<0.05$) but not in the remaining three intervals: Interval 2 (Mann-Whitney U Test: $U=45$, $n_1=15$, $n_2=5$, $p=0.72$), Interval 3 (Mann-Whitney U Test: $U=40$, $n_1=14$, $n_2=5$, $p=0.69$), Interval 4 (Mann-Whitney U Test: $U=16$, $n_1=7$, $n_2=3$, $p=0.27$) (Figure 6).

However when directly comparing the early post-parturition After period to the late-lactation Interval 4, Male Friends experienced a significant increase in testosterone concentration (After: 27.23 ± 2.16 , Interval 4: 31.85 ± 6.81 , Mann-Whitney U Test: $U=84$, $n_1=20$, $n_2=7$, $p<0.05$) converging with the testosterone profile observed in Controls (After: 37.29 ± 2.27 , Interval 4: 35.70 ± 5.10) (Figure 7). There was a significant post-parturition (After) difference between the two groups (Mann-Whitney U test: $U=51$, $n_1=12$, $n_2=5$, $p<0.05$) but no significant difference at Interval 4 (Mann-Whitney U test: $U=16$, $n_1=7$, $n_2=3$, $p=0.27$). Testosterone in Male Friends, after a parturition decline, increased back to levels similar to that in Controls by 16 weeks post-lactation. There was no significant change in testosterone concentrations from After to Interval 4 in Controls

(Mann-Whitney U Test: $U=8$, $n_1=5$, $n_2=3$, $p=1.00$). The testosterone difference between Male Friends and Controls remained insignificant through the remaining 16 weeks of lactation. Data are consistent with our prediction that testosterone levels in males in friendships will correspond with the timing of infant development and that levels of testosterone late in the lactation phase will be higher than those experienced shortly after parturition.

DISCUSSION

As they navigate their social environments, testosterone provides one proximate mechanism for adult male vertebrates, including humans and other primates, to adjust among short-term behavioral options and long-term strategies to maximize reproductive fitness (Corter and Flemming, 1995; Carter, 1998; Storey *et al.*, 2000; Wynne-Edwards, 2001; Gray *et al.*, 2007). In males mammals, suppression of testosterone, the primary androgen, appears to critically facilitate paternal behaviors by shifting male social focus from competitive mating effort to parental effort (Bercovitch and Ziegler, 1990, 2002; Ziegler 2000). In our study, baboon males who were friends with lactating females experienced testosterone profiles strikingly similar to those observed in paternal care-giving callitrichids and human fathers (Wynne-Edwards, 2001; Nunes, 2001, 2002; Gray *et al.*, 2002, 2006, 2007; Wynne-Edwards and Timonin, 2007). Our findings were consistent with each of four predictions of the paternal care model of testosterone association with friendship. First, testosterone levels were significantly lower in males involved in friendships with females than in Controls. Second, Male Friends, but not controls, experienced a significant periparturition decrease in testosterone concentration.

Third, while testosterone concentrations did not vary significantly in Controls, testosterone in Male Friends significantly increased from early post-parturition to 32 weeks post-lactation.

Fourth, hormonal profiles differed in the two categories of male friends: Male-Responsible—those more responsible than the females for maintaining proximity to females during lactation, and Female-Responsible—those who were less responsible than females for maintaining proximity. The periparturition testosterone decrease was nearly 1.5 times greater in Male-Responsible friends than in Female-Responsible friends. Preparturition testosterone levels, but not post-parturition levels, were significantly different in the two categories of males. In other words the trend towards decrease in periparturition testosterone in Male Friends was primarily a result of Male-Responsible friends while Female-Responsible friends (with lower testosterone than controls) simply maintained a low testosterone profile both before and after parturition. The small sample size (4) of Female-Responsible friends precluded further statistical analysis of this group, but it should be noted that periparturition testosterone increased, rather than decreased, in two of the four of these males (Figure 3B). In Male-Responsible friends, periparturition increase only occurred in four of the 11 males (Figure 3A). The relationship between these variations and additional behavior parameters associated with friendship are being further investigated.

Males provide direct infant care in approximately 5 percent of mammalian species (Clutton-Brock, 1991; Kleiman, 1977; Kleiman *et al.*, 1981). Even in the absence of paternity confirmation, these behaviors are generally referred to as paternal care. In primates, paternal care patterns range from intensive care-taking observed in titi monkeys

(*Callicebus sp.*) and callitrichids, to the more general affiliations with infants observed in baboons and other cercopithecines (Whitten, 1987). Alternatively, van Schaik and Paul (1996) argue that most “paternal” care in primates may be interpreted as mating effort, *i.e.*, care directed towards an infant that ultimately functions to increase future mating access to its mother. They note that in primates clear examples of both strategies occur and may be functionally inseparable in a given species. Determination of genetic paternity coinciding with behavioral data may help to sort out when and how these alternative strategies are expressed in species, groups or even individual males. The test for “true parental-care” (*sensu* Buchan *et al.*, 2003) is whether or not care is directed preferentially towards genetic offspring and if this care then results in enhanced fitness for the recipient (Trivers, 1972; van schaik and Paul, 1996). Buchan *et al.* (2003), providing one example in yellow baboons, observed that adult males preferentially supported juveniles that were genetic offspring during agonistic disputes. Applying the test for true parental care to friendship has been problematic in traditional behavioral studies of baboons, in part because of lack of independent physiological or genetic data. Our study was designed to complement purely observational research and determine whether male friends experience a “paternal hormone profile” coinciding with their affiliative relationships with lactating females and their infants.

Unlike serum testosterone measures, which indicates endocrine activity immediately prior to sampling, fecal testosterone reflects an averaged or accumulated testosterone response to events occurring from several hours to several days prior to sampling (Whitten *et al.*, 1998). Therefore, fecal testosterone sampling does not permit for analysis of discrete pituitary-testicular axis response to transitory social stressors (*e.g.*,

particular fights), which would be necessary to gauge the long-term fitness costs of lowered testosterone in male friends (Whitten *et al.*, 1998). However, Beehner *et al.* (2006) assert that in male chacma baboons, low basal testosterone (as seen in olive baboon friends) generally results in a direct fitness cost for males. These males are less successful at competing for rank, which reduces long-term mating success. Friendship, paternal care-giving (as mediated by lowered testosterone) and reduced immediate mating success might prove to be a successful long-term strategy for both genetic fathers and non-fathers alike if lactating females are more likely to conceive future infants with past friends. However the potential mating costs of lowered testosterone would obviously have fewer fitness consequences for friends who are actually the genetic fathers of friends' current infants. (Trivers, 1971).

In summary, the hormone profile of male olive baboon friends is consistent with those for human fathers and other paternal care-giving primates. The data reveal an association between lowered testosterone and the onset of friendship coinciding with parturition. Further, testosterone concentrations remain low in male friends during infant development, eventually rising to preparturition levels late in the lactation phase. While our data support the parental care hypothesis for friendship in male olive baboons, they do not exclude mating effort as a potential simultaneous strategy.

TABLES AND FIGURES

Table 1. Mean testosterone concentrations (ng/g) of males before and after the birth of their friends' infants, periparturition change, percent change and Hinde's Index.

Male x Female Friendship	Before	After	Periparturition Change	Percent Change	Hinde's Index
TDxXN	35.86	14.10	21.76	60.68	-2.60
TDxTH	26.84	18.40	8.44	31.45	-45.20
TDxAT	22.02	33.27	11.25‡	51.09‡	* 26.80
CHxSL	22.08	19.72	2.36	10.69	-24.70
GGxSL	37.69	25.11	12.58	33.38	-37.50
LZxKT	20.29	29.45	9.16‡	45.15‡	-43.10
SExTT	40.69	35.14	5.55	13.64	-21.50
ARxZA	48.70	33.65	15.05	30.90	NA
GLxVD	59.37	40.96	18.41	31.01	-12.80
GLxLT	40.76	41.85	1.09‡	2.67‡	-4.80
BGxVD	18.09	21.11	3.02‡	16.69‡	* 13.10
LExNM	30.76	21.12	9.64	31.34	* 14.70
LExTN	30.76	21.12	9.64	31.34	-7.00
LExGW	24.99	29.04	4.05‡	16.21‡	-11.10
BLxNM	35.09	14.77	20.32	57.91	-9.10
BLxTN	24.93	26.24	1.31‡	5.25‡	-6.90
IRxTN	42.34	19.92	22.42	52.95	-8.90
IRxNM	42.34	16.82	25.52	60.27	* 1.60
IRxGW	44.93	22.55	22.38	49.81	-16.00
SXxVD	42.15	35.25	6.90	16.37	-21.20

‡ Increase

* Females responsible for maintenance of proximity

NA—Insufficient approach/withdraw data to calculate Hinde's Index

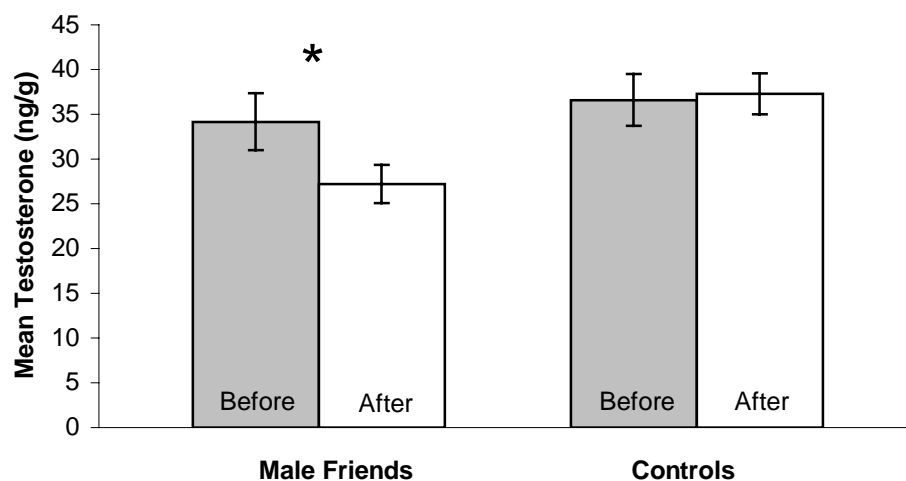


Figure 1. Mean testosterone concentrations (ng/g mean \pm SEM) before and after the birth of infants: in Male Friends and in Controls

*** indicates significant difference in Before/After concentrations**

Before = 2 weeks preparturition

After = 2 weeks post-parturition

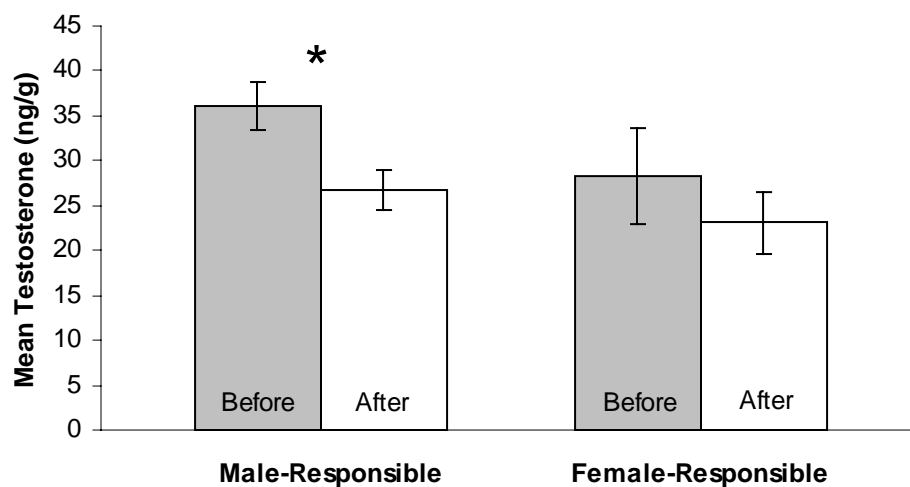
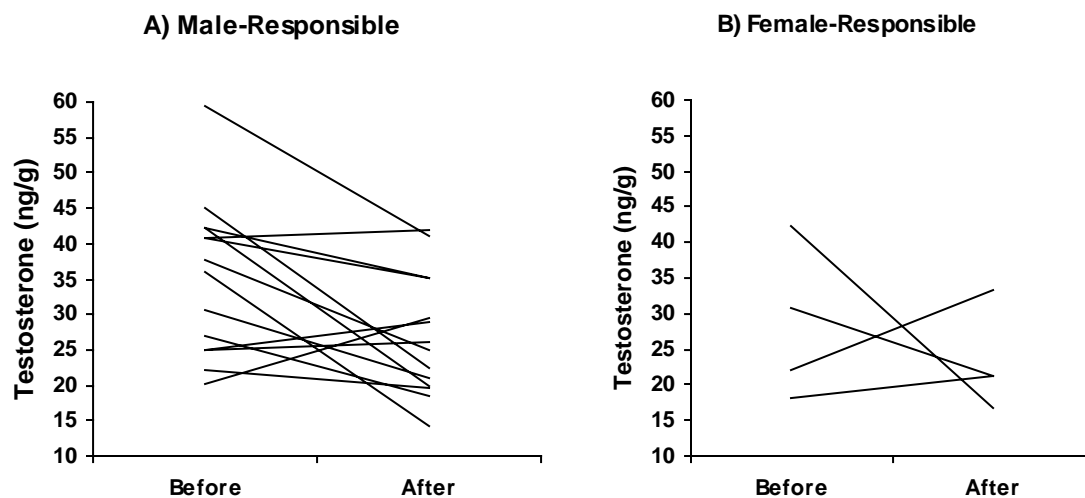


Figure 2. Mean testosterone concentrations (ng/g mean \pm SEM) before and after the birth of infants: in Male-Responsible Friends and in Female-Responsible Friends

*** indicates significant difference in Before/After concentrations**

Before = 2 weeks preparturition

After = 2 weeks post-parturition



**Figure 3. Mean testosterone concentrations (ng/g) before and after parturition in A) Male-Responsible Friends (n=15); B) Female-Responsible Friends (n=4).
Before = 2 weeks preparturition
After = 2 weeks post-parturition**

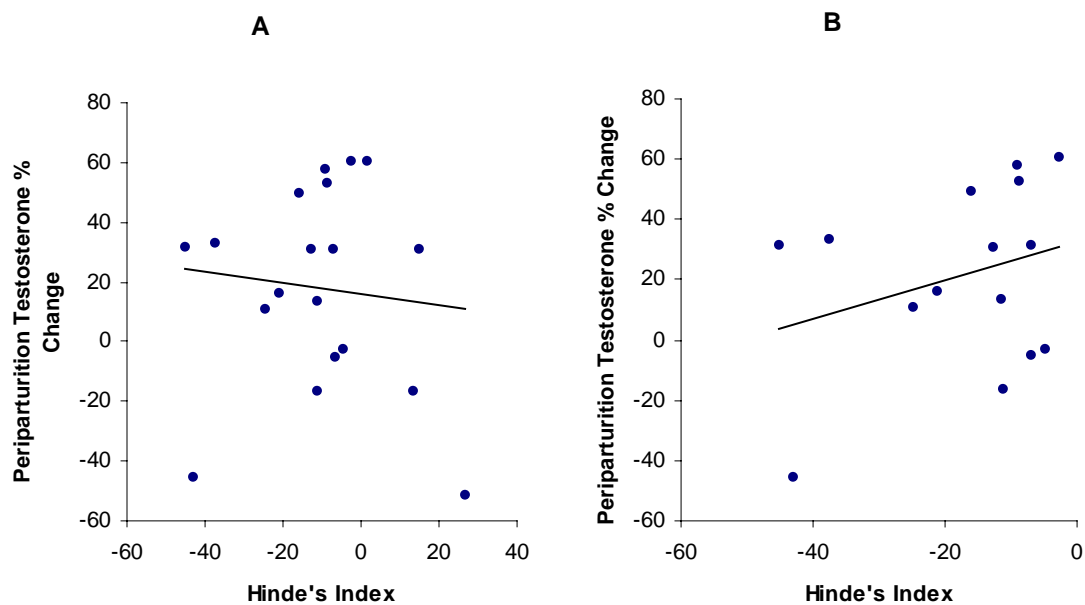


Figure 4. Association between Hinde's Index and periparturition testosterone percent change in Male Friends. A) Male-Responsible and Female-Responsible Friends; B) Male-Responsible Friends only.

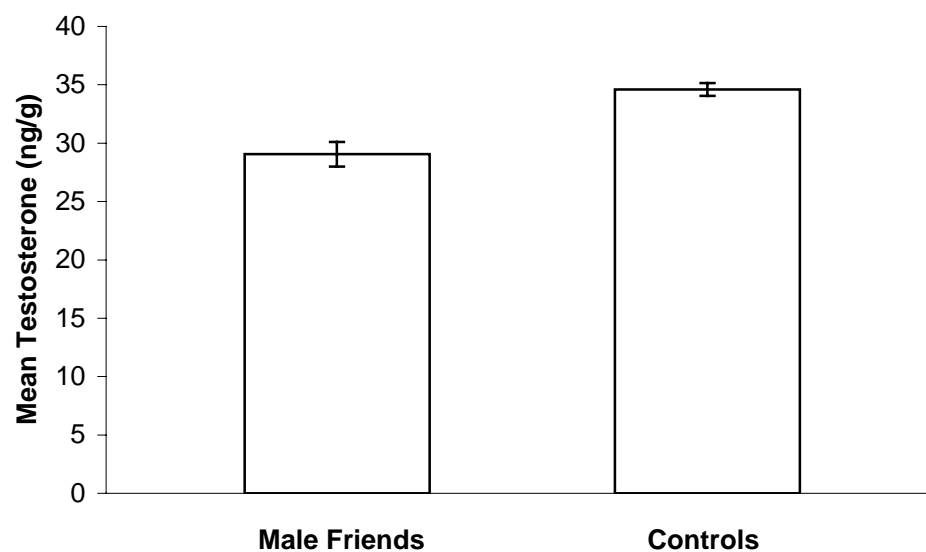


Figure 5. Difference in mean testosterone concentrations (mean of Interval 1-4 means; ng/g \pm SEM) in Male Friends and in Controls during the first 32 weeks of lactation (Mann-Whitney U Test: $U=24$, $n_1=4$, $n_2=4$, $p<0.05$).

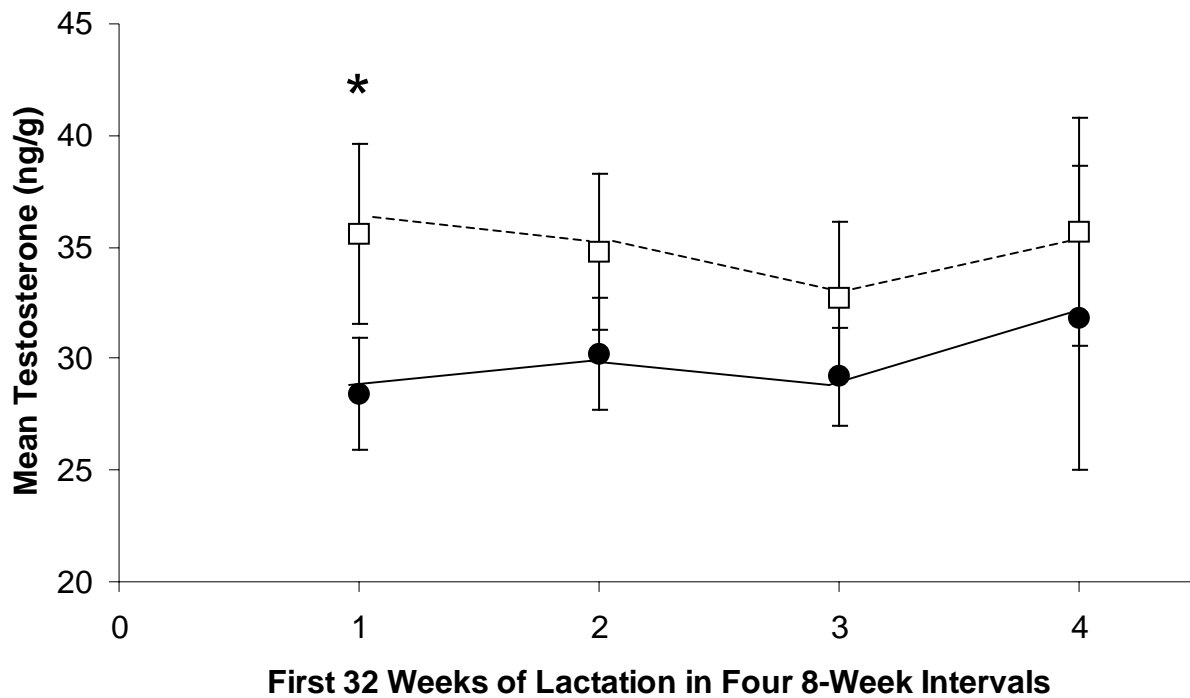


Figure 6. Testosterone concentrations (ng/g mean \pm SEM) in Male Friends (solid circles) and in Controls (open squares) during first 32 weeks of lactation.

*** Significant difference between Male Friend/Control concentrations**

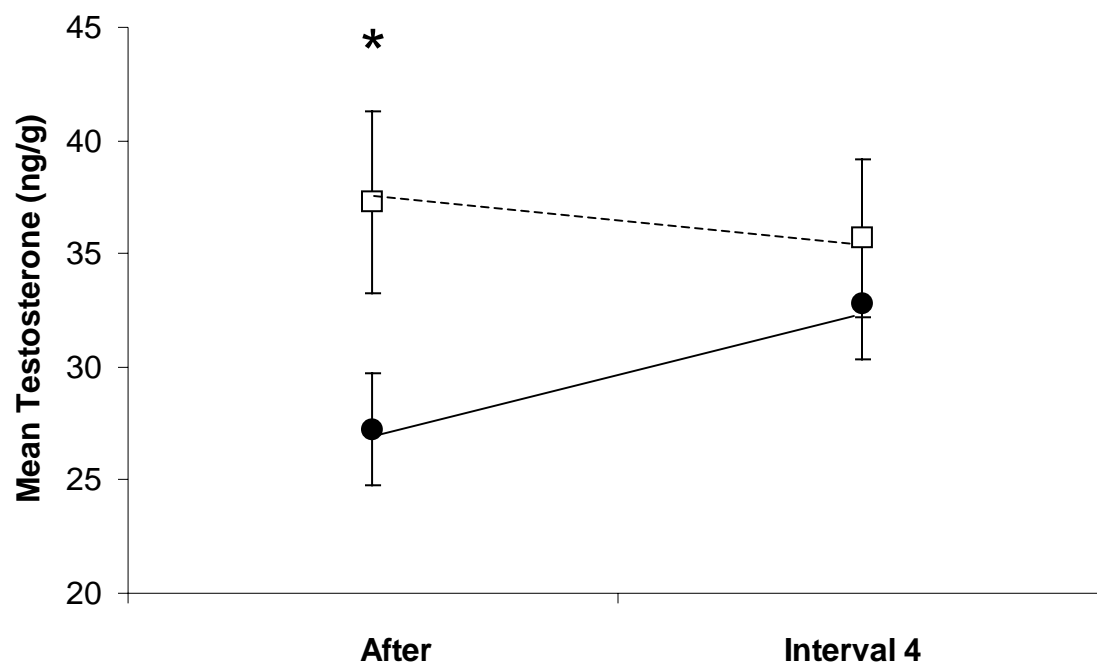


Figure 7. Testosterone concentration (ng/g mean \pm SEM) change from After (2-weeks post-parturition) to Interval 4 (Week 24-32) in Male Friends (solid circles) (Mann-Whitney U Test: $U=84$, $n_1=20$, $n_2=7$, $p<0.05$) and in Controls (open squares) (Mann-Whitney U Test: $U=8$, $n_1=5$, $n_2=3$, $p=1.00$).

*** Significant difference between Male Friend/Control concentrations**

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CHAPTER TWO

ASSOCIATION BETWEEN MALE GLUCOCORTICOID CONCENTRATIONS AND FORMATION AND MAINTENANCE OF FRIENDSHIP WITH LACTATING FEMALES IN WILD OLIVE BABOONS (*Papio hamadryas anubis*)

INTRODUCTION

The mammalian stress response is the comprehensive physiological process following stress that serves to mobilize the body to action and then safely return its functions to homeostasis (Selye, 1976). The stress response comprises an array of systems either stimulated or inhibited by stressors. Control over these systems involves one of two generalized endocrine pathways. Both are initiated by hypothalamic detection of a stressor, resulting in a hormonal cascade beginning with corticotropin-releasing-hormone (CRH) along with activation of the sympathetic nervous system (Sapolsky, 1993b). The hormonal end-products of these processes are either glucocorticoids or catecholamines. In addition, neuropeptides and opioid peptides are secreted by the posterior pituitary as a byproduct of pituitary activation by CRH and production of adrenocorticotrophic hormone. These peptides serve to stimulate glucocorticoid production by the adrenal cortex.

Within minutes of a perceived stressor, elevated serum levels of glucocorticoid can be detected. Along with the catecholamines, these glucocorticoids (primarily cortisol in primates and corticosterone in rodents and many other animals) provide the body's two critical chemical control mechanism during stress (Sapolsky, 1993b). The function of glucocorticoids is most readily apparent in the metabolic component of the stress response. Glucocorticoids inhibit pancreatic production of insulin, which is the primary hormone responsible for storage of fats as triglycerides, amino acids as proteins, and

glucose as glycogen in muscle tissue. Stress-response mobilizes metabolic systems and increases bodily demand for nutrients. By suppressing insulin storage reaction to high levels of circulating glucose, glucocorticoids ensure the body's uncompromised access to these nutrients. The catecholamines epinephrine and norepinephrine complement glucocorticoid activity during the stress response and provide the chemical mechanism whereby hypothalamic stimulation of the sympathetic branch of the autonomic nervous system regulates arousal and maximizes oxygen availability and energy transportation to appropriate tissues.

In addition to its adaptive functions, glucocorticoids, particularly when chronically activated during prolonged stress response, can have a number of pathological effects (Munck *et al.*, 1984; Abbott *et al.*, 2003, Sapolsky, 2002). These can include glycogen storage inhibition myopathy, hypertension (from prolonged vascular tone increase), osteoporosis, peptic ulcers, anovulation and amenorrhea in females, and impotence in males. Glucocorticoids also suppress the immune system, a process that although seemingly counterintuitive, is understandable as a crucial autoregulatory function, keeping the body from reacting with perilous immune response hyperactivity during times of stress. As with other glucocorticoid effects, short-term immunosuppression benefits can become costly with chronic stress response activation. The collective maladaptive effect of long-term glucocorticoid level elevation can have dire consequences on both individual and reproductive fitness (Mostl and Palm, 2002; Sapolsky, 2002)

Sapolsky's (1982, 1983a, 1983b, 1990) early detailed research of male dominance and aggression in olive baboons (*Papio hamadryas anubis*) provided much of what we

know about the association between glucocorticoids and social behavior in primates. For example, during periods when the dominance hierarchy was stable, higher-ranking males not only had the lower basal cortisol levels, but also more efficient endocrine response to stressors (Sapolsky, 1982, 1983a). Further, even during unstable periods, when higher-ranking males had elevated basal cortisol levels, the profile was only characteristic of those who were consistently being challenged by lower ranking males (Sapolsky, 1992). When male olive baboons were clustered according to predominant characteristics or behavioral styles (marked by high rates of mutual grooming and other positive social interactions with lactating females), high standing in the *affiliative* category (see Strum, 1982) was correlated negatively with basal cortisol concentration (Ray and Sapolsky, 1992).

In contrast to these early findings on olive baboons, Bergman *et al.* (2005), identified the opposite trend in chacma baboon (*P. h. griseipes*) males. Males who had high rates of affiliative interactions with lactating females such as grooming, approaches, and tolerated infant handling exhibited higher glucocorticoid levels than other males. However, consistent with earlier studies, infanticide risk associated with a new immigrant male rapidly rising to alpha status was the strongest predictor of glucocorticoid elevation across all males. Other positive correlates included recent dispersals and consortships with estrous females. Demographic or ecological variables such as age, rank, and season did not affect glucocorticoid profiles.

A meta-analysis of seven primate species (including wild olive baboons) has clarified the relationships among glucocorticoid level, stress and dominance in primates (Abbott *et al.*, 2003). Generally, social subordinates do experience higher basal

glucocorticoid levels in response to stressors; over time these individuals will adjust basal levels to a hypercortisolism set-point. This effect can be mediated by a number of factors however, the most critical being opportunities for social support from either close kin or other group members (Levine *et al.*, 1989). This point is particularly relevant in olive baboon societies characterized by large, complex groups coupled with hierarchies that are heavily influenced by both overt aggression and long-lasting supportive relationships among adults (Strum, 1985; Sapolsky, 1990; Abbot *et al.*, 2003).

One such association, first described as *friendship* by Strum (1974), typically commences at parturition between lactating females and unrelated adult males. These non-sexual relationships, identified by high rates of proximity and mutual grooming, have become widely recognized and studied by field researchers (Smuts, 1985; Palombit *et al.*, 1997; Palombit 2003a). Both males and females may be of any rank in their respective dominance hierarchies. Although friendships may occasionally extend beyond the females' six to eighteen month lactation phase, they are strongest and most conspicuous during this period.

Numerous observational data along with innovative field experiments have provided insights into the question of adaptive significance of friendship for male olive baboons but the explanations continue to be debated (Collins *et al.*, 1984; Smuts, 1985; Strum, 1987; Bercovitch, 1995; Palombit *et al.*, 1997; Palombit, 2003b). The analysis of hormones serves behavioral researchers as an independent test of various hypotheses to explain friendship.

In this study, we tested the parental care hypothesis for baboon friendship based on a "fatherhood" model of glucocorticoid profiles found in male pair-bonded

callitrichids and humans. If friendships constitute a form of parenting, male friends should show a periparturition and lactation phase glucocorticoid “paternal profile” (*sensu* Reburn and Wynne-Edwards, 1999; Storey *et al.*, 2000; Nunes *et al.*, 2001, 2002; Berg and Wynne-Edwards, 2001). An association between glucocorticoids and paternal behavior is broadly supported by studies of callitrichids as well as humans (Wynne-Edwards, 2001; Wynne-Edwards and Timonin, 2007). Ziegler *et al.* (2004) speculate that an observed mid-gestation rise in glucocorticoids in male cotton-top tamarins (*Saguinus oedipus*), which corresponds to a slightly earlier glucocorticoid increase in female partners, may play an important role in activating paternal care. At periparturition, levels rose and then fell in all males, but remained low in the early lactation period only in experienced fathers, not in first-time fathers (Ziegler *et al.*, 1996). In pair-bonded black tufted-ear marmosets, *Callithrix kuhlii*, glucocorticoid levels declined immediately following the birth of a male’s infant and the onset of his infant carrying, and were lower in “high investor” fathers than in males who carried their infants less (Nunes *et al.*, 2001). In male common marmosets, *Callithrix jacchus*, levels of glucocorticoids were similarly elevated shortly before parturition, but there was no difference in post-parturition levels between infant-carrying and non-carrying fathers (da Silva Mota *et al.*, 2006). In contrast to previous findings on cotton-top tamarins, experienced common marmoset fathers maintained higher post-parturition levels of glucocorticoids than first-time fathers.

Studies of glucocorticoid association with parenthood in men have yielded more consistent results. These build on earlier research on women indicating that post-parturition adrenocortical activation is the best predictor of maternal responsiveness and infant bonding (Fleming *et al.*, 1997a, 1997b; Wang, 1997; Stallings *et al.*, 2001). The

pre-parturition rise and rapid subsequent post-parturition decline in glucocorticoids seen in male callitrichids has also been observed in human fathers (Storey *et al.*, 2000; Berg and Wynne-Edwards, 2001). Human fathers maintained reduced post-parturition cortisol (for the three month period analyzed in the study) compared to controls (Berg and Wynne-Edwards, 2001). An experimental study demonstrated that hearing a 20-minute recording of an (unrelated) infant crying, induced a continuous increase in cortisol among new fathers, which gradually decreased following stimuli cessation; control subjects exhibited no such stimuli-related hormonal changes (Fleming *et al.*, 2002).

Based on consortship records of olive baboons, researchers have concluded that the majority of females' friendships are with possible fathers (see Bercovitch, 1995; Palombit *et al.*, 1997) and friendship may serve functions similar to those of reproductive pair-bonds in some primates. Adult males may protect infants against general harassment from other group members, infanticide, or predation, which essentially constitutes parental-effort (Hamilton, 1984; Palombit *et al.*, 1997; Weingrill, 2000). Male support could have long-term fitness benefits for offspring including resource and future rank acquisition (Borries *et al.*, 1999). This explanation is supported by field studies that indicate that males may be able to assess paternity of youngsters and they tend to behave in a manner consistent with paternal investment. For example, Buchan *et al.* (2003) observed that in agonistic disputes involving juveniles, male yellow baboons (*P. h. cynocephalus*) are more likely to support genetic offspring than unrelated individuals. In playback experiments with chacma baboons, the strength of a male's response to his friend's screams was correlated positively with his dominance rank at the time of infant conception (which is generally associated with his sexual access to estrous females)

(Palombit *et al.*, 2001). The “infanticide protection” hypothesis for friendship has gathered considerable support in chacma baboons in which sexually selected infanticide is an important factor in infant mortality, but less so in olive baboons in which infanticide is infrequent (Strum, 1995; Palombit *et al.*, 1997; Palombit 2003a, 2003b). Rather, protection against non-lethal forms of harassment may be a more crucial function of friendship in olive baboons.

We tested the following predictions of the parental care hypothesis of friendship in olive baboons. First, periparturition glucocorticoid levels will decrease in males in friendships but not in control males matched for the time period. Second, throughout lactation, glucocorticoid levels will be lower in males with female friends than in controls. Third, we predicted that glucocorticoid concentration would be negatively associated with a male’s relative investment in the friendship (in the form of proximity maintenance). Since each partner’s relative contribution to maintaining the friendship varies in baboons, the degree to which males benefit from friendships should be reflected in their effort at maintaining them (Trivers, 1972; Smuts, 1985; Palombit *et al.*, 1997). More relevant to our study, if males receive an important fitness benefit as a result of parental effort, male responsibility for maintaining friendships should co-vary with glucocorticoid profile. Finally, we predicted that glucocorticoid levels in males with female friends would increase in the late lactation phase, signaling a shift from parenting strategy to mating strategy as harassment threat to infants decreases, interactions with female friends abate and other reproductive contingencies arise, *e.g.*, consorting with estrous females (Huck *et al.*, 2005; Bergman *et al.*, 2005, 2006).

The “future mating-effort” (*sensu* Low, 1978) hypothesis is an additional explanation for friendship in male baboons. Male protection of females and their infants may only be consequences of a longer-term strategy to secure greater mating access to the females in subsequent estrus periods. This alternative explanation is not mutually exclusive from the parenting-effort hypothesis and has been argued for both baboon friendship and other forms of male-female relationships in primates (Smuts and Gubernick, 1992; van Schaik and Paul, 1996). These hypotheses will no doubt continue to be debated as paternal data from genetic analysis of baboon groups become available.

In summary, adrenocortical hormones are adaptively secreted in response to stress activation but may prove harmful when concentrations remain chronically elevated. We tested the parental care hypothesis for baboon friendship based on a paternal glucocorticoid profile model of pair-bonded non-human primates and humans. Data from other primates yield two broad conclusions regarding the associations between glucocorticoids and social behavior. First, a general trend in primates indicates that while social subordinates may experience greater stress as indicated by glucocorticoid concentration, rank-status and other social stressors can be powerfully mediated by access to conspecific social support. Second, primates seem to experience highly specific associations between glucocorticoids and fatherhood and paternal responsiveness. Any mediating effects appear to be embedded within larger social contexts and specific reproductive strategies relevant to each species.

METHODS

Study Site and Subjects

This study took place at Segera Ranch, which is located on the Laikipia plateau (36°50'E, 0°15'N), Laikipia District, Kenya, 260 km North of Nairobi. The site lies at an altitude of 1,700m; mean annual temperature range is 10-22 degrees Celsius, and annual rainfall averages approximately 500mm (Palombit, unpublished data). The habitat is characterized by mixed grassland with patchy *Acacia drepanolobium*. *Acacia xanthophloea* dominate areas around waterways including the overnight sleeping locations most frequented by baboons.

Olive baboons live in groups of 20-100 individuals typically comprising females in ranked matriline, their offspring, and unrelated adult males (Hall and DeVore, 1965; Altmann, 1980; Smuts, 1985). Females remain in the natal group and form stable long-term linear dominance hierarchies (Smuts, 1985). Males emigrate into nearby groups at adolescence where they begin to compete for rank in the male dominance hierarchy. As males rise in rank, they are able to gain sexual access to estrous females and increase their mating success in the promiscuous mating system.

We conducted quantitative behavior sampling and fecal sampling for hormone analysis on two groups of habituated baboons (KAT and TDM). Group composition changed slightly during the study in KAT, which comprised 37-42 individuals (9-11 adult males, 18-20 adult females, juveniles and infants). The second group, TDM, comprised 89-95 individuals (19-21 adult males, 26-30 adult females, juveniles and infants). Dominance interactions had been scored by direction of supplants and aggressive interactions for KAT for the previous five years and for TDM for the previous four years.

While one male study subject shifted between groups several times, no adult males permanently transferred out of either group. One adult male immigrated into the large group late in the study but remained minimally habituated, did not form friendships and otherwise remained peripheral to most group activities.

The vast majority of adult male olive baboons participate in friendships (Smuts, 1985). Male Friends, determined by C-score (see below) were resident adult males of all ranks and ages. Male-controls were resident adult males of all ranks and ages who were not involved in friendships with lactating females at any point throughout the study and who were not observed to consort with any estrous females within two days prior to fecal sample collection. In all analyses, Male Friends and Controls were matched for time period by comparing glucocorticoid concentrations of each group in relation to the parturition and lactation periods of female friends. Twenty-six adult males at the beginning of the study and all lactating females were considered subjects. Upon giving birth, new females were added to the subject pool resulting in a total of twenty-two females. One primiparous female was eliminated as a subject when she resumed cycling shortly after her infant disappeared three weeks after parturition.

Behavioral Observations and Analysis

Research took place from September 2004 to August 2005. We collected data from approximately 7:00h to 14:00h each day, for a total of approximately 900 contact hours. In addition to *ad libitum* observations on consortships, following patterns, reproductive states, diet, dominance, predation, injuries, births, deaths and disappearances, we collected a total of 1,966 focal samples on 22 females and 26 males

(Altmann, 1974). A focal behavior sample consisted of a 10-minute observation period during which 57 predetermined relevant behaviors were recorded continuously, and nearest neighbor spatial relations at 2-minute intervals. Nearest neighbor data listed all individuals within 6m of the subject and their distances from the subject. All behavioral data were collected on a hand-held Psion Workabout MX Basic data recorder (Raco Industries, Cincinnati, Ohio) and downloaded into a base-camp computer at the end of the day.

Dominance ranks for males and females in each of the two groups were based on the direction of decided dyadic interactions including supplants, bare-teeth displays, and aggressive chases (Hall, 1962). A supplant occurred when one individual withdrew within 5 seconds of another individual's approach within 2m (Palombit *et al.*, 2001). The hierarchy was determined by plotting relevant dyadic interactions on a dominance matrix (Martin and Bateson, 1993). Since the linearity of hierarchy constructions was not entirely certain and placement of closely ranked individuals, particularly males, was sometimes ambiguous in these study groups, individuals were divided into either "high" (top half of all ranks) or "low" rank (bottom half of all ranks) (Bergman *et al.*, 2005). We observed no conspicuous indications that any individual changed category during the study.

The composite proximity score (or "C-score") is a standard method for identifying baboon friendships (Smuts, 1985; Bentley-Condit and Smith, 1999; Palombit *et al.*, 1997, 2001; Silk, 2002). During focal observations, we measured continuously the time that subjects were in *close proximity* as the proportion of time that two individuals spent within 2m of one another, beginning when one individual approached the other

within 2m and ending when either individual withdrew further than 2m away.

Additionally, all individuals within 2-6m of a subject were recorded by instantaneous sampling at 2-minute intervals throughout the focal period. C-scores were calculated as the percentage of time spent within each of two distance categories summed (Palombit *et al.*, 1997; modified from Smuts, 1985):

$$C = 1(\%Time_{0-2m}) + 0.25(\%Time_{2-6m})$$

Each category was weighted by a constant determined from the reciprocal of the mid-point of the inner and outer limits of that category. Since the average length of the lactation phase in female subjects was 32.5 weeks (s=8.1, n=16), C-scores were calculated for each lactating female-male dyad in the two groups based on the time period from parturition to 32-weeks post-parturition (or until a female resumed cycling). A discontinuous distribution of C-scores indicated a friendship with one or more males (Palombit *et al.*, 1997). On this basis, a total of 30 friendships were identified involving 17 males and the 16 lactating females.

Once identified by C-score, we assessed the relative contribution of each partner towards maintenance of the friendship as indicated by “Hinde’s Index” (Hinde and Atkinson, 1970). The difference between the percentage of approaches within 2m (A) by the female and the percentage of withdrawals (W) by the female was calculated according to the following equation:

$$A_F/(A_F+A_M)-W_F/(W_F+W_M)$$

A positive Hinde’s Index score in the range 0 to 100 indicated that the female was responsible (Female-Responsible) for close proximity maintenance while a negative score (-100 to 0) indicated that the male was responsible (Male-Responsible). We set the

timeframe for Hinde's Index score calculations from parturition to 32 weeks post-parturition. This corresponded to the time period used to calculate C-Scores and maximized the number of friendships analyzed while still meeting the minimum data requirements for Hinde's Index calculations.

Hormone Sampling and Analysis

A total of 674 fecal samples from 26 males were collected. A combination of opportunistic and targeted sampling (*sensu* Bergman *et al.*, 2005) was employed which allowed for one fecal sample per individual to be collected approximately every eight days. This resulted in an even distribution of samples across subjects. Our methodology for fecal hormone extraction and assay followed Beehner and Whitten (2004). Briefly, sampling was conducted only from 6:00h-12:00h to reduce hormone concentration variations due to fecal hormone excretion daily cycle fluctuations (Whitten *et al.*, 1998). Once a fecal sample was obtained from a positively identified individual, it was homogenized with a wooden spatula and approximately 0.5g of the sample was thoroughly mixed into 10ml of methanol:acetone (4:1). Within 10 hours after collection, 4ml of the homogenate was separated from solid fecal material and filtered using a 0.2- μ m polytetrafluoroethylene (PTFE) syringe filter. This solution was diluted 1:2 with filtered water, loaded onto solid-phase extraction cartridges (Sep-Pak Plus C18 cartridge, Waters Associates, Milford, Massachusetts, U.S.A.), primed according to the manufacturer's instructions, and washed with a 0.10% sodium azide solution preservative. Cartridges were placed in individual Whirl-Pak bags with silica gel beads to absorb moisture and stored in a standard freezer (-10° C). Once all field-collection was complete, samples were transported to the Laboratory of Reproductive Ecology and

Environmental Toxicology at Emory University where they were stored at subzero temperature (-80°C). Prior to assay, samples were brought to room temperature and hormones were eluted with 3ml of methanol. Duplicate aliquots of samples to be analyzed were evaporated under nitrogen and reconstituted in phosphosaline gelatin working buffer. Samples were radioimmunoassayed (RIA) for glucocorticoid metabolites using a modification of a corticosterone I-125 RIA kit (MP Biomedicals, Costa Mesa, CA). We had previously validated this kit for use with baboon fecal glucocorticoids. Unless otherwise noted, glucocorticoid concentration is expressed as either individual duplicate mean concentration or category mean concentration in ng/g fecal sample dry weight. Interassay coefficients of variation were $6.23 \pm 0.12\%$ (high control, $n=27$), $10.47 \pm 0.04\%$ (low control, $n=27$), Intra-assay coefficient of variation was $8.28 \pm 0.20\%$ (fecal extract pool, $n=6$).

We determined mean glucocorticoid concentrations for each male from all samples obtained throughout the study. The difference in mean concentrations between males in the two groups was not significant (Mann-Whitney U test: $U=100$, $n_1=17$, $n_2=9$, $p=0.22$); data on both groups were pooled for all subsequent analyses. Glucocorticoid concentration was unrelated to dominance rank in all males combined (Mann-Whitney U test: $U=82$, $n_1=16$, $n_2=10$, $p=0.93$) and in the subset of Male Friend subjects (Mann-Whitney U test: $U=18$, $n_1=7$, $n_2=5$, $p=1.00$).

In order to reduce effects not related to parturition while maintaining sufficient behavior and hormonal data for analysis, the periparturition period was defined as the 2-week period before (Before) and the 2-week period after (After) the birth of a female friend's infant. Glucocorticoid concentrations from multiple fecal samples (minimum-

two, maximum-four) collected during each two-week period from any male were averaged for each time period. We collected minimum combined periparturition behavioral and hormonal data to include 20 friendships in this set of analyses. Among these friendships five males had multiple (either two or three) friendships during the study. Although there were no overlaps in any individual male's friends' periparturition periods, friendships were analyzed in two ways. First, to ensure the independent contribution of data from each male, Before-mean and After-mean glucocorticoid concentrations for any males' multiple friendships were calculated. Second, in particular analyses (see Figures 2-4) any males' multiple friendships were considered independently to allow for comparison between friendships in which males versus females maintained responsibility for proximity maintenance. There was no significant difference between the two methods for calculating the sample Before and After means (Mann-Whitney U test: $U=120$, $n_1=20$, $n_2=12$, $p=1.60$).

To evaluate temporal variations in glucocorticoid concentration during lactation, the 32-week period of lactation was divided into four 8-week intervals (Figure 6). In order to assess a change in glucocorticoid level from early post-parturition to late-lactation, the two-week After period (rather than Interval 1) was compared to Interval 4 (Figure 7). The shorter After period better represents glucocorticoid levels immediately after parturition than the 8-week Interval 1.

Statistical Analysis

We used nonparametric tests for all analyses. All tests were two-tailed with α at 0.05. Wilcoxon Paired-Sample Tests were used to compare periparturition glucocorticoid

concentrations in Male Friends versus Controls and among Male Friends only, to compare periparturition glucocorticoids in Male-Responsible versus Female-Responsible friends. To analyze temporal variation in glucocorticoid levels in Controls and Male Friends, the 32-week period of lactation was divided into four 8-week intervals. The Kruskal-Wallis test was used to compare data sets for each interval. The Mann-Whitney U Test was used to compare glucocorticoid levels in Male Friends versus Controls during the 32-week lactation phase. Spearman's Rank Correlation Test was used to analyze the association between periparturition glucocorticoid change and Hinde's Index. All statistics were performed with StatistiXL (version 1.7) statistical software for Microsoft Windows.

RESULTS

Male Glucocorticoid Concentrations Before and After Parturition

We rejected the prediction that periparturition glucocorticoid levels will decrease in males in friendships. Glucocorticoid level in Male Friends and Controls were not different in the 2-week period before parturition (Mann-Whitney U test: $U=36$, $n_1=12$, $n_2=5$, $p=0.57$). However, Male Friend glucocorticoid concentration increased significantly from Before (178.99 ± 13.84) to After (213.02 ± 17.15) parturition (Wilcoxon Paired-Sample Test, $T=13$, $n=12$, $p<0.05$). There was no change in Controls Before (188.26 ± 11.94) to After (186.19 ± 6.15) (Wilcoxon Paired-Sample Test, $T=7$, $n=5$, $p=1.00$). (Figure 1)

We also rejected the prediction that glucocorticoid concentration would be negatively associated with a male's relative investment in the friendship. Calculation of

Hinde's Index for each friendship indicated that 4 females and 15 males were responsible for proximity maintenance in the 20 friendships used for these analyses (Table 1). Males involved in both Male-Responsible and Female-Responsible friends experienced an increase rather than decrease in periparturition glucocorticoid concentration (Male-Responsible: Wilcoxon Paired-Sample Test, $T=39$, $n=15$, $p<0.05$; Female-Responsible: Wilcoxon Paired-Sample Test, $T=0$, $n=4$, $p=0.10$) (Figure 2). The average percent increase was greater among the Male-Responsible friends (28.8%) than the Female-Responsible friends (13.8%) (Figure 3). Although the periparturition increase in Female-Responsible friends (in contrast to a periparturition decrease in Male-Responsible friends) was predicted, the result was not significant and may be an artifact of the small sample size of Female-Responsible friends (4). In a comparison of Male-Responsible and Female-Responsible friendships, the glucocorticoid concentrations in males in the two categories were not different Before (Mann-Whitney U test: $U=34.00$, $n_1=4$, $n_2=15$, $p=0.74$) or After parturition (Mann-Whitney U test: $U=36.00$, $n_1=4$, $n_2=15$, $p=0.59$). Thus, males in both categories experienced similar glucocorticoid profiles in the two weeks prior to parturition and again in the two weeks after parturition.

There was no association between male investment and periparturition glucocorticoid change in Male-Responsible and Female-Responsible friendships ($r_s=0.00$, $DF=19$, $p=1.00$) and in Male-Responsible friends alone ($r_s=-0.05$, $DF=15$, $p=0.85$), (Figure 4).

Male Glucocorticoid Concentrations During First 32 Weeks of Lactation

We predicted that throughout lactation, glucocorticoid levels would be lower in males with female friends than in controls during the first 32 weeks of lactation. Results were not consistent with this prediction; 32-week mean (average of four interval means) glucocorticoid levels were significantly higher in Male Friends (182.53 ± 5.21) than Controls (171.98 ± 5.47) (Mann-Whitney U Test: $U=12$, $n_1=4$, $n_2=4$, $p<0.05$) (Figure 5). Male Friends glucocorticoid concentrations were significantly higher in Intervals 1 (Mann-Whitney U Test: $U=43$, $n_1=15$, $n_2=5$, $p<0.05$) and Interval 4 (Mann-Whitney U Test: $U=42$, $n_1=12$, $n_2=5$, $p<0.05$) but not in Intervals 2 or 3 (Figure 6). We found a significant difference among four intervals during the first 32 weeks of lactation in Male Friends (Kruskal-Wallis Test: $F=0.84$, $DF_1=3$, $DF_2=52$, $p<0.05$) but not in Controls (Kruskal-Wallis Test: $F=0.82$, $DF_1=3$, $DF_2=15$, $p=0.51$). In Male Friends there was a significant decrease in glucocorticoid concentration from Interval 3 to Interval 4 (Mann-Whitney U test: $U=114$, $n_1=14$, $n_2=13$, $p<0.05$) but not for any other two adjacent periods.

Finally, having predicted a periparturition decrease in glucocorticoid concentrations in Male Friends, we also predicted that their post-parturition levels would then increase in the late lactation phase. However, as reported above, periparturition glucocorticoid concentrations significantly increased in male friends from the 2-week Before period to the 2-week After period. Male Friends' concentrations in the After period (213.02 ± 17.14) were significantly higher than Controls' (186.19 ± 6.15) (Mann-Whitney U test: $U=37$, $n_1=12$, $n_2=5$, $p<0.05$). Subsequently, Male Friends experienced a significant decrease in glucocorticoid concentration over 32 weeks of lactation from the

post-parturition After period (213.02 ± 17.14) to Interval 4 (160.61 ± 10.70) (Mann-Whitney U Test: $U=110$, $n_1=12$, $n_2=12$, $p<0.05$) (Figure 7). There was not a change in glucocorticoid concentrations from After (186.19 ± 6.15) to Interval 4 (171.94 ± 12.12) in Controls (Mann-Whitney U Test: $U=15$, $n_1=5$, $n_2=5$, $p=0.69$). Friends' glucocorticoids levels fell significantly below Controls' at Period 4 (Mann-Whitney U test: $U=42$, $n_1=12$, $n_2=5$, $p<0.05$).

DISCUSSION

The results of our tests of the parental care hypothesis for friendship in male olive baboons based on a “paternal glucocorticoid profile” found in male pair-bonded callitrichids and humans (Reburn and Wynne-Edwards, 1999; Storey *et al.*, 2000; Nunes *et al.*, 2001, 2002; Berg and Wynne-Edwards, 2001) were not consistent with four predictions. First, we predicted that periparturition glucocorticoid levels will decrease in males with female friends. Instead, concentrations increased in association with the birth of females' infants and the beginning of lactation. This pattern contrasts with findings in pair-bonded primates. For example, in human fathers, Storey *et al.* (2000) and Berg and Wynne-Edwards (2001) found a significant periparturition decrease in cortisol concentrations.

Rather than prematurely reject the parental care hypothesis for male baboon friendship, our result leads us to reevaluate the glucocorticoid profile model used to generate predictions. Baboon friends are clearly not “bonded” in the same sense as reproductive pairs of co-parenting callitrichids and humans. Friendships are most conspicuous during lactation and do not serve an immediate reproductive benefit (Smuts,

1985). They typically wane when infants become independent and when the females resume cycling. Friendships, like all relationships, are embedded within a larger, more complex social network specific to each species. We expect social relationships to be behaviorally malleable and adaptable in response to varied ecology and social environments. Adaptive behavioral mediation by a complex milieu of circulating hormones should be just as flexible in response to varied ecology and social environments that individual species face (Bercovitch and Ziegler, 2002; Mendoza *et al.*, 2002). Even among males in pair bonded primates, the functional role of glucocorticoids during pregnancy, parturition and lactation is not clearly understood. Elevated glucocorticoids may facilitate attachment between co-parents or between fathers and infants (Carter and Altemus, 1997; Carter, 1998; Wynne-Edwards and Reburn, 2000; Ziegler *et al.*, 2004; da Silva Mota *et al.*, 2006) or during gestation, may prime fathers to bond with future offspring (Storey *et al.*, 2000; Wynne-Edwards and Reburn, 2000; Ziegler *et al.*, 2004). Likewise, in baboon friendships, a periparturition glucocorticoid elevation may facilitate a male's attachment to his friend's infant, or enhance his bond with the female. Alternatively, and more germane to the outcome of our first test, stressors related to a female friend's parturition may stimulate an adaptive glucocorticoid increase in the male, allowing him to maintain a heightened state of arousal at a time when his friend and her infant are most vulnerable to ecological and social threats. This contingency may be particularly relevant in matrilineal species like baboons, where lactating females are regularly harassed by adult males and only nominally defended by female relatives (Smuts, 1985).

Second, we predicted that glucocorticoid concentration will be negatively associated with a male's relative investment in the friendship in the form of proximity maintenance. We found no correlation however, between a male's investment in the friendship and his periparturition glucocorticoid percentage change. This aspect of our study warrants further investigation with a more sensitive gauge of "investment" in friendships. Moreover, measure of relationship investment (relative proximity maintenance) may not be functionally equivalent to the measure used in studies of pair bonded callitrichids (relative duration of infant carrying in "high investor" versus "low investor" fathers) (*sensu* Nunes *et al.*, 2001). Future analysis might incorporate relative rates of allogrooming between friends or affiliative interactions between male friends and infants.

Third, we predicted that throughout lactation, glucocorticoid levels would be lower in males with female friends than in controls and finally, that glucocorticoid levels in male friends will increase in the late lactation phase, possibly signaling a shift from parenting strategy to mating strategy. As with our previous predictions, these were based on the glucocorticoid profile typically displayed in male pair bonded callitrichids and humans: lowered post-parturition glucocorticoid concentrations are maintained early during lactation, eventually rising and returning to preparturition levels late in lactation (Storey *et al.*, 2000; Nunes *et al.*, 2001, 2002) In contrast, baboon male friends experienced higher 32-week mean glucocorticoid concentrations than did controls. The most robust difference was in the initial 2-weeks post-parturition period, but concentrations remained significantly higher than controls' for the first eight weeks. Concentrations in friends declined after the first eight weeks post-parturition to levels

similar to controls', until finally at weeks 25-32, they fell significantly below controls'. A critical factor to interpreting these results is that basal glucocorticoid levels in male friends remained significantly elevated above controls' for an extended period of time. This physiological state has considerable individual fitness and reproductive costs (Selye, 1976; Sapolsky 2002). We suggest that chronic basal elevation of glucocorticoid levels is being sustained only with equal or greater benefits to male friends' reproductive fitness. These may come about as the result of hormonal synergistic affects as posited by other researchers (Reburn and Wynne-Edwards, 2000; Berg and Wynne-Edwards, 2001, Ziegler *et al.*, 2003; Huck *et al.*, 2005)

Glucocorticoid mediation of testosterone (and its behavior correlates) is one candidate to investigate further. Our research indicates an inverse relationship between male friend glucocorticoid and testosterone concentrations both at periparturition and across 32 weeks of lactation (see Chapter 1). While these data can not specify the temporal order of hormone effect in the subjects, there is evidence in olive baboons for glucocorticoid suppression of testosterone but not for the converse (Sapolsky, 1983a, 1985). Suppressed testosterone has been widely implicated in the onset, facilitation, amplification and maintenance of paternal behavior in primates, presumably leading to enhanced reproductive fitness in fathers (in *Saguinus oedipus*, Ziegler *et al.*, 1996; in *Callithrix kuhlii*, Nunes *et al.*, 2000, 2001; in human males Fleming *et al.*, 1997a, 1997b; Storey *et al.*, 2000; Berg and Wynn-Edwards, 2001; Wynne-Edwards, 2001; Gray *et al.* 2002, 2006, 2007). We thus believe that elevated glucocorticoids in male baboons during the lactation phase of their female friends functions to decrease testosterone and thereby

adjust male behavioral strategies from male-male competition and sexual consortships to friendship focused on lactating females and their infants.

We propose two adjustments regarding the glucocorticoid profile model for testing the parental care hypothesis for friendships. While both infant protection and interactive forms of care-giving such as carrying or provisioning are forms of male parental-effort (*sensu* Hamilton, 1984), they are not functionally equivalent and may be associated with very different hormonal profiles. We might look to non-primate taxa that form multi-male groups for a glucocorticoid model of true male parental care that manifests as protection and defense rather than holding, carrying or provisioning, characteristic of pair-bonded primates. We also propose that the model should take into account the precise timing of parenting stressors most relevant to the particular species and its social ecology. Finally, we should consider that instead of directly facilitating paternal behavior in male baboon friends, the more important effect of periparturition and lactation phase glucocorticoids may be suppression of testosterone and indirect mediation of parenting effort.

TABLES AND FIGURES

Table 1. Mean glucocorticoid concentrations (ng/g) of males before and after the birth of their friends' infants, periparturition change, percentage change, and Hinde's Index.

Male x Female Friendship	Before	After	Periparturition Change	Percent Change	Hinde's Index
TDxXN	202.61	181.25	21.36	0.11	-2.60
TDxTH	232.91	106.69	126.23	0.54	-45.20
TDxAT	181.44	245.84	64.40‡	0.35‡	26.80*
CHxSL	155.15	227.96	72.81‡	0.47‡	-24.70
GGxSL	177.83	262.32	84.49‡	0.48‡	-37.50
LZxKT	128.84	148.09	19.25‡	0.15‡	-43.10
SExTT	212.62	227.35	14.73‡	0.07‡	-21.50
ARxZA	273.46	332.31	58.85‡	0.22‡	NA
GLxVD	213.10	168.80	44.30	0.21	-12.80
GLxLT	132.82	184.15	51.34‡	0.39‡	-4.80
BGxVD	230.97	236.31	5.34‡	0.02‡	13.10*
LExNM	156.76	183.24	26.48‡	0.17‡	14.70*
LExTN	170.00	74.21	95.79	0.56	-7.00
LExGW	144.30	153.95	9.65‡	0.07‡	-11.10
BLxNM	152.44	216.89	64.44‡	0.42‡	-9.10
BLxTN	102.89	330.89	228.00‡	2.22‡	-6.90
IRxTN	73.00	169.55	96.56‡	1.32‡	-8.90
IRxNM	118.88	119.40	0.51‡	0.00	1.60*
IRxGW	129.08	139.43	10.35‡	0.08‡	-16.00
SXxVD	198.74	213.73	14.99‡	0.08‡	-21.20

‡ Increase

* Females more responsible than males for maintaining proximity in friendships

NA—Insufficient approach/withdraw data to calculate Hinde's Index

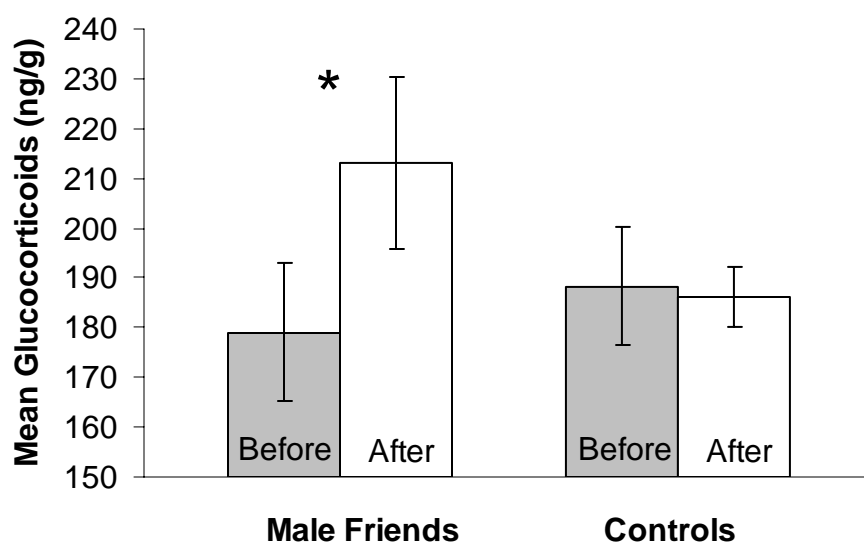


Figure 1. Mean glucocorticoid concentrations (ng/g mean \pm SEM) before and after the birth of infants: in Male Friends and in Controls

*** Significant difference in Before/After concentrations**

Before = 2 weeks preparturition

After = 2 weeks post-parturition

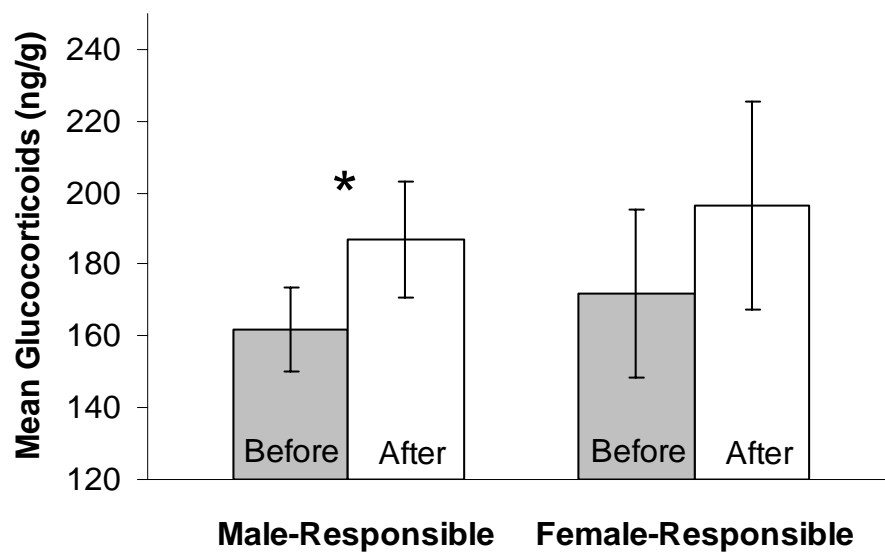


Figure 2. Mean glucocorticoid concentrations (ng/g mean \pm SEM) before and after the birth of infants: in Male-Responsible Friends and in Female-Responsible Friends

*** Significant difference in Before/After concentrations**

Before = 2 weeks preparturition

After = 2 weeks post-parturition

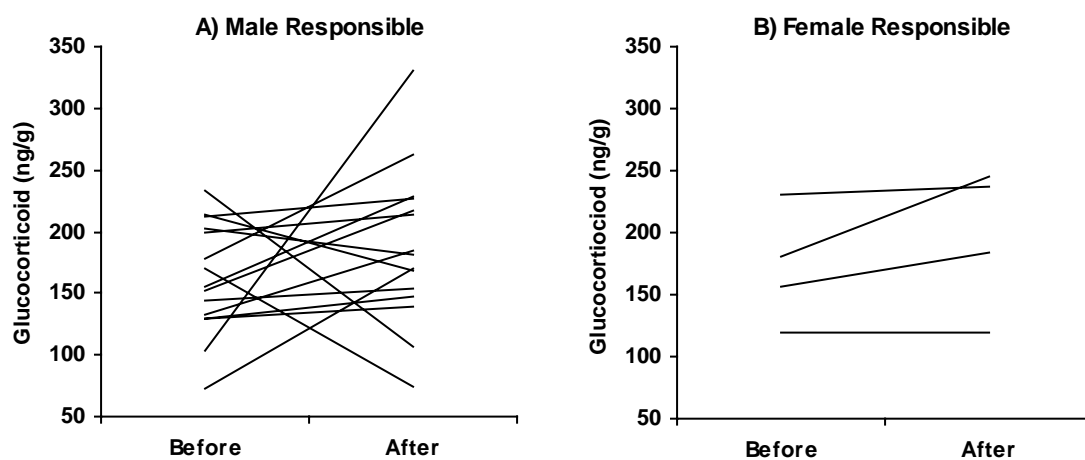


Figure 3. Mean glucocorticoid concentrations (ng/g) Before and After parturition in A) Male-Responsible Friends (n=15); B) Female-Responsible Friends (n=4).
 Before = 2 weeks preparturition
 After = 2 weeks post-parturition

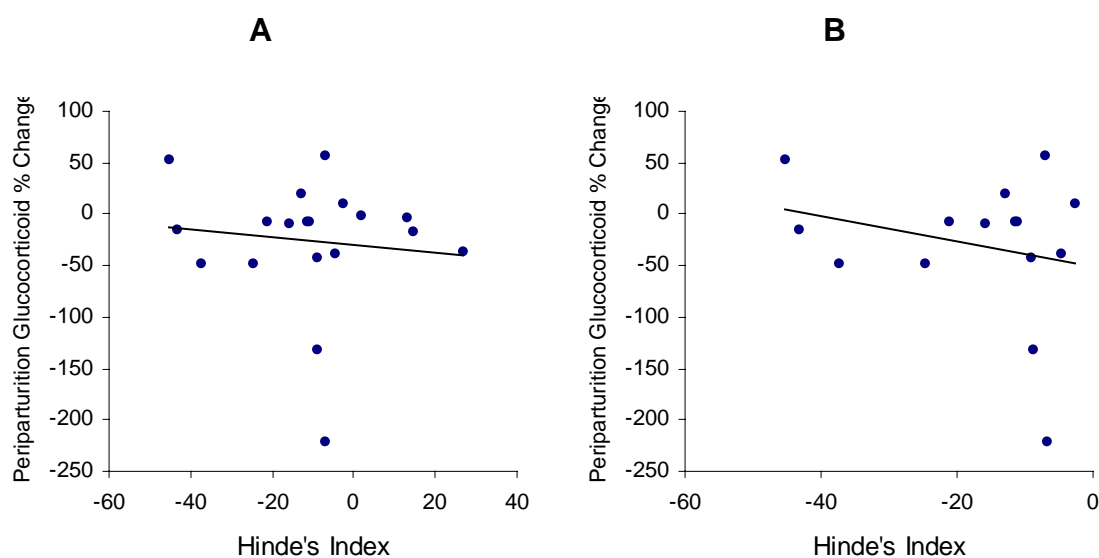


Figure 4. Association between Hinde's Index and periparturition glucocorticoid percent change in Male Friends. A) Male-Responsible and Female-Responsible Friends; B) Male-Responsible Friends only.

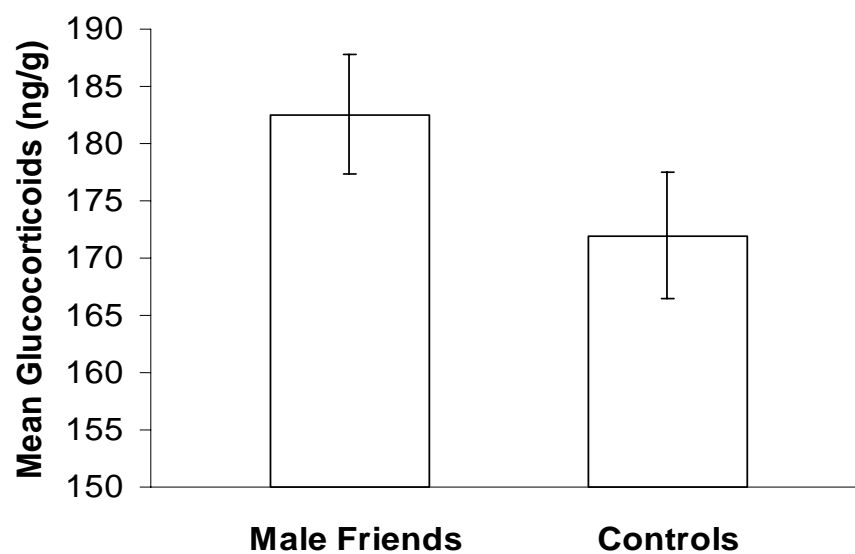


Figure 5. Difference in mean glucocorticoid concentrations (mean of Interval 1-4 means; ng/g \pm SEM) in Male Friends and in Controls during the first 32 weeks of lactation (Mann-Whitney U Test: $U=12$, $n_1=4$, $n_2=4$, $p<0.05$).

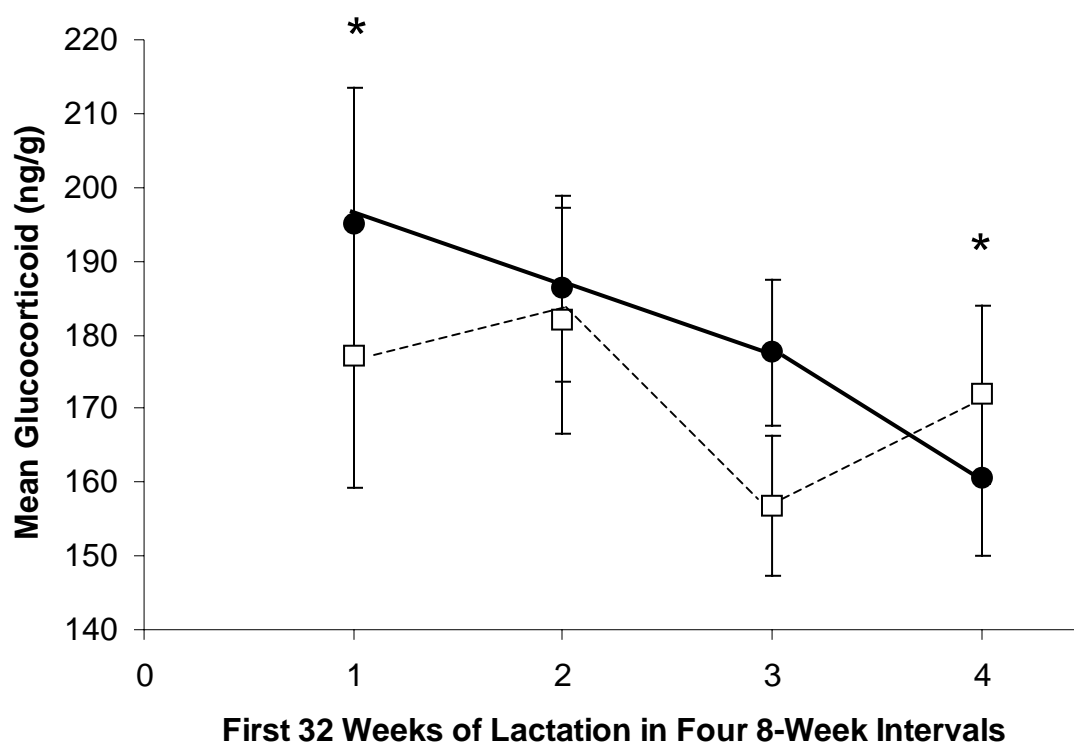


Figure 6. Glucocorticoid concentrations (ng/g mean \pm SEM) in Male Friends (solid circles) and in Controls (open squares) during first 32 weeks of lactation.

* Significant difference between Male Friend/Control concentrations

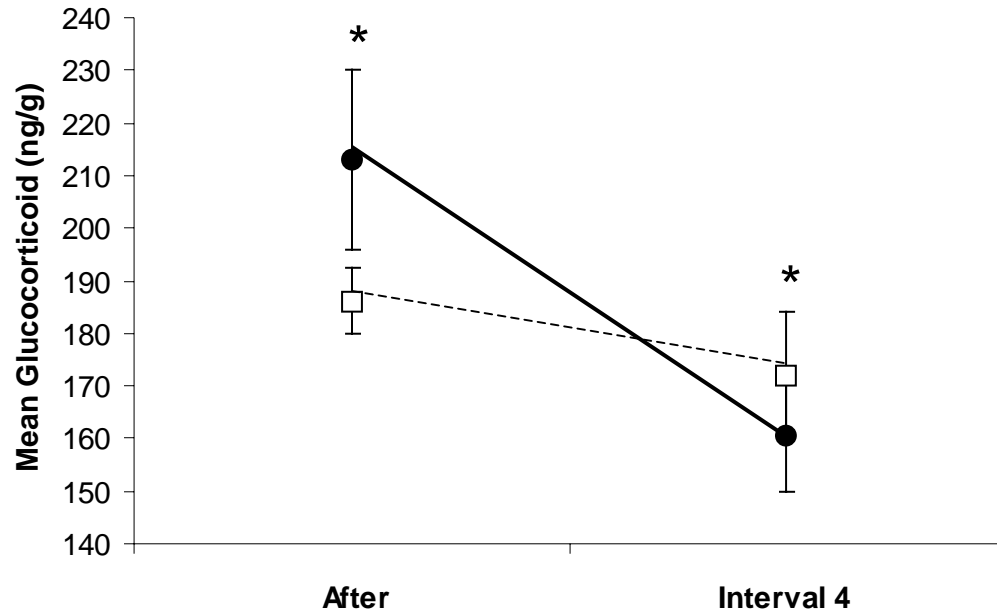


Figure 7. Glucocorticoid concentration (ng/g mean \pm SEM) change from After (2 weeks post-parturition) to Interval 4 (Week 24-32) in Male Friends (solid circles) (Mann-Whitney U Test: $U=110$, $n_1=12$, $n_2=12$, $p<0.05$) and in Controls (open squares) (Mann-Whitney U Test: $U=15$, $n_1=5$, $n_2=5$, $p=0.69$).

* Significant difference between Male Friend/Control concentrations

CHAPTER 2 – REFERENCES CITED

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CHAPTER THREE

DO ADULT MALES PROTECT LACTATING FEMALES FROM CONSPECIFIC HARASSMENT? THE ASSOCIATION BETWEEN FEMALE GLUCOCORTICOID CONCENTRATIONS AND FRIENDSHIP IN OLIVE BABOONS (*Papio hamadryas anubis*)

INTRODUCTION

The term “friendship” was first applied to olive baboons (*Papio hamadryas anubis*) by Strum (1974) to describe non-sexual relationships between certain adult males and lactating females. Friendships, characterized by high rates of affiliative proximity maintenance and grooming, are highly conspicuous and widely recognized in wild populations of baboons (Ransom and Ransom, 1971; Smuts, 1982, 1983, 1985; Palombit, 2003a). Although there are subtle differences in patterns, these associations are also observed in yellow baboons (*P. h. cynocephalus*) and chacma baboons (*P. h. griseipes*). The relationships typically commence at parturition and are strongest during the female’s lactation phase (Palombit *et al.*, 1997). Although a male friend may be of any rank in the dominance hierarchy, studies of chacma baboons indicate that females may compete for higher-ranking friends (Palombit *et al.*, 2001). Since males emigrate at adolescence while females remain in the natal group, males are typically unrelated to their female friends (Strum, 1985; Palombit, 2003a).

Smuts (1985) outlined several hypotheses for the adaptive value of friendships to female baboons. One important reproductive benefit may be the facilitation of a long-term male-support association that forms between the male friend and infant during lactation (Ransom and Ransom, 1971; Seyfarth, 1978; Packer, 1980; Stein, 1984; Smuts, 1985; Collins, 1986; Strum, 1987; Smuts and Gubernick, 1992; Buchan *et al.*, 2003).

Nicolson, (1982) showed that as an infant becomes increasingly independent from its mother, it tends to restrict associations with adult males to its mother's friend even more so than she does. Whether or not these associations confer protection, they result in greater tolerance for close proximity and co-feeding between infants and their mothers' friends, as well as affiliative behavior such as holding, carrying and grooming (Altmann & Altmann, 1970; Packer, 1980; Nicolson, 1982). The trend continues as infants develop. As juveniles, they maintain high rates of association with male friends even as they become independent from their mothers. These relationships persist through at least the first four years of the juvenile's life (Johnson, 1984).

More directly, females may derive a reproductive benefit when male friends protect infants from either non-lethal harassment (Male Harassment hypothesis) or sexually selected infanticide from other adult males (Infanticide hypothesis). Male infanticide is a considerable cause of infant mortality in chacma baboon groups (Cheney *et al.*, 2004), where forming friendships may be a critical protective counterstrategy for females (van Schaik, 1996; Palombit *et al.*, 1997, 2001, 2003b; Weingrill, 2000; Beehner *et al.*, 2006). Playback experiments have helped to clarify male friend reaction patterns (Palombit *et al.*, 1997). These males responded more strongly to screams of female friends than to control female screams, *e.g.*, visual scanning or moving in the direction of the speaker. More tellingly, they responded more to the combination of female friend scream/infanticidal male threat vocalization than to female friend scream/non-infanticidal male or female scream/alpha-female threat vocalizations. While male infanticide does occur in olive baboons, it is far less frequent than in chacma baboons and may be a less critical reason for females to form friendships (Palombit, 2003b; Henzi and Barrett,

2003). Rather, female olive baboons may develop friendships with males for protection against general aggression and non-lethal harassment (directed to either themselves or their infants) from other adult males (Altmann, 1980; Wasser, 1983; Rhine *et al.*, 1988; Wasser and Starling, 1988). Each adult male, upon immigration into a new group, is typically able to dominate each female. Overt aggression directed towards females is common (DeVore, 1965). Smuts (1985) found that females are victims of male aggression about five times per week, and one-fourth of attacks involve potentially serious injuries such as bloody gashes, cuts and slow-healing wounds to the legs, arms and shoulders. Almost all male defenders are male friends. In the majority of these circumstances, males actively and successfully defend their friends by chasing, threatening or attacking the aggressor.

Protection against aggression and harassment from higher-ranking females (Female Harassment hypothesis) may also be an important function of olive baboon friendship for lactating females. Although female aggressors rarely do serious harm to either lactating females or their infants, females may fall victim to aggression from other, higher-ranking females even more frequently than from males (Altmann, 1980; Smuts, 1985). Periods of lactation in particular can be precarious for both mothers and infants. Lactating females and their new infants become highly attractive to other group members, especially adult females. Their curiosity and heightened attentiveness results in increased frequency of approaches and attempts to touch, handle, pull or even kidnap infants (Strum, 1974; Altmann, 1980; Smuts, 1985). Occasionally, rough handling or kidnapping by adult females can be fatal to infants (Strum, 1974; Collins *et al.*, 1984; Shopland and Altmann, 1987; Brain, 1992; Kleindorfer and Wasser, 2004). Compared to

protection from adult males involving physical aggression, protection from ongoing harassment from other females may be much more subtle and discreet; the mere presence of adult male friends is oftentimes sufficient to inhibit stressful interactions with other females (Strum, 1985). As harassment episodes by dominant females accumulate, the fitness and reproductive benefits of friendship to low-ranking female victims may best be measured over the course of her reproductive life (Stein, 1981).

Hormones provide an important alternative to strictly behavioral observations to test hypotheses regarding the adaptive fitness of social relationships such as friendship (Levine *et al.*, 1989; Bercovitch and Ziegler, 1990, 2002; Whitten *et al.*, 1998). For example, elevated levels of glucocorticoids (primarily cortisol in primates) are an indicator of stress and can be evaluated in relation to harassment by group members (Sapolsky, 1982, 1990, 1992; Weingrill *et al.*, 2004; Beehner *et al.*, 2005; Bergman *et al.*, 2005). The term *stress* denotes any disruptions or challenges to homeostasis, which may include adverse social interactions. The *stress-response*, which includes temporarily increasing glucocorticoid production, comprises the physiological processes following stress that mobilize the body to action and then safely return its functions to homeostasis (Selye, 1976, Sapolsky, 1993a). Although generally serving an adaptive function, glucocorticoids, when chronically elevated during prolonged stress, have a number of pathological effects including anovulation and amenorrhea in female mammals (Munck *et al.*, 1984; Sapolsky, 2002; Abbott *et al.*, 2003). Collectively, the maladaptive effects of long-term elevated glucocorticoid concentrations may have severe consequences on both individual and reproductive fitness (Mostl and Palm, 2002; Sapolsky, 2002). In chacma baboons, the strongest correlate of glucocorticoid elevation in lactating females is the

occurrence of infanticide in the group but even recent immigration of new (potentially infanticidal) males results in marked increases (Beehner *et al.*, 2005; Engh *et al.*, 2006). Lactating females with a male friend, however, experience less robust elevations than those without a friend (Beehner *et al.*, 2005; Engh *et al.*, 2006). Friendships in olive baboons, as in chacma baboons, may help mitigate stress.

We had two main objectives for this study. First, we tested the hypothesis that olive baboon male friends buffer females from harassment-induced stress as indicated by glucocorticoid concentration, predicting that lactating females with friends would have lower levels than those without friends. We were unable to test this hypothesis in this form however, because, consistent with findings by Smuts (1985), all lactating females in our study had at least one friend. Instead, we focused on testing two predictions based on individual and temporal variation in the nature and number of friendships and hormonal profiles of females.

Prediction 1: There is considerable variation in relative investment of each partner in maintaining the friendship (Smuts, 1985; Palombit *et al.*, 1997). The adaptive significance of this variation remains unclear, but evidence that lactating female chacma baboons compete for social access to male friends suggests that the nature of a friendship influences a female's accrual of the benefits offered by these associations (Palombit *et al.*, 2001). If so, then measures of friendship quality, partially the relative investment of the female, should co-vary with female glucocorticoid profile in a manner similar to that reported for male baboons (Sapolsky *et al.*, 1997). If friendship serves to mitigate the negative effects of social harassment for females, greater male investment should result in greater stress mitigation for females. Thus, we predicted that basal glucocorticoid

levels in lactating females will be positively correlated with the relative female responsibility for maintaining friendship, *i.e.*, relatively more investment by a female in a friendship will correlate with higher female glucocorticoid level.

Prediction 2: Occasionally, a female's friendship with a particular male undergoes a temporary waning. This might be for a number of reasons but is particularly noticeable when the male has friendships with other lactating females. Under this circumstance, a lactating female experiences reduced proximity and social interaction with her male partner. If friendships serve to protect females from harassment, these periods may thus expose females to a greater risk of aggression, and therefore be more stressful for females. We predicted that when established friendships (according to C-Score during the first 32-weeks of lactation—see Methods below) are weakened for a period of time, female glucocorticoid concentrations will be higher than periods before or after, when male friends are present. Like males, females may have simultaneous multiple friendships. As Smuts (1985) noted, a lactating female may share a strong “primary” relationship with a particular male, and less cohesive (but nonetheless distinctive) relationships with one or two other males. Multiple simultaneous friends are common among female olive baboons (Smuts, 1985; Palombit, 2003a). It is important to take account of this pattern when testing predictions. Consequently, the above prediction was tested with reference to: (1) a lactating female's “cumulative” or mean hormone concentration in relation to her friendship status with multiple friends, and (2) a lactating female's hormone concentration in relation to her “primary” friendship.

Second, we investigated the Male Harassment versus Female Harassment explanations for the benefit of friendship to lactating females. These alternative

hypotheses make contrasting predictions about the adrenocortical profiles of lactating females. From the Male Harassment hypothesis (but not the Female Harassment hypothesis) we predicted that basal glucocorticoid level in lactating females will be negatively correlated with the rank of their male friends. The effectiveness of a male protector will vary more when the harasser of a lactating female is another male than when it is a female. This is because all adult males are typically dominant to all adult females. Consequently, even the lowest ranking male is potentially useful to a lactating female as a shield against harassment from a high-ranking female. Thus, if friendships function to buffer females from harassment from higher-ranking females, we predicted that glucocorticoid level and female dominance rank will be inversely correlated in lactating females. The same cannot be said, however, if harassment originates from adult males, since some of these may be dominant to the male friend, and since females of all ranks are potential targets of harassment by any adult male

METHODS

Study Site and Subjects

Research was conducted at Segera Ranch and adjacent areas located on the Laikipia plateau (36°50'E, 0°15'N), Central, Kenya. The site lies at an altitude of 1,700m with a mean annual temperature range of 10-22 degrees Celsius (Palombit, unpublished data). Annual rainfall averages approximately 500mm (Palombit, unpublished data). The habitat is dominated by grasslands and scattered *Acacia drepanolobium* scrub. The baboons in this area most commonly converge and overnight in stands of *Acacia xanthophloea* that lie along rivers and other waterways.

We conducted quantitative behavior sampling and fecal sampling for hormone analysis on two habituated groups (KAT and TDM), studied since 2000 by Palombit and colleagues. Group composition changed only minimally during the study. KAT comprised 37-42 individuals (9-11 adult males, 18-20 adult females, juveniles and infants) and TDM comprised 89-95 individuals (19-21 adult males, 26-30 adult females, juveniles and infants). Dominance interactions had been scored by direction of supplants and aggressive interactions for KAT for the previous five years and for TDM for the previous four years.

Both groups remained demographically stable throughout the study period. One adult male transferred from TDM to KAT for several weeks before returning to TDM but no adult or subadult males permanently transferred out of either group. One apparently elderly adult male immigrated into the TDM late in the study, but remained minimally habituated. He did not form any friendships with females and remained peripheral to most group activities. Initial subjects included the 26 adult males at the beginning of the study and the 22 females who were lactating during the study. One KAT primiparous female was eliminated at three weeks post-parturition when her infant disappeared and she quickly resumed cycling.

Behavioral Observations and Analysis

Research took place from September 2004 to August 2005. Data were collected from 7:00h to 14:00h for a total of approximately 900 contact hours. We recorded 1,966 focal samples and *ad libitum* observations on consortships, female reproductive states, diet, dominance, and demography (Altmann, 1974). A focal behavior sample consisted of

a 10-minute observation period during which 57 predetermined relevant behaviors were recorded continuously, and nearest neighbor spatial relations at 2-minute intervals. Nearest neighbor data included all individuals and their distances from the focal subject within 6m of the subject. All behavioral data were collected on a hand-held Psion Workabout MX Basic data recorder (Raco Industries, Cincinnati, Ohio) and downloaded into a computer at the end of the day.

Friendships were determined from all possible male-female dyads by calculating composite proximity score (or “C-score”) a standard method for identifying affiliates in baboons (Smuts, 1985; Bentley-Condit and Smith, 1999; Palombit *et al.*, 1997, 2001; Silk, 2002). To determine C-Score, we collected proximity data in two measures concurrently with focal subject observations. First, the time in *close proximity* was the proportion that two individuals spent within 2m of one another, beginning when one individual approached the other within 2m and ending when either individual withdrew further than 2m away. Second, the proportion of time the subjects spent within 2-6m of others was calculated from instantaneous sampling of nearest neighbors. For any female-male dyad, the percentage of time spent within each of the two distance categories was multiplied by a constant (the reciprocal of the mid-point of the inner and outer limits of that category). Weighted proximity times were summed to arrive at the composite score (Palombit *et al.*, 1997; modified from Smuts, 1985):

$$C = 1(\%Time_{0-2m}) + 0.25(\%Time_{2-6m})$$

Since the average length of the lactation phase in female subjects was 32.5 weeks (s=8.1, n=16), C-scores were calculated based on the time period from parturition to 32-weeks post-parturition (or until cycling actually resumed). A discontinuous distribution

of C-scores indicated a friendship with a male (see Palombit *et al.*, 1997). If more than one friendship score was clearly separated from the scores for other males, the male with the highest C-score was designated the “primary friend” and additional friends considered “secondary.” We identified a total of 30 friendships, which involved 17 males and the 16 lactating females.

In order to assess relative responsibility for maintaining proximity in the friendship, an important measure of each partners’ investment or contribution to the relationship, we calculated “Hinde’s Index” (Hinde and Atkinson, 1970). The difference between the percentage of approaches within 2m (A) by the female and the percentage of withdrawals (W) by the female was calculated according to the following equation:

$$A_F/(A_F+A_M)-W_F/(W_F+W_M)$$

A positive Hinde’s Index score in the range 0 to 100 indicated that the female was more responsible (Female-Responsible) for close proximity maintenance while a negative score (-100 to 0) indicated that the male was more responsible (Male-Responsible).

Although the quality of friendships may change over time with each partner’s relative responsibility for maintaining friendship proximity potentially shifting, we set the timeframe for Hinde’s Index score calculations from parturition to 32 weeks post-parturition. This corresponded to the time period used to calculate C-Scores and maximized the number of friendships analyzed while still meeting the minimum data requirements for Hinde’s Index calculations.

Separate dominance ranks for males and for females were calculated according to the direction of decided dyadic interactions including supplants, bare-teeth displays, and aggressive chases (Hall, 1962). A supplant occurred when one individual withdrew

within 5 seconds of another individual's approach within 2m (Palombit *et al.*, 2001). Dyadic interactions were plotted on a dominance matrix to determine the dominance hierarchy (Martin and Bateson, 1993). Following Bergman *et al.*, (2005), individuals were divided into either "high-rank" (top half of all ranks) or "low-rank" (bottom half of all ranks) since linear placement of some closely ranked individuals, particularly in the male hierarchy, was uncertain. As predicted from previous studies of long-term stability in female dominance hierarchies, female rank relationships during the study period were similar to those noted in previous years (Palombit, unpublished data). We observed no evidence of an individual male or female shifting from one rank category to the other during the study.

Hormone Sampling and Analysis

We followed the fecal sampling method used by Beehner and Whitten (2004). Individuals were targeted randomly (*sensu* Bergman *et al.*, 2006) for fecal collection with no individual repeated in the target cycle until a sample had been collected from all other subjects. However, samples were also collected opportunistically from an individual as they became available during target follows, and if a sample was needed from a particular subject in the appropriate time frame. This regime generated an even sample distribution across subjects and minimum collection of one sample per individual approximately every eight days (Whitten *et al.*, 1998, Beehner and Whitten, 2004; Bergman *et al.*, 2005). We collected a total of 355 samples from the 22 females. All sampling was conducted from 6:00h-12:00h to control for daily fecal hormone excretion cycles and to reduce resulting hormone concentration variations. (Whitten *et al.*, 1998).

Feces were prepared for collection by first removing seeds, rocks and similar solid material, and then homogenizing the mass with a wooden spatula to eliminate any potential areas of hormone concentration. Approximately 0.5g of the sample was mixed into 10ml of methanol:acetone (4:1) solution. Within 10 hours after collection, 4ml of the homogenate was separated from any concentrated solid fecal material and filtered using a 0.2- μ m polytetrafluoroethylene (PTFE) syringe filter. This solution was diluted 1:2 with filtered water, loaded onto solid-phase extraction cartridges (Sep-Pak Plus C18 cartridge, Waters Associates, Milford, Massachusetts, U.S.A.), primed according to the manufacturer's instructions, and washed with a 0.10% sodium azide preservative solution. Cartridges were initially stored with silica gel beds to absorb moisture in individual Whirl-Pak bags and kept in a standard freezer (-10° C).

Once all field-collection was complete, samples were transported to the Laboratory of Reproductive Ecology and Environmental Toxicology at Emory University and stored at subzero temperature (-80° C) prior to assay. In final preparation for assay, cartridges were brought to room temperature and hormones were eluted with 3ml of methanol. Duplicate aliquots of samples to be analyzed were evaporated under nitrogen and reconstituted in phosphosaline gelatin working buffer. Samples were radioimmunoassayed (RIA) for glucocorticoid metabolites using a modification of a corticosterone I-125 RIA kit (MP Biomedicals, Costa Mesa, CA). This assay kit had been previously validated for use with baboon fecal glucocorticoids in this laboratory. Unless otherwise noted, glucocorticoid concentration is expressed as either individual duplicate mean concentration or category mean concentration in ng/g fecal sample dry weight. Interassay coefficients of variation were $6.23 \pm 0.12\%$ (high control, n=27), $10.47 \pm 0.04\%$

(low control, n=27), Intra-assay coefficient of variation was $8.28 \pm 0.20\%$ (fecal extract pool, n=6).

Analysis Methods

Two subjects were eliminated from these analyses because their glucocorticoid concentrations were extreme outliers. The first was a high-ranking lactating female (see Table 1 - NM) that began experiencing chronic genital bleeding shortly after parturition. This coincided with elevated glucocorticoid levels approximately twice the mean value experienced by other subjects. This condition was also seen in three other females who were not selected as subjects. The second subject eliminated was a low-ranking apparently elderly female (Table 1 - TT) that also experienced extremely high glucocorticoid levels post-parturition. *Ad libitum* observations indicate that she appeared frail and in general poor health throughout most of the study. Of the 30 friendships observed, there were sufficient combined hormonal and behavioral data to include 26 friendships in this component of the analysis. Nine females had either two or three friends simultaneously.

All lactating females in our study formed readily distinguishable friendships during the 32-week post-lactation analysis period. Thus, we were not able to test directly whether females with friends experienced different glucocorticoid concentrations than females without friends. We divided the 32-week period into four 8-week intervals (Interval 1: week 1-8, Interval 2: week 9-16, Interval 3: week 17-24, Interval 4: week 25-32) (Table 1). These were the shortest intervals that allowed for C-score analysis that distinguished a female's friendships from other dyadic associations. Intervals in which no

adult male emerged as a friend, via C-score distributions, were designated as “Friend-Absent” periods. These intervals were compared to intervals when one or more friends were designated by C-score for that female (Table 2).

In one test of the Harassment hypothesis (Figure 3), there were combined behavioral and hormonal data in three 8-week lactation intervals to allow for glucocorticoid profile comparisons among females in three categories: “Friends Absent”, “Any Friend Present” (any friend designated by the 32-week C-score that was also designated a friend by the particular 8-week interval C-score), and “Only Primary Friend Present” (only the friend designated by the highest 32-week C-score was also designated a friend in the particular 8-week interval C-score). In the subsequent temporal analysis (Figure 4), within-individual comparisons were made between females in two categories: “Primary Friend Present” (a female’s primary friend, determined by 32-week C-score, was also a friend in the particular 8-week interval C-score), and “Primary Friend Absent” (a female’s primary friend, determined by 32-week C-score, was not designated a friend in the particular 8-week interval C-score). Glucocorticoid concentrations were compared first when individual females went from the “Friend Present” to the “Friend Absent” condition in any two consecutive intervals and second, when individual females went from the “Friend Absent” to the “Friend Present” condition in any two consecutive intervals.

Finally, glucocorticoid concentrations during the first eight weeks (Interval 1) and during the first 16 weeks (Intervals 1 and 2 combined) of lactation were analyzed to test the Male Harassment versus Female Harassment hypothesis since hormonal data beyond 16 weeks for some females was incomplete.

Statistical Analysis

Nonparametric tests were used for all analyses to address friendship sample sizes. All tests were two-tailed with α set at 0.05. Mann-Whitney U Tests were used to compare glucocorticoid concentrations in lactating females who were either in Male-Responsible or Female-Responsible friendships. This was followed by Spearman Rank Correlation analysis to test the association between female glucocorticoid concentrations and Hinde's Index scores. Kruskal-Wallis Tests were used to compare glucocorticoid concentrations in females in three categories across three post-lactation time periods. Wilcoxon Paired-Sample tests were used to compare female glucocorticoid concentration changes in consecutive intervals during lactation. Mann-Whitney U Tests were used to compare glucocorticoid concentrations in females with only low-ranking male friends with those with at least one high-ranking male friend and to compare glucocorticoid concentrations in females who were themselves low-ranking versus high-ranking. All statistics were performed with StatistiXL (version 1.7) statistical software for Microsoft Windows.

RESULTS

Do Male Friends Buffer Females from Harassment-induced Stress?

If friendships help buffer females from harassment, we predicted that basal glucocorticoid levels in lactating females will be positively correlated with the relative female responsibility for maintaining friendship. During the first eight weeks of lactation, females in Female-Responsible friendships (with their primary or only friend) maintained significantly higher glucocorticoid concentrations (191.37 ± 1.54 ng/g, $n=2$) than females in Male-Responsible friendships (with their primary or only friend), (141.57 ± 5.93 ng/g,

n=11), (Mann-Whitney U Test: $U=22$, $n_1=2$, $n_2=11$, $p<0.05$) (Figure 1). Through 16 weeks of lactation, females in Female-Responsible friendships continued to experience higher glucocorticoid concentrations (Female-Responsible, 203.63 ± 28.39 ng/g, $n=2$; Male-Responsible, 154.26 ± 6.31 ng/g; $n=11$; Mann-Whitney U Test: $U=20$, $n_1=2$, $n_2=11$, $p=0.10$). By 16 weeks post-lactation, however, the effect was not significant. In summary, at least in the first several months post-parturition, lactating females that invested more (or who's male partner invested less) in maintaining proximity to their friends experienced higher levels of glucocorticoids, an indicator of stress. These results were consistent with the first prediction

Correlation analysis, however, indicated no association through eight weeks of lactation between female glucocorticoid concentrations and relative investment in maintaining proximity in friendships either when females' primary friendships' Hinde's Index scores were considered ($n=13$, $r_s=0.32$, $DF=13$, $p=0.28$) or when any female's multiple friendships' Hinde's Index scores were averaged to arrive at a composite score ($n=13$, $r_s=0.42$, $DF=13$, $p=0.15$) (Figure 2). By 16 weeks post-lactation there was still no correlation in either treatment (primary friendship scores only: $n=13$, $r_s=-0.16$, $DF=13$, $p=0.60$; composite scores: $n=13$, $r_s=-0.13$, $DF=13$, $p=0.68$).

The results of our analyses of lactating females in three categories during lactation ("Friends Absent", "Any Friend Present", and "Only Primary Friend Present") were not consistent with the prediction that female glucocorticoid concentrations will be higher during periods when friendships temporarily wane. There were no differences among the three categories in any of the three intervals (Figure 3). In the subsequent within-individual analysis, however, which compared glucocorticoid concentration temporal

change in lactating females in two consecutive 8-week interval categories (“Primary Friend Present” and “Primary Friend Absent”), results were consistent with the prediction and supported the hypothesis that friendships buffer lactating females from stress (Figure 4). Females experienced a significant increase in glucocorticoid concentration when they went from a “Primary Friend Present” interval (155.75 ± 18.14 ng/g, $n=7$) to a “Primary Friend Absent” interval (236.75 ± 17.40 ng/g, $n=7$), (Wilcoxon Paired-Sample Test, $T=2$, $n=7$, $p<0.05$). Likewise they experienced a decrease (approaching significance) in glucocorticoid levels when they went from a “Primary Friend Absent” interval (222.38 ± 19.10 ng/g, $n=5$) to a “Primary Friend Present” interval (118.98 ± 8.73 ng/g) (Wilcoxon Paired-Sample Test, $T=0$, $n=5$, $p=0.06$).

Do Male Friends Buffer Females from Male Harassment or Female Harassment?

Results were consistent with the Male Harassment hypothesis that predicts that basal glucocorticoid level in lactating females will be negatively correlated with the rank of their male friends. In the first 16 weeks post-parturition, females that had only low-ranking male friends (208.71 ± 23.30 ng/g, $n=2$) had higher glucocorticoid concentrations than females that had a high-ranking male friend (156.4 ± 13.20 ; $n=12$) (Mann-Whitney U Test: $U=23$, $n_1=2$, $n_2=12$, $p<0.05$) (Figure 5). However the difference was not significant during the first 8 weeks (low-ranking male friends: 179.73 ± 10.09 ng/g, $n=2$; high-ranking male friends: 149.15 ± 7.67 ng/g, $n=12$; Mann-Whitney U Test: $U=21$, $n_1=2$, $n_2=12$, $p=0.13$).

The Female Harassment hypothesis prediction that lactating females’ glucocorticoid levels and their dominance ranks will be inversely correlated was rejected.

There was no association between glucocorticoid profile and female rank through the first 8 weeks (Mann-Whitney U Test: $U=24$, $n_1=6$, $n_2=8$, $p=1.00$) or first 16 weeks (Mann-Whitney U Test: $U=29$, $n_1=6$, $n_2=8$, $p=0.57$) post-parturition (Figure 6).

DISCUSSION

For lactating females, reduced level of harassment, from both males and females, is an important proposed outcome of a friendship with adult males (Smuts, 1985). Using Hinde's Index to test the association between a lactating female's investment in friendship and her stress levels, data indicate that having a male friend does help buffer females against stress. Friendships among the olive baboons in our study were more often maintained by males than by females. This contrasts notably with chacma baboons in which females are by far more responsible for proximity maintenance, presumably because the threat of male sexually selected infanticide in this population (Palombit *et al.*, 2001). This threat appears to be much less significant in olive baboons (Palombit, 2003a). For olive baboon females, protection from non-lethal harassment by other group members could be an important motivation for staying near an adult male friend (Smuts, 1985).

If friendships serve a harassment-guarding function, we predicted that a female's responsibility for maintaining proximity to her friend would be positively correlated with her susceptibility to stress as measured by her glucocorticoid profile. The small sample size of "Female-Responsible" friendships ($n=2$) for which we had sufficient data to compare to "Male-Responsible" friendships ($n=11$) constrains interpretation of our findings but females in "Female-Responsible" friendships showed higher glucocorticoid

levels during the first eight weeks post-parturition. Our alternative analyses, first considering only Hinde's Index scores of friendships with primary friends, and second, calculating composite Hinde's Index scores for any females' multiple friendships combined with scores for single friendships indicated there was no correlation between glucocorticoid concentrations and Hinde's Index scores either eight or sixteen weeks post-lactation.

Our analysis of variation in glucocorticoids within four 8-week periods in females with friends present or absent yielded mixed results. We predicted that when established friendships temporarily wane for a period of time, female glucocorticoid concentrations will be higher than in periods before or after, when male friends are present. There was, however, no glucocorticoid concentration difference among the three categories ("Friends Absent", "Any Friend Present", and "Only Primary Friend Present") in any of the first three time periods but our conclusions are limited by small sample numbers, especially in the "Friends Absent" category. In contrast, a within-individual temporal analysis suggests support for the Harassment hypothesis. Glucocorticoid levels increased when lactating females went from periods when their primary friends were present to periods when their primary friends were temporarily absent. The opposite glucocorticoid trend was seen when lactating females went from periods when their primary friends were absent to periods when their primary friends were present. The within-individual analysis may be the more appropriate test of our prediction since it controlled for any individual variation in rank, age, health status or other factors that potentially influenced stress levels.

If an important benefit of friendship for lactating females is protection from harassment, and females face greater harassment related stress when their friends are

absent, why do females not play a larger role in maintaining friendships in our study? Why are males relatively more responsible for maintaining close proximity (0-2m) to their friends? There are a number of possible explanations. First, our data show that females do take some responsibility for friendships, and in fact, some females are even more responsible than their male friends for maintaining proximity. Second, it is important to note that while females receive stress-reducing benefits from friendships, males may be receiving even greater benefits from friendships if their participation is a form of parental effort resulting in enhanced reproductive fitness (see Chapters 1, 2). Male friends also obtain additional benefits in the form of grooming from female friends, which they can receive only in close proximity. Smuts (1985) noted that in established friendships, males were more responsible than females for maintaining close proximity (0-1m), while females were more responsible for maintaining proximity in distances from 1-5m. Consistent with Smuts (1985), we argue that a female may try to stay close to male friends, but not *too close*. By doing so, she can receive the protective benefits of friendship but reduce the potential of being harassed by the friend himself. Male friends are responsible for one-fifth of all harassment (threats, chases, and attacks) and a large amount of severe aggression (attacks) received by females (Smuts, 1985).

We were able to gain insights into whether friendships help buffer females more from male harassment or female harassment with two additional analyses. The Male Harassment hypothesis was tested by comparing glucocorticoid concentrations in females that had only low-ranking male friends with females that had at least one high-ranking male friend. Compared to high-ranking males, low-ranking males should be less desirable protectors since they can effectively protect against fewer threatening males. Our results

support this hypothesis. For the first 16 weeks post-lactation, lactating females with only low-ranking friends had significantly higher glucocorticoid concentrations than females with at least one high-ranking male friend. The Female Harassment hypothesis predicts that the friend's rank will be irrelevant since even the lowest-ranking male can physically dominate the highest-ranking female. Our results thus reject this hypothesis.

For females toward the bottom of the dominance hierarchy, the lactation phase may be a particularly distressing time since females of all ranks become very interested in new infants. Higher-ranking females can demand access to infants and even manage to kidnap them from subordinate mothers who have little recourse against their attention. Occasionally, kidnapping may be fatal when mothers are unable to retrieve their infants (Strum, 1974; Collins *et al.*, 1984). Females of all ranks potentially benefit equally from harassment mitigation from male friends but low-ranking females (by definition) are disproportionately the targets of stressful interactions with higher-ranking females (Smuts, 1985). Thus, the Female Harassment hypothesis predicts that glucocorticoid concentrations in lactating females will be inversely correlated with individual rank if harassment by females constitutes a primary benefit of maintaining friendships. Low-ranking females in our study, however, had similar glucocorticoid concentrations as high-ranking females during the first 16 weeks post-lactation. There are a number of ways to interpret this result. Low-ranking females may become habituated to harassment from higher-ranking females, which may be an expected and tolerated feature of group-living in matrilineal societies with stable female dominance hierarchies. This explanation suggests that friendships do not serve an important female-harassment function and the Female Harassment hypothesis can be rejected. Alternatively, male support may be so

effective at buffering against harassment stress from other females that even lower-ranking mothers fail to experience an elevated stress reaction (Abbott *et al.*, 2003, Sapolsky, 2005). Abbott *et al.* (2003) suggest that in group-living primates, even the opportunity for social support may have this stress mediating effect (Abbott *et al.*, 2003).

Comparing females with and without friends was not possible in this study without dividing the lactation phase into intervals to find periods when friendships temporarily waned. Still, the number of females without friends, even in these intervals, made statistically testing hypotheses problematic. Friendships appear to be quite valuable to participants and lactating females are rarely found without at least one friend. Future studies might incorporate additional and more subtle measures of friendship to determine finer grades of relative investment.

In summary, our results suggest that for lactating females, having a male friend is an effective agent mediating stress. Females that are behaviorally investing more in maintaining proximity to their friends, are experiencing higher stress levels than females that invest less. The alternative interpretation is that female's with friends that invest less in maintaining proximity than they do, experience higher stress levels than females with friends that invest more. This association is significant early in lactation but becomes less pronounced by 16 weeks post-parturition. Male status as "primary" or "secondary" friend does not seem to play an important role in stress reduction in any period of the lactation phase but relative "presence" or "absence" of primary friends during the lactation phase is important. Glucocorticoid concentrations increase when primary friendships wane and decrease when they strengthen. A male's rank is also important: females with at least one high-ranking male friend experience significantly lower levels of glucocorticoids during

the first 16 weeks post-parturition than females with only low-ranking friends. There is not a significant association between glucocorticoid levels and rank in lactating females. These results are consistent with the Male Harassment but not the Female Harassment hypothesis for friendships providing a selective advantage to lactating females.

TABLES AND FIGURES

Table 1: All friendships identified by C-Score; female rank (L=Low, H=High); glucocorticoid concentrations (ng/g) associated with four 8-week periods post-parturition; Hinde's Index score calculated from parturition to 32-weeks post-parturition.

Female x Male Friendship	Female Rank	Interval 1 Week 1-8	Interval 2 Week 9-16	Interval 3 Week 17-24	Interval 4 Week 25-32	Hinde's Index
ATx(TD)	L	192.90	167.58	NA	NA	(26.80)*
GWx(IR)	H	152.38	137.80	NA	NA	(-16.00)
GWxLE	H	152.38	137.80	NA	NA	-11.10
HZx(FD)	H	102.84	191.81	101.29	145.33	(-15.80)
HZxCH	H	102.84	191.81	101.29	145.33	NA
IGx(GL)	H	152.72	174.86	144.88	220.95	(-1.90)
IGxBG	H	152.72	174.86	144.88	220.95	-9.20
IGxLE	H	152.72	174.86	144.88	220.95	5.80*
JUx(LY)	L	189.83	274.19	109.3	165.01	(30.80)*
KTx(LZ)	H	175.31	191.84	137.96	NA	(-43.10)
LTx(GL)	L	138.15	165.15	NA	NA	(-4.80)
LUx(TD)	L	126.26	201.69	141.89	162.44	(-35.70)
NMx(BL)	H	470.54	277.86	82.57	111.48	-9.10‡
NMxLE	H	470.54	277.86	82.57	111.48	14.70*‡
NMxIR	H	470.54	277.86	82.57	111.48	1.60*‡
SLx(CH)	L	129.64	201.18	234.54	102.84	(-24.70)
SLxLY	L	169.64	201.18	234.54	102.84	NA
SLxGG	L	129.64	201.18	234.54	102.84	-37.50
THx(TD)	L	150.91	153.53	292.02	110.91	(-45.20)
THxVO	L	150.91	153.53	292.02	110.91	-33.60
TNx(LE)	H	125.65	86.92	66.93	NA	(-7.00)
TNxBL	H	125.65	86.92	66.93	NA	-6.90
TNxIR	H	125.65	86.92	66.93	NA	-8.90
TTx(SE)	L	309.19	209.31	NA	NA	-21.50‡
VDx(GL)	L	157.17	198.52	293.04	148.50	(-12.80)
VDxBG	L	157.17	198.52	293.04	148.50	13.10*
VDxSX	L	157.17	198.52	293.04	148.50	-21.20
XNx(GY)	L	146.23	133.38	88.60	274.50	(-28.70)
XNxTD	L	146.23	133.38	88.60	274.50	-2.60
ZAx(AR)	H	209.34	224.38	NA	NA	NA

Male Friends in parentheses are either the primary or only friend.

Hinde's Index scores in parentheses correspond to either a female's primary or only friendship.

* Females relatively more responsible for maintaining proximity than males

‡ Eliminated from analyses (see Methods—Behavioral Observations)

NA – Insufficient data

Table 2: Lactating females, Male Friends and associated glucocorticoid (GLC) concentrations (ng/g) in four 8-week lactation intervals.

	Week 1-8		Week 9-16		Week 17-24		Week 25-32	
<u>Female</u>	<u>Male Friend</u>	<u>GLC</u>	<u>Male Friend</u>	<u>GLC</u>	<u>Male Friend</u>	<u>GLC</u>	<u>Male Friend</u>	<u>GLC</u>
AT	(TD)	192.90	absent	167.58	absent	NA	NA	NA
GW	(IR)	152.38	(IR), LE	137.80	absent	NA	NA	NA
HZ	(FD)	102.84	CH	191.81	(FD), CH	101.29	(FD), TD	145.33
IG	(GL), BG, LE	152.72	(GL), BG, LE	174.86	(GL)	NA	NA	NA
JU	(LY)	189.83	(LY)	274.19	(LY)	109.30	LY	165.01
KT	absent	175.31	absent	191.84	(LZ)	137.96	NA	NA
LT	(GL)	138.15	(GL)	165.15	absent	NA	NA	NA
LU	absent	126.26	absent	201.69	(TD)	141.89	absent	162.44
SL	(CH), LY	169.64	(CH)	201.18	absent	234.54	CH	102.84
TH	(TD), VO	150.91	(TD)	153.53	VO	292.02	TD	110.91
TN	(LE), BL	125.65	(LE), BL, IR	86.92	(LE)	66.93	NA	NA
VD	(GL), SX, BG	157.17	(GL), SX, BG	198.52	(GL), SX, BG	293.04	(GL), BG	148.50
XN	(GY), TD	146.23	(GY), TD	133.38	(GY), TD	88.60	absent	274.50
ZA	(AR)	209.34	absent	224.38	NA	NA	NA	NA

Male Friends in parentheses are either the primary or only friend.

NA – insufficient data

absent – no friendship distinguishable from other male-female dyads (according to C-Score)

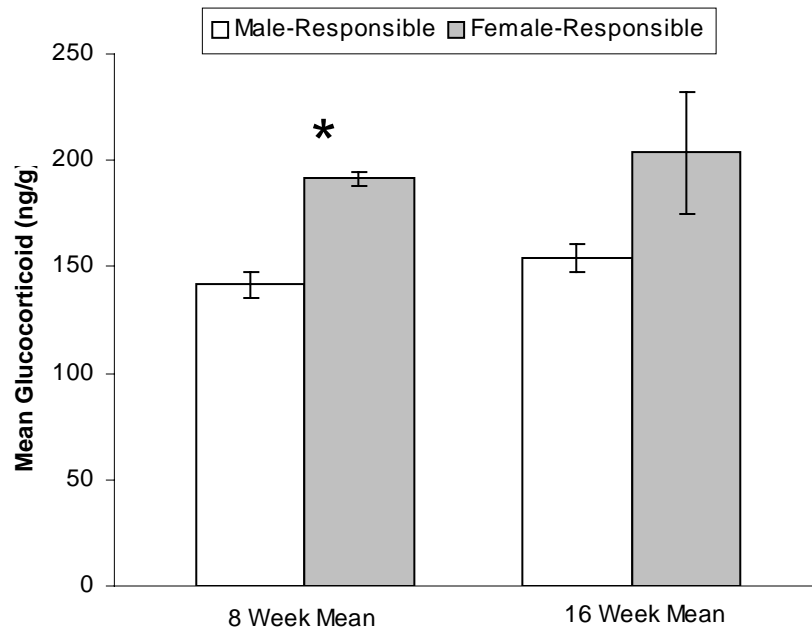


Figure 1. Female glucocorticoid concentrations (ng/g mean \pm SEM) during the first 8 weeks of lactation in Male-Responsible versus Female-Responsible friendships (Mann-Whitney U Test: $U=22$, $n_1=11$, $n_2=2$, $p<0.05$) and during the first 16 weeks of lactation in Male-Responsible versus Female-Responsible friendships (Mann-Whitney U Test: $U=20$, $n_1=11$, $n_2=2$, $p=0.10$).

***Significant difference**

Male-Responsible friendships = males relatively more responsible for maintaining proximity than females

Females-Responsible friendships = females relatively more responsible for maintaining proximity than males

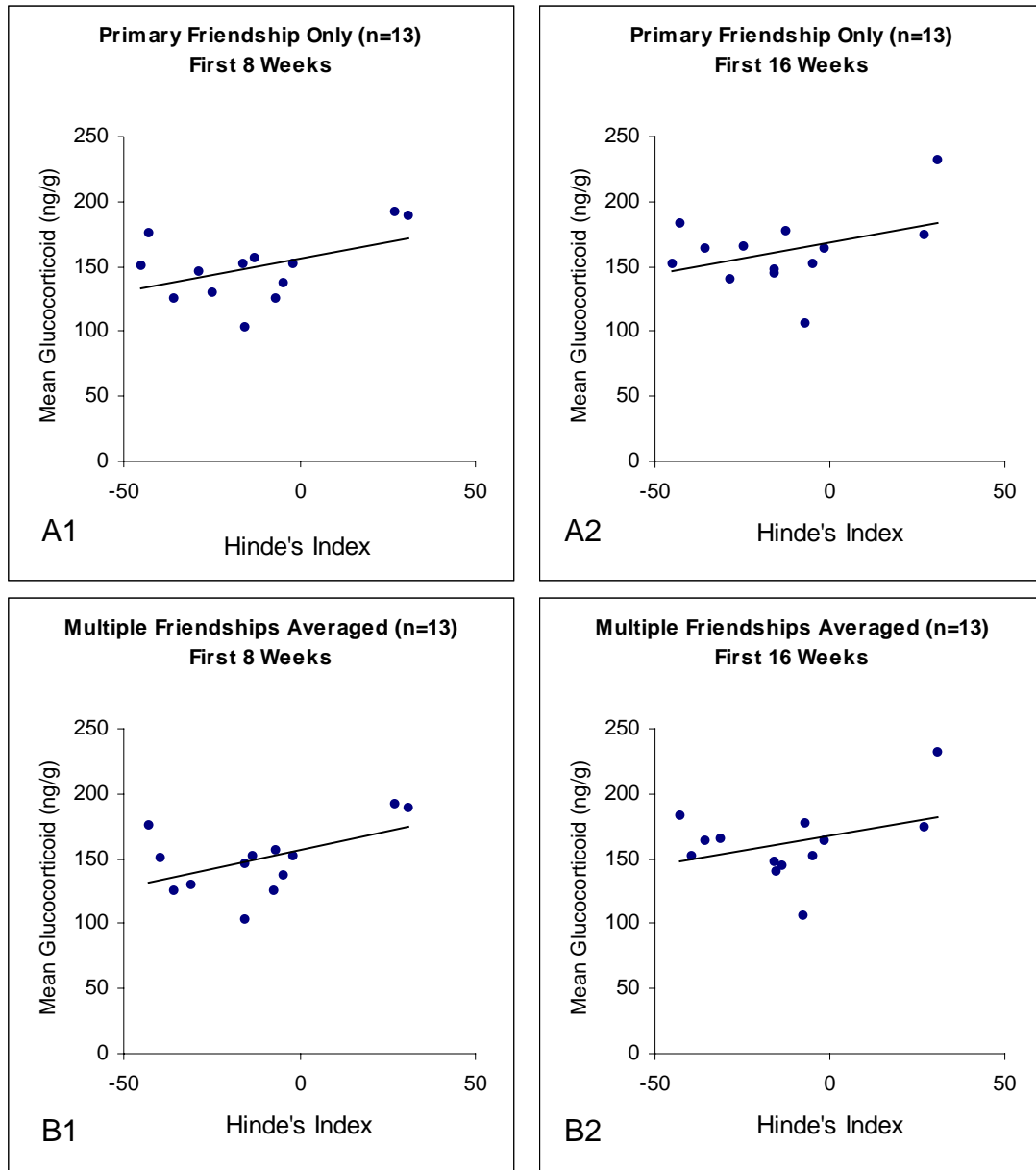


Figure 2. Association between female glucocorticoid concentrations and Hinde's Index score:
A1) Hinde's Index scores for primary friendships only for the first 8 weeks post-parturition
 ($r_s=0.32$, $DF=13$, $p=0.28$).

A2) Hinde's Index scores for primary friendships only for the first 16 weeks post-parturition
 ($r_s=-0.16$, $DF=13$, $p=0.60$).

B1) Mean Hinde's Index scores for multiple friendships of any individual female. Samples include composite scores and single scores for females with only one friendship for the first 8 weeks post-parturition ($r_s=0.42$, $DF=13$, $p=0.15$).

B2) Mean Hinde's Index scores for multiple friendships of any individual female. Samples includes composite scores and single scores for females with only one friendship for the first 8 weeks post-parturition ($r_s=-0.13$, $DF=13$, $p=0.68$).

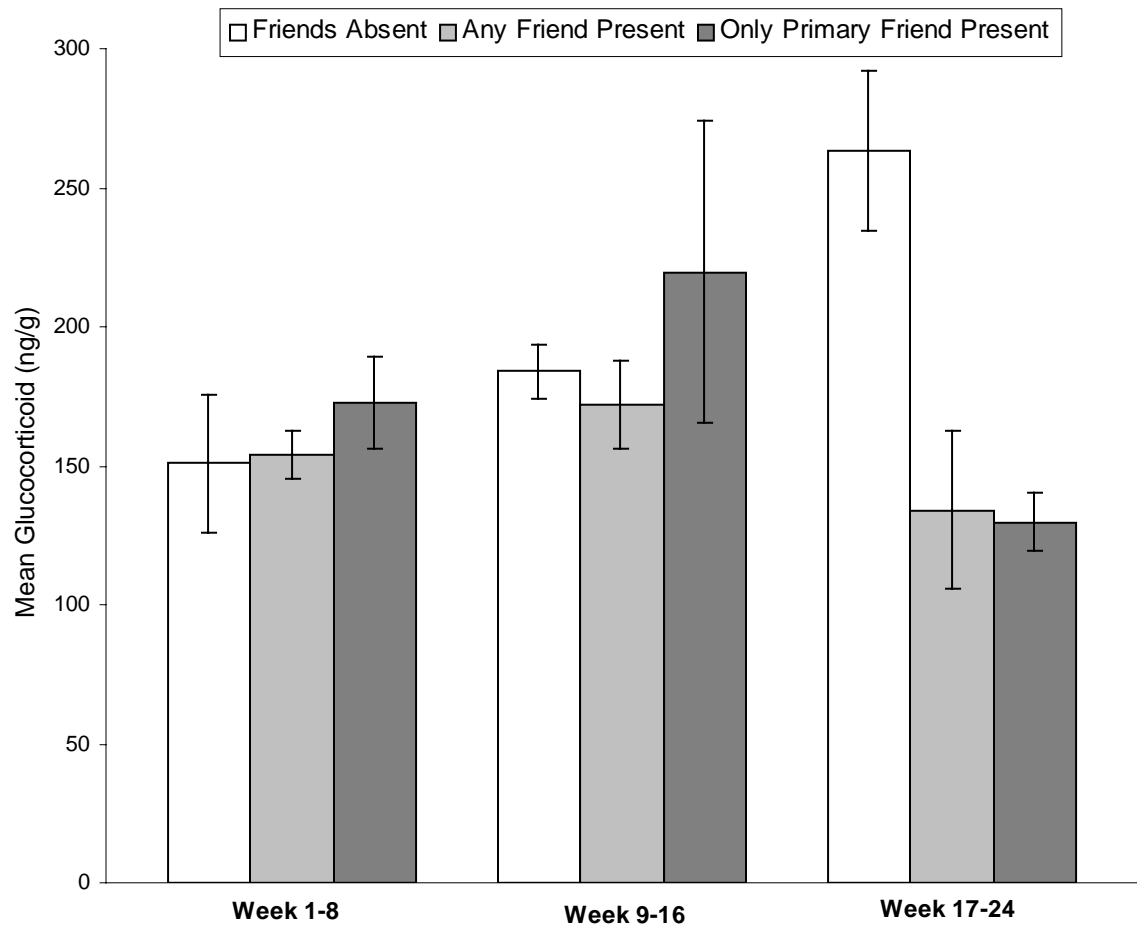


Figure 3. Lactating female glucocorticoid concentration (ng/g mean \pm SEM) in three 8-week intervals during the first 24 weeks post-parturition. Differences among categories were not significant in any interval. Interval 1 (Week 1-8): Kruskal-Wallis Test: $F=0.62$, $DF_1=2$, $DF_2=14$, $p=0.55$; Friends Absent: 150.78 ± 24.53 , $n=2$; Any Friend Present: 153.97 ± 8.80 , $n=12$; Only Primary Friend Present: 172.56 ± 16.38 , $n=4$. Interval 2 (Week 9-16): Kruskal-Wallis Test: $F=0.60$, $DF_1=2$, $DF_2=12$, $p=0.56$; Friends Absent: 183.87 ± 9.45 , $n=4$; Any Friend Present: 171.73 ± 5.88 , $n=10$; Only Primary Friend Present: 219.67 ± 54.52 , $n=2$. Interval 3 (Week 17-24): Kruskal-Wallis Test: $F=2.00$, $DF_1=2$, $DF_2=8$, $p=0.20$; Friends Absent: 263.28 ± 28.74 , $n=2$; Any Friend Present: 134.15 ± 28.29 , $n=7$; Only Primary Friend Present: 129.72 ± 10.27 , $n=3$.

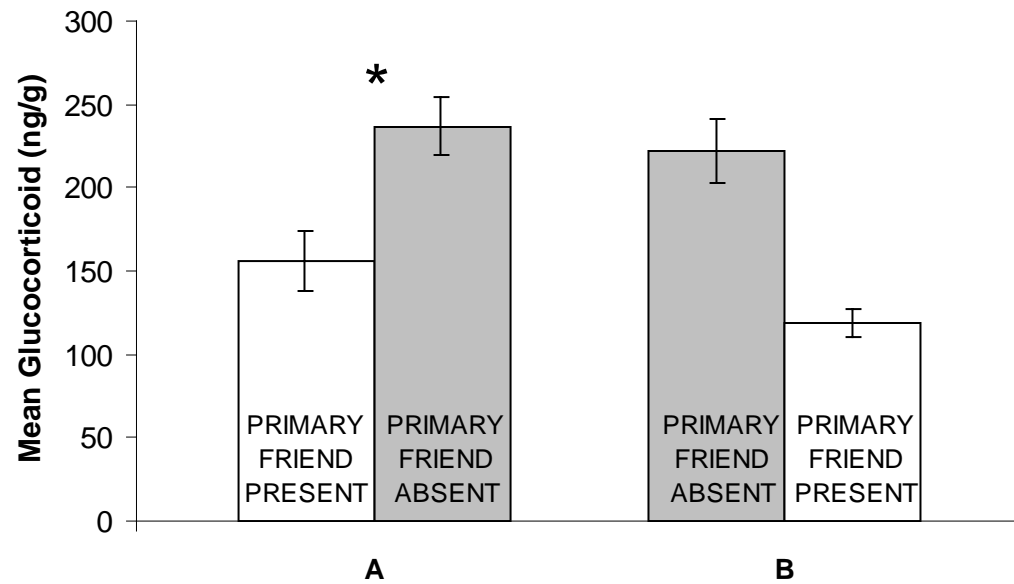


Figure 4. Lactating female glucocorticoid concentrations (ng/g mean \pm SEM) in any two consecutive 8-week lactation intervals when:

A) Primary Friend Present followed by Primary Friend Absent (Wilcoxon Paired-Sample Test, $T=2$, $n=7$, $p<0.05$)

B) Primary Friend Absent followed by Primary Friend Present (Wilcoxon Paired-Sample Test, $T=0$, $n=5$, $p=0.06$)

***Significant difference**

Primary Friend Present = A female's primary friend (determined by 32-week C-score) was also a friend in a particular 8-week interval

Primary Friend Absent = A female's primary friend (determined by 32-week C-score) was not a friend in a particular 8-week interval

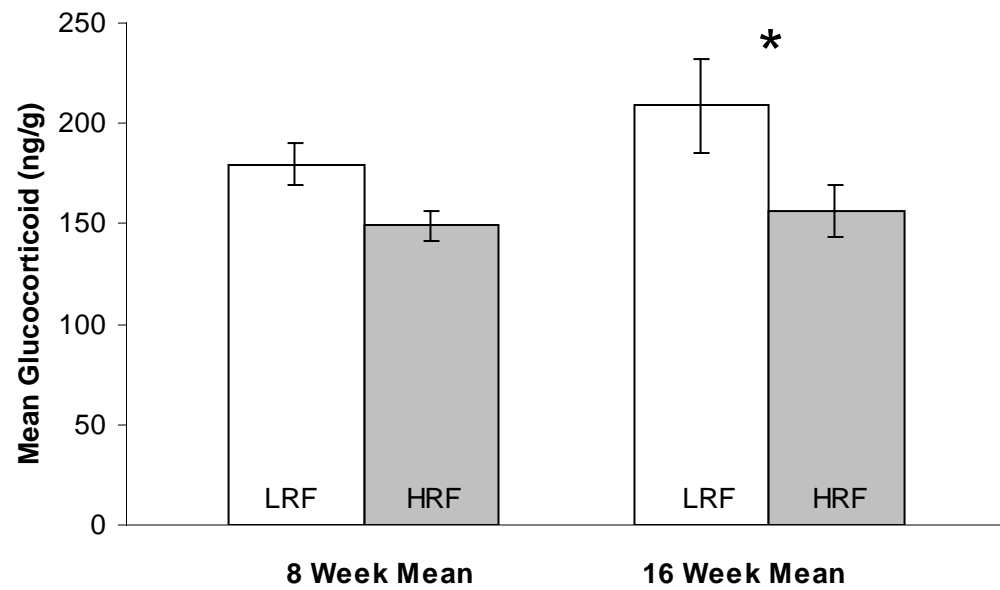


Figure 5. Glucocorticoid concentrations (ng/g mean \pm SEM) during the first 8 weeks and first 16 weeks of lactation in females with only low-ranking male friends and females with at least one high-ranking male friend (8 weeks: Mann-Whitney U Test: $U=21$, $n_1=2$, $n_2=12$, $p=0.13$; 16 weeks: Mann-Whitney U Test: $U=23$, $n_1=2$, $n_2=12$, $p<0.05$).

***Significant difference**

LRF = females with only low-ranking male friends

HRF = females with at least one high-ranking male friend

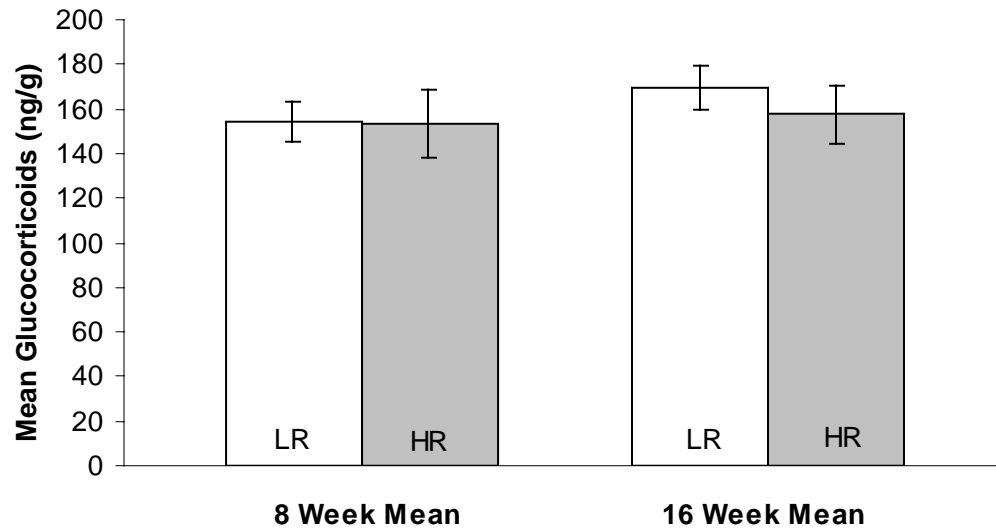


Figure 6. Glucocorticoid concentrations (ng/g mean \pm SEM) during the first 8 weeks and first 16 weeks of lactation in low-ranking and in high-ranking females

8 weeks: Mann-Whitney U Test: $U=24$, $n_1=6$, $n_2=8$, $p=1.00$; LR: 153.89 ± 8.96 , $n=8$;

HR: 153.04 ± 15.21 , $n=6$.

16 weeks: Mann-Whitney U Test: $U=29$, $n_1=6$, $n_2=8$, $p=0.57$; LR: 169.76 ± 9.97 , $n=8$;

HR: 157.15 ± 13.10 ; $n=6$.

LR = low-ranking female

HR = high-ranking female

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CONCLUSION

This study of friendship in olive baboons was designed to test hypotheses concerning the adaptive significance of friendship for each sex. There were three principal components:

1) Association Between Male Testosterone and Friendship

The Parental Care hypothesis for friendship in adult males was tested by analyzing male testosterone profiles associated with parturition and lactation in female friends. I based four predictions on the testosterone profiles shown in male mammals such as rodents, nonhuman primates and humans, which suggest a general mammalian trend: fatherhood and active paternal care are correlated with suppressed testosterone at parturition and during lactation (Ziegler *et al.*, 1996; Fleming *et al.*, 1997a, 1997b; Nunes *et al.*, 2000, 2001; Storey *et al.*, 2000; Berg and Wynn-Edwards, 2001; Wynne-Edwards, 2001; Gray *et al.*, 2002, 2006, 2007). My results were consistent with each prediction.

First, testosterone levels were lower in males involved in friendships than in control males.

Second, male friends, but not controls, experienced a significant periparturition decrease in testosterone concentration.

Third, in male friends, but not in controls, testosterone increased from early post-parturition to 32 weeks post-parturition.

Fourth, males who were relatively more responsible for maintaining friendships (than their female partners) experienced a greater periparturition testosterone decrease than male friends who invested less in their friendships. Thus, I argue that testosterone

concentrations in male baboons suggest a hormonal mechanism underlying friendship and paternal solicitude similar to that in other mammals. These results were consistent with the functional hypothesis that friendship behavior in males constitutes paternal care of offspring.

2) Association Between Male Glucocorticoids and Friendship

The results of my test of the Parental Care hypothesis for friendship in male olive baboons based on a “paternal glucocorticoid profile” found in male pair-bonded mammals were not consistent with each of four predictions. First, rather than decrease as predicted, periparturition glucocorticoid levels increased immediately following the birth of females’ infants.

Second, in contrast to the prediction that glucocorticoid concentration will be negatively associated with a male’s relative investment in friendships, there was no correlation between a male’s investment in the friendship and his periparturition glucocorticoid percentage change.

Third, I predicted that throughout lactation, glucocorticoid levels would be lower in males with female friends than in controls. Baboon male friends, however, experienced higher 32-week mean glucocorticoid concentrations than did controls.

Fourth, I predicted that glucocorticoid levels in male friends would increase in the late lactation phase, but concentrations in friends steadily declined after the first eight weeks post-parturition to levels below controls’ by the end of 32 weeks post-parturition. There were two related challenges to interpreting the results of the second component of this study. The first was the efficacy of the “paternal care” model (based on pair bonded

rodents, nonhuman primates and humans) to predict glucocorticoid profiles in olive baboons, a non-pair bonded species. Parental-effort can be expressed differently as either infant protection or as direct care giving, such as holding or carrying, displayed by pair bonded species. These two forms of parental-effort may manifest very different glucocorticoid profiles. Other mammals that live in bisexual social groups and provide indirect parental care in the form of protection and guarding against predators may provide a more useful comparison and glucocorticoid model. Currently, there is a dearth of meaningful data to formulate such a model. Lonstein and De Vries (2000:669), however, suggest reevaluating hormonal associations with paternal behaviors in uni-parental (maternal) rodent species including Norway rats, *Rattus norvegicus*, common mice, *Mus musculus*, and Siberian hamsters, *Phodopus sungorus*, with more broadly defined categories of parental care including not only nurturing behaviors such licking or retrieval of pups, but also *responsiveness* which “indicates a general propensity of an animal to act parentally towards young.” I propose adding an additional category, “paternal protectiveness” in analysis of hormonal associations with paternal care in non pair bonded rodents and other mammals as the next step in developing a paternal care model for analysis of hormone association with baboon friendship.

The second challenge was interpreting the striking difference between glucocorticoid profiles in male baboon friends and pair bonded mammals. Should the parental care hypothesis be rejected? On the one hand yes, because glucocorticoid concentration patterns were the opposite of what was predicted. On the other hand, the results from analysis of testosterone in male friends were notably consistent with the

hypothesis. In fact my results of the two hormones indicated an inverse association in each of four corresponding tests of the hypothesis.

This leads me to an alternative conclusion: periparturition and chronic elevation of glucocorticoids in male baboons during the lactation phase of their female friends functions to decrease testosterone and thereby divert male behavioral strategies from male-male competition and mating effort toward friendship with lactating females (and their infants). There are two lines of evidence that support this conclusion. First, glucocorticoids have been implicated in testosterone suppression in mammals, including olive baboons, but the converse has not been demonstrated (Sakamura *et al.*, 1975, Johnson *et al.*, 1982; Sapolsky 1983a, 1985). Second, reduction in testosterone has a widely recognized role in the onset, facilitation, amplification and maintenance of paternal behavior in primates, which likely enhances reproductive fitness in fathers (Ziegler *et al.*, 1996; Nunes *et al.*, 2000, 2001; Fleming *et al.*, 1997a, 1997b; Storey *et al.*, 2000; Berg and Wynn-Edwards, 2001; Wynn-Edwards, 2001; Gray *et al.* 2002, 2006, 2007).

3) Association Between Female Glucocorticoids and Friendship

I analyzed glucocorticoid concentrations in lactating females first to test the hypothesis that friendships buffer lactating females from harassment. I predicted that a female's responsibility for maintaining her friendship (relative to her partner's contribution) would be positively correlated with her susceptibility to stress as reflected by her glucocorticoid profile. Females in "Female-Responsible" friendships did show higher glucocorticoid levels during the first eight weeks post-parturition. A within-

individual temporal analysis also suggested support for the Harassment hypothesis. Glucocorticoid levels increased when lactating females went from periods when their primary friends were present to periods when their primary friends were temporarily absent. Glucocorticoid levels decreased when lactating females went from periods when their primary friends were absent to periods when their primary friends were present.

Next, I analyzed the glucocorticoid concentrations to test two contrasting hypotheses: friendships protect against harassment from adult males versus higher-ranking females. The results supported the Male Harassment hypothesis. Lactating females with only low-ranking friends had higher glucocorticoid concentrations than females with at least one high-ranking male friend. This result also rejected the Female Harassment hypothesis, which predicts that the friend's rank will be irrelevant to glucocorticoid fluctuations since even the lowest-ranking male can physically dominate the highest-ranking female. The Female Harassment hypothesis also predicts that glucocorticoid concentrations in lactating females will be inversely correlated with individual rank if harassment by females constitutes a primary benefit of maintaining friendships. My results indicated that both low- and high-ranking females had similar glucocorticoid profiles. This suggests that friendships do not serve an important female-harassment function and lead to my rejection of the Female Harassment hypothesis.

Two principle challenges constrained analysis and interpretation of results in the third component of this research. All lactating females formed friendships with adult males during the study. Of course, I believe this outcome reflects the significant adaptive value of these relationships to females. But it did mean that I could not compare hormone profiles in females with and without friends. Instead, I divided the lactation phase into

intervals to identify periods when friendships temporarily waned. Still, the number of these intervals remained small.

Data were also insufficient to test for an association between the magnitude of glucocorticoid concentrations and female rank when male friends were “temporarily absent,” *i.e.*, when friendships temporarily waned. The Male Harassment hypothesis predicts that “temporary absence” of a male friend should generate similar glucocorticoid increases in females of all dominance ranks. The Female Harassment hypothesis, however, predicts that lower-ranking females will experience disproportionately more risk of harassment than their higher-ranking counterparts, and therefore show greater relative increases in glucocorticoids (Abbott *et al.*, 2003). Both hypotheses predict that glucocorticoid levels in lactating females will be higher when their primary male friend is absent. But only the Female Harassment hypothesis predicts that the magnitude of glucocorticoid increase during periods of male friend absence will be inversely correlated with the rank of the female friend.

The difficulty in executing this analysis was twofold. First (as mentioned previously), there were few discrete periods of time when friendships waned and females could be considered “without a friend.” Moreover, there were too few periods to analyze statistically subjects further divided by female rank. Second, I was unable to isolate short-term male-absent periods defined by short-term behavioral events, (*e.g.*, consortships with estrous females lasting a single day), that were still long enough to allow adequate fecal sampling. Unlike glucocorticoids in serum and their more immediate correspondence with stressful experience, fecal hormones are best considered a general or composite measure of stress accumulated and “averaged” over a number of hours or even

days prior to excretion (Whitten *et al.*, 1998). Even if lactating females were very stressed during periods when their male friends were focused elsewhere, it is unlikely that fecal hormones would meaningfully correspond to periods of only a few hours. While this study was well suited to investigating accumulated stress over the course of a female's lactation phase, analyses of fecal hormones associated with behavioral events and short-term changes in the social environment were limited. The incompatibility of realistic fecal sampling regimens with investigations of short-term behavioral periods or events continues to be a challenge for field socioendocrinology studies.

Future Research

There are numerous possible directions for future research of hormonal correlates of baboon friendships and their adaptive significance. Two suggestions for future studies expand upon this one. The first would be to analyze testosterone profiles of lactating females in friendships. Although testosterone is conventionally associated with male behavior and sexual development, it also plays an important and often analogous functional role in females (reviewed in Baum *et al.*, 1977; Carter, 1993; Dabbs *et al.*, 1997; Staub and De Beer, 1997; Beehner *et al.*, 2005b). In baboons (*Papio spp.*), Beehner *et al.* (2005b) found associations between testosterone and female rank, and a within-individual association between testosterone and aggression. Given that female chacma baboons compete for access to male friends (Palombit *et al.*, 2001), these findings could have important implications for future analysis of friendships in females.

There is also increasing evidence suggesting a vital role of estrogens in female primate behavior, especially during parturition and lactation phases (Numan, 1994; Pryce

et al., 1994; Maestripieri, *et al.*, 1995; Pryce, 1996; Dahl, 1999; Storey *et al.*, 2000; Bardi *et al.*, 2001). For example in Japanese macaque, *Macaca fuscata*, mothers, Bardi *et al.*, (2001) reported an inverse association between estrogen levels and social interactions with other group members (both males and females), measured by spatial proximity, approaches, withdraws and grooming. Periparturition social interactions decreased in association with an increase in the mothers' estrogen levels. Later, post-parturition social interactions increased in association with a decrease in estrogen. Similar finding have been reported in human mothers (Storey *et al.*, 2000). If low post-parturition estrogen is associated with an increase in social behaviors, particularly the manifestations of friendships, I would expect low levels of estrogen to be associated with greater female responsibility for maintaining friendships. As an infant matures, increasing estrogen levels should correspond to declining female responsibility for maintaining friendships.

Future research might further investigate the behavioral components of the friendships to see if they were consistent with my conclusions from the hormonal analysis. For example, the Parental Care hypothesis predicts an association between the late-lactation rise in testosterone in males and an increase in their mating behaviors with estrous females (which may later include female friends that resume cycling). A revised "Protective" Parental Care hypothesis would predict that the post-parturition rise and lactation phase elevation in male glucocorticoids would be associated with increased male-male aggression or other evidence of protective behaviors. In lactating females, particularly those in Female-Responsible friendships, evidence of lower rates of harassment by other group members towards females with more or stronger friendships would support the Harassment hypothesis.

Future studies will continue to focus on the relationships between social behavior and these and other hormones, but they should not neglect considering the mediating and synergistic effects that hormones may have on one another. Finally, as the science of socioendocrinology continues to mature, it is imperative that researchers redouble their efforts to inform each step of the research process, from development of hypotheses to interpretation of results, with considerations of the dynamic reciprocal nature of hormone-behavior interactions.

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