ENDOCRINE CORRELATES AND FITNESS CONSEQUENCES OF VARIATION IN THE MOTHER-INFANT RELATIONSHIP IN WILD BABOONS (*PAPIO CYNOCEPHALUS*) IN AMBOSELI, KENYA

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ABSTRACT

For animals, mammalian neonates are unusually dependent on their mothers for growth and survival, and a major goal of mammalian reproductive biology is to understand the causes and consequences of variation in infant caretaking behaviors among mothers. I investigated the endocrine correlates and fitness consequences of variation in the mother-infant relationship in five groups of wild baboons (*Papio cynocephalus*) of known demographic history and genealogical relationships in Amboseli, Kenya. I used non-invasive techniques to measure excreted steroid hormones from mothers across the perinatal period, and data from both patterns of behavior between parents, infants and other group members, and the long-term (>30 years) genetic, demographic and reproductive records for this population.

First, I show that fecal glucocorticoid levels during late pregnancy predicted maternal responsiveness to infant distress cries after birth. This study provides the first evidence for the preparative actions of glucocorticoids for responding to a predictable challenge (i.e. motherhood) in a wild animal population. Second, I show that sex differences in the mother-infant relationship exist during the early postnatal period, differences that are consistent with the lives of offspring as adults. I show that mothers are more permissive of male than female infants, and that maternal dominance rank and fecal estrogen levels during late pregnancy are more predictive of the suckling behavior of female than male infants. My results suggest that the mother's social world has a greater influence on the lives of female infants, and are among the first evidence of sex differences in the mother-offspring relationship during infancy in wild primates. Third, I examine the patterning of associations between adult males and new mothers during the early postnatal period and evaluate

two hypotheses for why close associations (or 'friendships') between males and females might be adaptive for each sex. I show that friendships with males provide mothers and infants protection from harassment by other females, but are not associated with risk of infanticide by other adult males. Finally, I examine the predictors of birth intervals and explore the possible proximate pathways through which suckling behavior and postpartum progesterone may mediate the effects of maternal dominance rank on birth intervals in this and other mammal populations.

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GENERAL INTRODUCTION

For reproduction to be successful, parents must produce offspring that are themselves able to survive and reproduce. In some species, offspring require assistance from one or both parents to reach the age of reproductive maturity (Clutton-Brock 1991). Mammals are unique among vertebrates in that mothers not only provide all prenatal care through gestation, they also provide, through lactation, the sole source of nutrition for young infants (Clutton-Brock 1991). Lactation in mammals thereby creates an obligate association between mothers and infants, limiting the contributions of males to offspring fitness in most species. The immediate impact of mothering behavior on offspring fitness suggests that individual plasticity in caregiving behavior may be of selective value as it may permit mothers to adjust infant care in relation to their own needs and in response to changes in their social and physical milieu. Mothers have limited physiological resources they can devote to reproduction, and expenditure on the current offspring can be costly in terms of the mother's ability to invest in other offspring (Trivers 1974; Pianka 1976). Mothers should thus adjust their expenditure on infant care in relation to both its benefits to the current offspring and its costs to themselves, as a means of maximizing their own inclusive fitness (Winkler 1987). Variation in infant caretaking, on the other hand, can have both negative and positive consequences for young infants and some of these short-term effects can have long-term consequences for offspring fitness (e.g. Fairbanks 1996; Fleming et al. 1999; Francis et al. 1999; Meaney 2001).

In this study, we examine the endocrine correlates and fitness consequences of variation in the mother-infant relationship in 34 mother-infant dyads of known demographic history and maternal lineage in five groups of wild baboons (*Papio cynocephalus*) in the Amboseli basin, Kenya. Using patterns of behavior, noninvasive fecal hormone sampling, and the long-term database for the population, we evaluate the extent to which (1) differences in the mother-infant relationship are predictable from differences among mothers in the profiles of four steroid hormones over late pregnancy and early lactation and (2) differences in the mother-infant relationship predict variation in the timing of mothers' future reproduction and in infant survival. In doing so, we build on and considerably extend previous studies of this topic in non-human primates, which have primarily been constrained to a few individuals of a few species, captive populations, one or two hormones, and invasive hormone sampling.

Chapters 1 and 2 of this thesis focus on the "causes" of variation in the mother-infant relationship, while Chapter 4 examines some of the "consequences" of this variation for mothers and offspring. More specifically, in Chapter 1, we examine the extent to which the steroid hormones glucorticoids predict variation in maternal responsiveness to infant distress cries. In Chapter 2, we evaluate the extent to which perinatal concentration of the ovarian steroids, estrogens and progesterone, are associated with variability in several measures of the mother-infant relationship, as well as the effects of maternal and infant characteristics on these associations. In Chapter 3, we examine the adaptive benefits of 'friendships' between new mothers, their newborn offspring, and adult males, and assess the influence of paternity on the patterning of male/mother-infant dyad interactions. Finally, in Chapter 4, we examine the effects of variation in the mother-infant relationship on offspring survival and the timing of mothers' future reproduction.

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CHAPTER ONE: Late Pregnancy Glucocorticoid Levels Predict Maternal Responsiveness in Wild Baboons (*Papio cynocephalus*)

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ABSTRACT

Glucocorticoids (GCs) are steroid hormones secreted in response to stressful stimuli and are believed to help organisms survive these challenges. During the peripartum period, GCs are hypothesized to increase maternal attraction and responsiveness to infant generated stimuli. We measured naturally occurring variation in maternal responsiveness to infant distress vocalizations during the first two months of infants' lives and used noninvasive techniques to measure excreted steroids during the two months prior to and after parturition in 34 wild mother-infant yellow baboon (*Papio cynocephalus*) dyads in Amboseli, Kenya. Fecal GCs exhibited a high degree of intra-individual stability across the peripartum period. Females with higher GC concentrations the month before parturition were more responsive to their infants' distress than females with lower GC concentrations. These patterns were not influenced by major maternal or infant characteristics. They are consistent with the hypothesis that late pregnancy elevations in GCs "prepare" pregnant females for responding to stimuli from their neonates. This study represents the first evaluation of the relationships between peripartum GCs and the expression of maternal behavior in a wild animal population and provides the first evidence among wild animals for the preparative actions of GCs for responding to predictable challenges.

INTRODUCTION

Maternal care is perhaps the single most significant measure of successful adaptation among female mammals (Rosenblatt 1995). Mammalian offspring require extensive care from their mothers in the postpartum period to live to reproductive age, and variability in the mother-offspring relationship can have dramatic fitness consequences for both the mother and her offspring (e.g. Fairbanks 1996; Francis et al. 1999; Short 1983; Trickett & McBride-Chang 1995). Variability in the mother-offspring relationship has been noted since the beginnings of systematic research. However, only recently have researchers begun to turn their attention to the role of physiological or neuroendocrine factors in mediating individual differences in maternal care (rats: Rees et al. 2004) (sheep: Dwyer et al. 2004) (nonhuman primates: Bales et al. 2002; Bardi et al. 2003a; Bardi et al. 2003b) (humans: Fleming et al. 1987; Fleming et al. 1997; Stallings et al. 2001), and in those cases where they are available, results have been inconsistent across studies and confined primarily to laboratory or captive populations. Recent advances in noninvasive techniques for measuring hormone concentrations now make comparable research on wild, free-living populations possible (Whitten et al. 1998). In this study, we extracted steroid hormones from feces and provide the first intensive investigation of the influence of hormones on the expression of maternal behavior in a wild animal population. In particular, we focus on glucocorticoids (GCs) and examine whether pre- and postpartum GC concentrations predict variation in maternal responsiveness to infant distress cries in a population of wild, free-living yellow baboons (*Papio cynocephalus*) in Amboseli, Kenya.

Glucocorticoids (GCs) are hormones secreted in response to stressful or challenging stimuli and are believed to help organisms survive these challenges (Sapolsky et al. 2000). In birds and rodents, the primary GC produced is corticosterone; however, in primates, including humans, it is cortisol. Sapolsky et al. (2000) distinguish between two classes of GC action: *modulating actions*, or those that affect an organisms' immediate response to a stressor; and *preparative actions*, or those that mediate the organisms' response to a future challenge.

The modulating actions of GCs on physiology and immunology have been studied since the 1950s (reviewed in Sapolsky et al. 2000), but recently researchers also have begun to consider the modulating actions of GCs on the expression of behavior (DeVries et al. 1995; DeVries et al. 1997). Evidence for modulating actions of GCs on the expression of maternal behavior comes from studies of human and nonhuman mammalian mothers, but findings have been inconsistent across studies and limited to human or captive populations. Postpartum GCs have been found to be positively associated with variation in maternal responsiveness to infant cues in humans (Fleming et al. 1987; Fleming et al. 1997; Stallings et al. 2001) and with rates of maternal behaviors in rats (Rees et al. 2004). These patterns are consistent with (Fleming 1990)'s suggestion that GCs increase mothers' general level of arousal and attentiveness and thus increase their attraction and responsiveness to infant generated cues during the early postpartum period. However, the extent to which the results of these studies can be generalized to other taxa or to wild settings remains unclear.

In contrast to modulating actions, the preparative actions of GCs are poorly understood (Sapolsky et al. 2000). Elevations of GCs in anticipation of future challenges require that stressors be predictable (Sapolsky et al. 2000). Major predictable stressors in the lives of female mammals include parturition and the postpartum care of offspring. Elevations in GC concentrations during gestation have been reported in humans, nonhuman primates and other mammals (Keller-Wood & Wood 2001). These elevations are typically believed to be important for promoting fetal growth and development (Gartner et al. 2002; Pepe & Albrecht 1995) but if GCs act in some contexts to prepare organisms for subsequent challenges as suggested by Sapolsky et al. (2000), these elevations may also reflect pregnant females' anticipation of the challenges associated with parturition and the postpartum care of offspring. Support for this idea would come from the demonstration that prepartum elevations in GCs are associated with variation in postpartum maternal behavior. To date, only three studies have considered this possibility (Bardi et al. 2004; Bardi et al. 2003a; Dwyer et al. 2004). They have, however, relied solely on captive animals and two of these studies found no relationship between prepartum GCs and postpartum maternal behavior (Bardi et al. 2003a; Dwyer et al. 2004). The extent to which this general finding is applicable to other taxa or to naturalistic settings remains unclear.

In the present study, we investigate both the potential preparative and modulating actions of GCs on maternal responsiveness to infant distress cries in 34 wild yellow baboon mother-infant dyads. We focus on maternal responsiveness, instead of on overt displays of maternal behavior without direct reference to infant stimuli such as nursing and grooming, because we believe maternal behavior in response to infant cues reflects, more accurately, differences in caregiving motivation among individuals (seeFarrell & Alberts 2002). Such differences in caregiving motivation, we believe, may have important life history consequences for mothers and infants. Indeed, consistent parental responsiveness to infant distress signals are important for normal social and cognitive development in human children (Ziv & Cassidy 2002) and, though data on the topic are unavailable, may be equally important for the well being of other primate offspring.

We test the hypothesis that peripartum GC concentrations increase maternal attention and responsiveness to infant generated cues. We measured naturally occurring variation in maternal responsiveness to infant distress vocalizations during the first two months of infancy and related differences among mothers in their responses to infant distress cries to differences among them in fecal GC concentrations during the two months prior to and after parturition. Consistent with the hypothesis that prepartum GCs "prepare" mothers for responding to their future offspring, we predicted that greater prepartum GC concentrations would result in greater postpartum maternal responsiveness to infant distress cries. We also predicted that, consistent with the hypothesis that postpartum GCs modulate ongoing maternal responsiveness, greater postpartum GC concentrations would be associated with greater maternal responsiveness.

METHODS

Subjects, Behavioral Sampling and Measurement

Thirty-four mother-infant dyads living in five groups in the Amboseli basin, Kenya were studied from Sep 2002 to Nov 2003. Subjects are part of a larger population of baboons that has been under continuous observation for over three decades (e.g. Alberts et al. 2003; Altmann 1980; Altmann 1998; Altmann & Altmann 1970). All pregnant females in the study groups who bore live young that survived the first two months of infancy were included in this study. Each female was sampled during the last two months, or last trimester, of her pregnancy. After parturition, each mother-infant dyad was observed throughout the first two months of the infants' life.

Each mother-infant pair was observed, on average, for 11.6 + 4.5 (SD) actual in-sight observation hours in 33.2 + 12.2 (SD), 20 min focal animal samples (Altmann 1974) during the first 8 postnatal weeks. During each 20 min sample on a mother-infant pair, continuous data were recorded on (1) all changes in mother-infant contact, (2) all occurrences of social and/or agonistic interactions between (a) mother and infant and (b) mother and/or infant and other members of their social group, and (3) all occurrences of infant distress.

Data on the sequence of social and agonistic interactions surrounding each distress bout were used to assign a cause of distress to each bout. A bout of infant distress began with the first distress vocalization given by an infant and ended when the infant no longer exhibited signs of distress in relation to the original cause of distress. If, in response to the onset of infant distress, mothers responded by making themselves available to infants by a change in their behavior, indicating they were focused on identifying and/or alleviating the cause of the infant's distress, an act of maternal support was recorded. All distress bouts not caused by mother-infant interactions and with known outcomes were included in our analyses.

Using these data, we computed two measures pertaining to distress for each dyad: distress rate and responsiveness. *Infant distress rate* was the number of distress bouts given by each infant for each hour he/she was observed. *Maternal responsiveness* was measured as the proportion of infant distress bouts responded to with support by mothers.

Infant and Maternal Characteristics

Mothers and infants were described by the following biographic measures: maternal rank, parity, and infant sex. Relative dominance ranks were assigned to each female based on the pattern of wins and losses in pairwise agonistic encounters (Hausfater 1975). A female's rank the month that her infant was conceived was considered her maternal dominance rank for that infant (Altmann 1980). Stability of dominance ranks throughout adulthood and even across generations has been documents for baboon and macaque females (Melnick & Pearl 1987; Pereira 1995). A mother's parity was defined as the mother's number of pregnancies, irrespective of their outcomes, and including the current infant (Altmann & Alberts 2005).

Fecal Hormone Sampling and Measurement

A total of 694 fecal samples were collected, giving an average of 1.3 fecal samples per female per week for each of the 8 weeks prior to and after parturition. Fecal samples were collected within minutes of deposit in a vial prefilled with 95% ethanol in a ratio of 2.5:1 ethanol to feces. Samples were stored in an evaporation cooler at ~15° (daily minimum) – 25 (daily maximum) °C in the field camp before they were transported, every two weeks, to the University of Nairobi. There the ethanol was evaporated and the samples were lyophilized and stored in a -20°C freezer. Samples were then transported to Princeton University where each was sifted through fine mesh and 0.2 g of sample was extracted into 2 ml of 90% methanol. The methanol extracts were then subjected to solid phase extraction (Waters, Milford MA, WAT094226) (Khan et al. 2002; Lynch et al. 2003).

The concentration of GCs in each fecal extract was assessed using I-125 radioimmunoassays. All samples were assayed in duplicate and mean concentrations were expressed as ng of hormone per g of dry fecal matter, to control for dietary differences between individuals and seasons (Wasser et al. 1993). Samples were assayed for GC metabolites using a corticosterone kit (ICN Diagnostics Division, Costa Mesa, California, USA) (see Khan et al. 2002). The primary antibody in this kit has high cross-reactivities with the major cortisol metabolites present in baboon feces and detects a rise in cortisol metabolites after a baboon is presented with an ACTH challenge (Goymann et al. 1999; Wasser et al. 2000). For assay validation, see Khan et al. (2002).

Endocrine data were $\log_{10}$ transformed to achieve an approximately normal distribution with uniform variance. GC data were divided into weeks relative to parturition, with the date of parturition considered the first day of "week 1", and the day before parturition considered the last day of "week -1". Mean daily values were calculated when multiple samples were available for a given female for a particular day and mean weekly GC values were calculated when multiple daily values were available for a particular week, so as to produce a single value for each female for each week. This yielded 376 weekly values.

Weekly means were averaged to produce monthly means for each of the two months prior to and after parturition and, for the analyses of within individual stability in peripartum GCs (see below), a single mean value for the entire prepartum and a single mean value for the entire postpartum period for each female. Because females varied in the number of weekly values they contributed to the dataset, and incomplete sampling can cause bias in analyses of inter- individual differences in GCs during a rapid period of changes in GC values, mean values were calculated only for the subset of females with adequate sampling for a given period. Monthly mean values were only calculated for females with at least 3 weeks of samples for 3 of the 4 months. Because of the 1-3 day lag time between steroid hormone secretion and excretion in feces (Wasser et al. 1993), values from the first postpartum week, presumed to reflect prepartum values, were excluded from subsequent analyses of the postpartum period. For the first postpartum month mean values were calculated for females with at least 2 of the 3 weeks of samples. This yielded 86 monthly means. Finally, a mean for the entire prepartum period was calculated for 28 females with samples from at least 5 of the last 8 weeks of pregnancy and a postpartum mean was calculated for 26 females with samples from at least 4 of the first 7 weeks after the first postpartum week.

Data Analysis

Our analysis strategy involved three steps. First, we determined whether there were individual differences in maternal responsiveness to infant distress; second, we determined whether there were individual differences in peripartum GC concentrations, and finally; we evaluated the sources and consequences of these individual differences. Most analyses were performed using SPSS 12.0 (SPSS Inc. 2003) and all analyses were two-tailed with $p<0.05$.

Individual differences in maternal responsiveness

We evaluated individual differences and assessed within individual stability in maternal responsiveness to infant distress to determine whether responsiveness represented a stable individual trait during the first two postpartum months. First, we used linear regression techniques to test whether an individual mothers' responsiveness during the first month of infancy predicted her responsiveness during the second month. Second, we calculated an alternative measure of responsiveness, mothers' latency in responding to infant distress, and examined the correlation between mothers' scores on both these measures using Pearson product moment correlation. A significant correlation would signify that individuals who responded more often also responded faster, providing further evidence of individual differences in maternal responsiveness to infant distress. To estimate the latency or speed of response, we plotted the proportion of distress bouts not yet responded to by mothers (on a logarithmic scale) against the latency of response (on a linear scale). We used the slope of this function to describe mothers' latency or timing to response to infant distress; the more negative the slope, the faster the mother was considered to have responded to her infant's distress cries.

Individual differences and within individual stability in peripartum fecal GCs

We also evaluated individual differences and assessed within individual stability in GCs to determine whether they represented stable individual traits during the peripartum period. We assessed whether individual identity, or week, or both, explained a significant proportion of the variance in weekly mean GC concentrations for the subset of females with samples from multiple weeks for the pre- (n=28 females with at least 5 weeks of data) and postpartum periods (n=26 females with at least 4 weeks of data) using general linear model (GLM) procedures. If individual identity emerged as the sole significant predictor of variance in GC concentrations for both the pre- and postpartum period, we could infer that stable individual differences in peripartum GC concentrations exist in this population.

Sources of individual differences

Given that any support for our hypotheses about the nature of the relationships between individual differences in GC concentrations and maternal behavior could be confounded by the effects of maternal and infant characteristics on peripartum GC concentrations or on maternal responsiveness, we evaluated whether responsiveness or GC concentrations were predictable from maternal dominance rank at conception, parity, infant sex, or infant distress rate. We examined whether responsiveness or mean GC values for the pre- and postpartum periods differed between mothers of male and mothers of female infants using a t-test. We then used linear regression analyses to determine whether maternal rank, parity, or infant distress rate predicted individual variation in responsiveness or GC concentrations

To examine the effects of peripartum GC concentrations on maternal responsiveness, we performed linear regression analyses using each of the four monthly mean GC values (2 prior to and 2 after parturition) to predict individual variation in responsiveness. If a significant relationship was found, we tested for the independent interaction effects of infant gender, maternal rank, and parity using GLM procedures, to determine if the relationship found was dependent on variation in any of these factors.

RESULTS

Mothers exhibited stable individual differences in their response to infant distress

Maternal support in response to infant distress varied from infant embraces when mother and infant were in contact to mothers reestablishing contact with infants when the two were separated at the outset of distress. Mothers varied in their tendency to support infants; mothers provided support to 33-92% of their own infant's distress bouts (mean+SD=67+14%, n=34). On average, mothers who responded to more distress bouts responded to them faster (r^2=-.138, p=.030). Because the two measures of responsiveness were highly correlated, for simplicity, we use only one, the proportion of distress bouts responded to by mothers, in subsequent analyses. Mothers were consistent in their response to infant distress during the first two months of their infants' life. Maternal responsiveness during the first postpartum month significantly predicted responsiveness during the second (r^2=.140, n=34, df=33, p=.029).

Peripartum fecal GC concentrations exhibited a high degree of within individual stability

Mean weekly GC concentrations varied little across the eight weeks prior to parturition and then declined precipitously after parturition (Fig. 1). That peripartum GC concentrations represented a stable individual trait was strongly supported by our statistical approaches. Individual identity was a highly significant predictor of mean weekly GC concentrations for both the prepartum ($F_{27, 142}$=4.8, n=28, p<.000) and postpartum period ($F_{25,100}$=2.85, n=26, p<.000). We infer from these findings that stable individual differences in GC concentrations exist, at least within a peripartum period, and we proceeded to apply regression and general linear model procedures to evaluate the sources and consequences of variation among individuals.

Maternal and infant characteristics do not predict variation in maternal responsiveness or peripartum GC concentrations

Infant distress rate ranged from 2.2-14.4 bouts/hr (mean+SD=6.19+2.83, n=34). Infants who cried more did not elicit greater responsiveness from mothers than infants who cried less (Table 1). In fact, individual variation in neither maternal responsiveness nor peripartum GC concentrations were predictable from any of the major maternal or infant characteristics measured (see Table 1).

Higher prepartum GC values predicted greater maternal responsiveness

Mean monthly GC concentrations for the month before birth significantly predicted postpartum maternal responsiveness (Table 1, Fig. 2a, r^2=.169, n=27, df=26, p=.033). There were no significant interaction effects of infant sex ($F_{1,23}$=.523, p=.477), maternal rank ($F_{5,7}$=.825, p=.570) or parity ($F_{6,11}$=.645, p=.694) on this relationship. We examined the emergence of this relationship over time by examining whether mean GC values for weeks -4 & -3 and weeks -2 & -1 predicted postpartum maternal responsiveness. We found that as females neared parturition, the relationship between GCs and maternal responsiveness grew stronger. Mean values for weeks -4 & -3 did not predict responsiveness (Fig. 2b, r^2=.062, n=18, df=17, p=.320), but mean GC concentrations for the two week period before parturition highly significantly predicted postpartum maternal responsiveness (Fig. 2c, r^2=.345, n=24, df=23, p=.003). Again, there were no significant interaction effects of infant sex ($F_{1,20}$=.673, p=.422), maternal rank ($F_{7,5}$=1.171, p=.446), or parity ($F_{7,7}$=.819, p=.601) on this relationship. These results are consistent with the hypothesis that prepartum GCs "prepare" females to respond to their future offspring.

No evidence of postpartum GCs modulating ongoing maternal responsiveness

Mean GC concentrations for the first and second postpartum months were not associated with variation in maternal responsiveness. Our results therefore do not lend support to the hypothesis that GC concentrations during the 1-2 months following parturition modulate ongoing maternal responsiveness.

DISCUSSION

The general pattern of change in GCs over the peripartum period observed in this study is consistent with those previously reported for this population (Altmann et al. 2004), for captive baboons and other catarrhine primates (Bahr et al. 1998; Bardi et al. 2003a; French et al. 2004), and resembles the pattern observed in human females (Scott et al. 1990). Fecal GC concentrations were elevated during late pregnancy and declined precipitously after parturition. Fecal GC concentrations among Amboseli yellow baboon females exhibited a high degree of within individual stability across the peripartum period. This finding suggests that GC concentrations possessed the characteristics of a stable individual trait, at least for a given peripartum period. We believe this is the first demonstration of within individual stability in GC concentrations in a wild animal population over any period. Moreover, the results of our study lend support to the hypothesis that GCs help 'prepare' animals for some predictable stressors, such as parturition and motherhood.

Preparative Actions of GCs

In a previous study of captive baboons, Bardi et al. (2004) reported that mothers with higher late pregnancy cortisol concentrations exhibited higher rates of some maternal behaviors (but not others) compared to mothers with lower prepartum cortisol concentrations. While maternal behaviors as examined by Bardi et al. (2004) provide a rough measure of maternal motivation to interact with infants, responsiveness as measured in our study provides a better measure of maternal motivation in that it examines a mother's responses to infant cries for aid and support. Such stimuli convey important information about an infant's sense of safety and can alert mothers to changes in the dyad's physical or social milieu that pose potential dangers to the infant. Variation in maternal responsiveness to some infant cues can therefore have important fitness consequences for infants. We believe ours is the first study to evaluate the hypothesis that late pregnancy elevations in GCs increase mothers' attention and responsiveness to infant-generated stimuli. Consistent with our prediction, females with higher GC concentrations the month before parturition were more responsive to their own infants' distress; these females responded to a greater proportion of distress bouts and did so at faster rates than females with lower GC concentrations.

The results of our analyses suggest that elevations in GCs the month before parturition may help mothers prepare for responding to their unborn infants, possibly by mobilizing available energy stores (REFS) or by 'activating' existing maternal neural networks towards enhanced attentiveness to infant generated stimuli (REFS) (Fleming et al. 1987; Fleming et al. 1997) Enhanced attraction to infant stimuli may contribute to greater maternal responsiveness to infant distress cries after birth. These effects are understandable from an adaptive standpoint: GCs typically mobilize energy reserves in response to a stressor and are believed to help animals cope with and survive these stressors, but elevations in GCs can also occur in anticipation of a challenge if these challenges are predictable in their occurrence and variability in response to these challenges has potential fitness consequences (Sapolsky et al. 2000). Parturition and the postpartum care of offspring represent major predictable life history challenges in the lives of female mammals, with fitness consequences for both mother and offspring, and as such provide potent stimuli for preparative secretions of GCs.

Our study provides the first demonstration of a preparatory role for GCs in anticipation of a challenge in a wild animal population. Preparative elevations in GCs are believed to help organisms cope with and survive predictable challenges. They have been observed in food-deprived rats presented with challenges before feeding (Levine et al. 1989) and humans before challenging events (Sapolsky 1994), but have not been reported for any wild animal population (Sapolsky et al. 2000). The subjects our study are naturally behaving animals which experience natural ecological conditions that exert selective pressures in the wild that are oftentimes absent from captive settings. Our data suggest that elevations in GCs in anticipation of predictable challenges can occur in naturalistic contexts, and highlight the possibility that they may occur in other taxa and in anticipation of a range of other predictable stressors, such as before periods of seasonal and climatic changes or before periods of intense male-male competition for mates (Sapolsky et al. 2000).

Modulating Actions of GCs

Studies of human and rat mothers have identified an important positive role for GCs in the modulation of ongoing maternal behavior in the first several days after parturition (Fleming et al. 1997, Stallings et al. 2001, Rees et al. 2004). In contrast, postpartum GCs have been found to be negatively associated with variation in maternal care in captive gorillas (Bahr et al. 1998), macaques (Bardi et al. 2003a), baboons (Bardi et al. 2004), and sheep (Dwyer et al. 2004). No biological explanations have been proposed to account for these disparate findings across taxa, though it remains possible that these differences are at least partially attributable to differences in study design (e.g. the timing of GC measurement after parturition), captive settings, or sample size across studies.

We evaluated the hypothesis that postpartum GCs play a positive role in the modulation of ongoing maternal behavior in wild baboons. Our study represents the first test of this hypothesis in a wild animal population. In contrast to our predictions, GC concentrations during the 1-2 months after parturition were not associated with ongoing maternal responsiveness. These results suggest that GCs may become less important as baboon mothers gain experience with their infants. This pattern may be due to the formation of maternal memory of infant stimuli or experiences (Rees et al. 2004). As elevations in GCs are energetically costly to maintain over long periods of time (Rabin 1999; Sapolsky 1993), such processes would enable mothers to remain responsive to their infants even after the high concentrations of GCs typical of late pregnancy are no longer present.

The results of our study join those from a growing number of other studies that have demonstrated important roles for steroid hormones in mediating the expression of mammalian maternal behavior (Fleming et al. 1997; Pryce et al. 1993; Rees et al. 2004). Despite advances in our understanding of the influence of neuroendocrine factors on the onset and maintenance of maternal behavior, little is known of the influence of these factors on variability in maternal care among individuals. Our study highlights the importance of evaluating the extent and sources of inter-individual variability in the evolution of maternal behavior and of GC action when considering the life-history consequences and evolution of these characteristics.

Fig. 1.1. Population profile of mean log-transformed fecal GC (ng/g feces) + SE by week from parturition (see METHODS for details). Numbers indicate the sample size or number of females sampled each week.

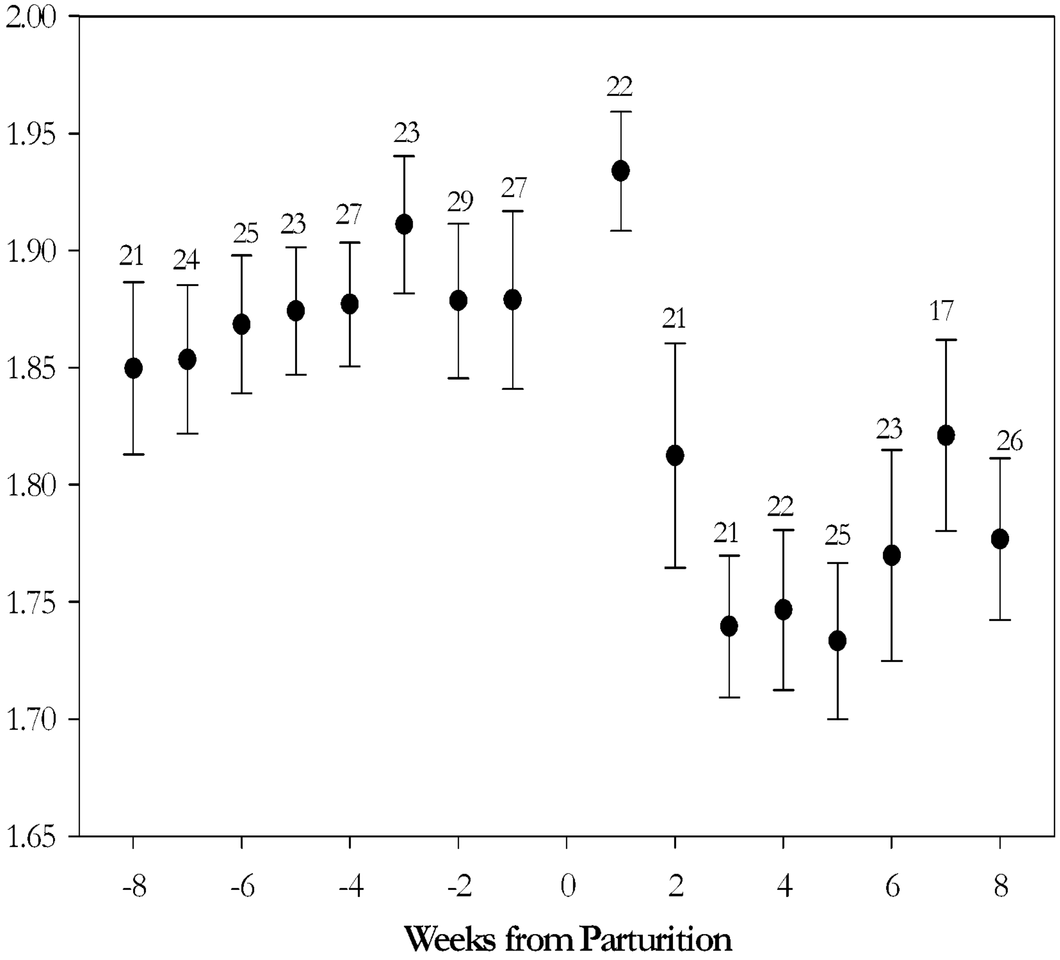
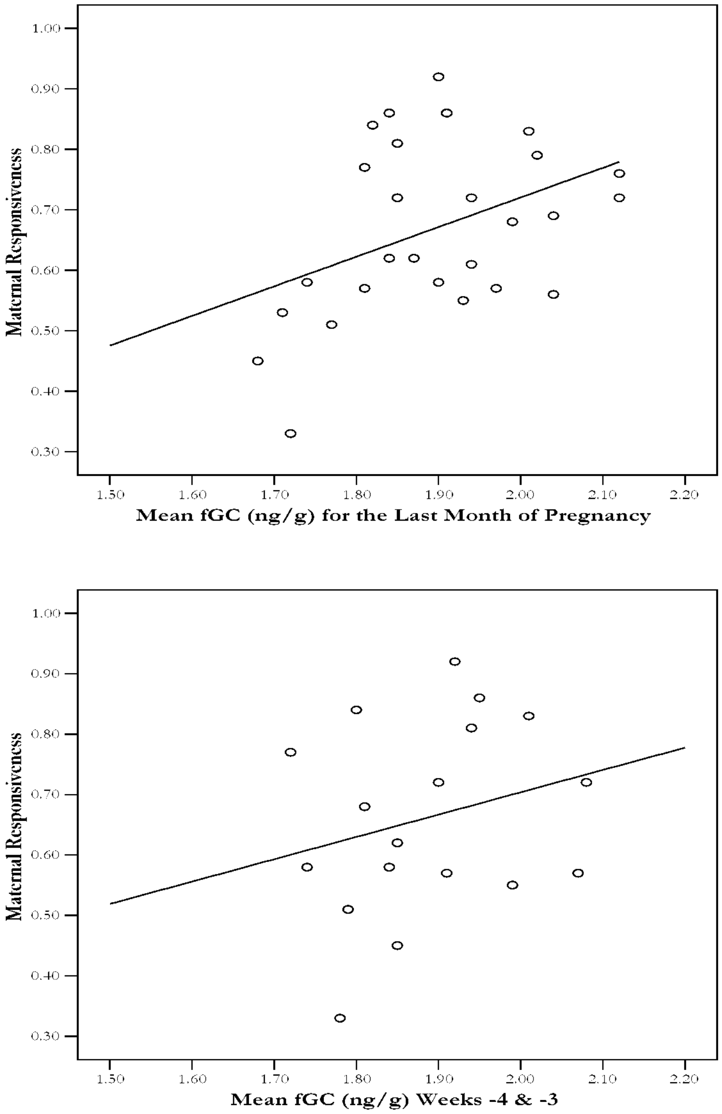


Fig. 1.2. The effect of prepartum fecal GC concentrations on maternal responsiveness to infant distress. Each point represents a single individual's mean fecal GC value for (A) the last month of pregnancy for subset of females with data for at least 3 of the 4 weeks (n=27), (B) weeks -4 & -3 for subset of females with samples from both weeks (n=18), and (C) weeks -2 & -1 for subset of females with samples from both weeks (n=24).



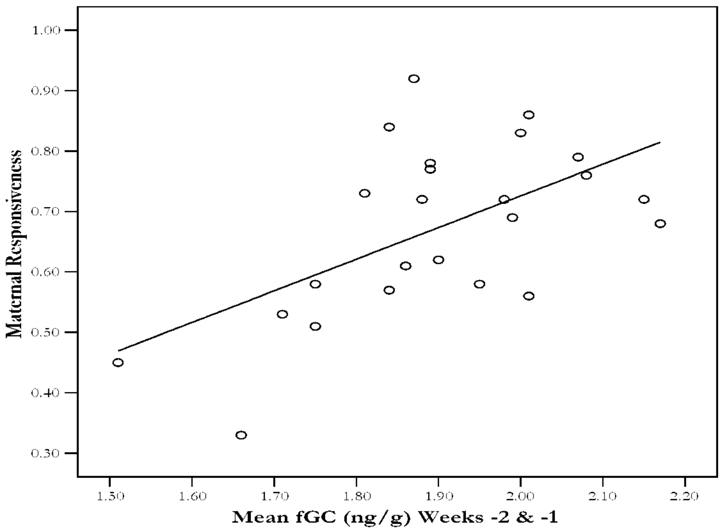

Maternal Responsiveness
1.00
0.90
0.80
0.70
0.60
0.50
0.40
0.30
1.50
1.60
1.70
1.80
1.90
2.00
2.10
2.20
Mean fGC (ng/g) Weeks -2 & -1

Fig. 1.3. Comparison of relative monthly mean fecal GC concentrations for the second to last month of pregnancy (weeks -8 to 5) to the last month of pregnancy (weeks -4 to -1).

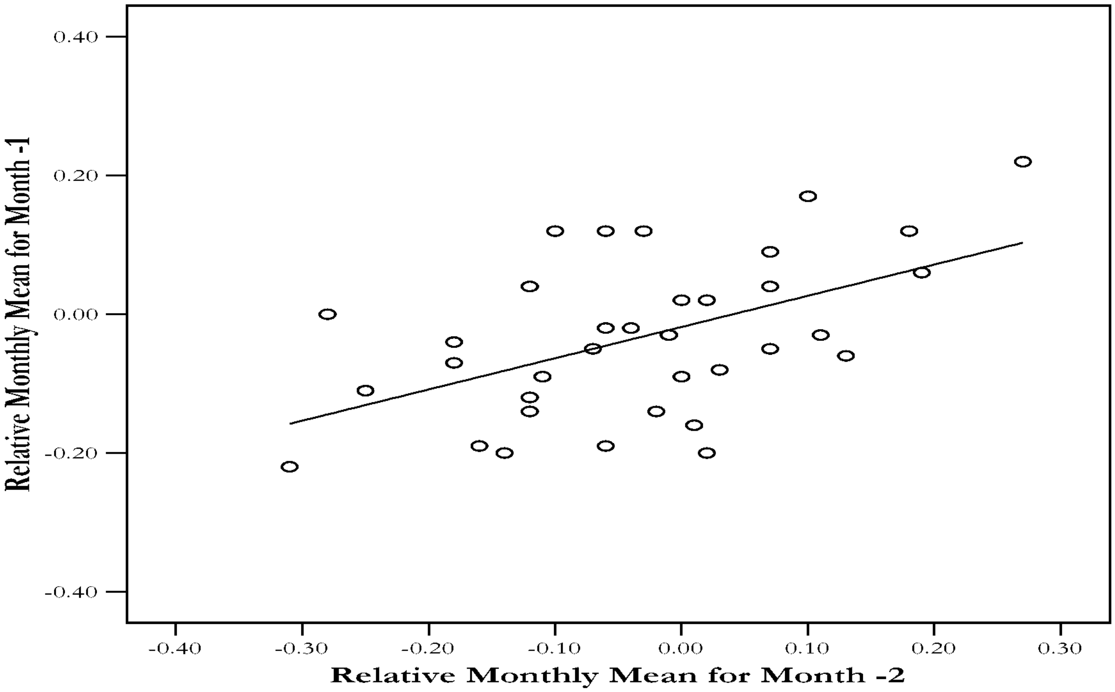


Table 1.I. Effects of maternal and infant characteristics on individual variation in maternal responsiveness to infant distress cries and peripartum fGC concentrations; results of linear regressions and t-tests showing that individual variation in neither responsiveness nor peripartum fGC concentrations were predictable from major maternal or infant characteristics. N=34 females unless otherwise noted.

Characteristic	**Responsiveness**	**Prepartum fGCs** [a]	**Postpartum fGCs** [b]
Maternal rank	r^2=.021 (p=.408)	r^2=.012 (p=.577)	r^2=.101 (p=.113)
Primipara vs. multipara	t_{32}=.271 (p=.788)	t_{26}=.435 (p=.667)	t_{24}=-.243 (p=.810)
Parity number among multipara	r^2=.022 (p=.447) [c]	r^2=.052 (p=.285)	r^2=.000 (p=.952)
Infant sex	t_{32}=1.29 (p=.207)	t_{26}=.438 (p=.665)	t_{24}=-.102 (p=.920)
Infant distress rate	r^2=.000 (p=.901)	r^2=.034 (p=.351)	r^2=.043 (p=.311)

[a] Mean value for females with at least 5 weeks of data for last 8 weeks of pregnancy (n=28)

[b] Mean value for females with at least 4 weeks of data for first 8 weeks after parturition, not including the first postpartum week (n=26)

[c] n=29

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CHAPTER TWO: Sex Differences in the Mother-Infant Relationship in Wild Baboons (*Papio cynocephalus*): Social and Hormonal Influences

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ABSTRACT

We examine hormonal and social factors as predictors of the patterning of mother-infant interactions during the first 8 weeks of life in 34 wild savannah baboon (*Papio cynocephalus*) mother-infant dyads in Amboseli, Kenya. We use contact and nursing behavior as measures of the mother-offspring relationship, and evaluate the extent to which perinatal ovarian steroids (fecal estrogens and progesterone), previous infant care experience, maternal dominance rank, and infant gender contribute to statistical explanation of variation in this relationship during a critical period of infant growth and development. Infants of more experienced mothers initiated higher rates of changes in mother-infant contact compared to infants of less experienced mothers. This pattern was found in both sexes, with male infants (n=19) initiating higher rates of transitions than female infants (n=15). Moreover, both high maternal rank and high prenatal estrogen concentrations predicted less suckling time for female infants but had no detectable effects on male infants' suckling time. Thus, while some factors, such as prior infant care experience, may affect the patterning of mother-infant interactions equally for both sexes, other factors, especially maternal rank, are more predictive for one sex than the other. Our results suggest that the mother's social world has a greater influence on the lives of female infants than on the lives of male infants. They highlight the emergence of developing sex differences in the behavior of newborn infant baboons that may become magnified during ontogeny.

INTRODUCTION

Among vertebrates, mammalian neonates are unusually dependent on their mothers for growth and survival. Lactation provides the sole source of nutrition for young infants, and in many species neonates also rely on their mothers for transportation, protection, and support (Clutton-Brock, 1991). As infants mature, however, they undergo rapid changes in their relationship with their primary caregiver. Over periods spanning several weeks in some species to several years in others, offspring must transition from complete reliance on their mothers to nutritional, locomotor and social independence (Clutton-Brock, 1991).

Individual differences in the mother-offspring relationship and in the timing of infant independence have been observed in a variety of mammalian taxa, from rodents (reviewed in McGuire and Bemis, in press) to nonhuman primates (reviewed in Fairbanks, 1996). These differences are believed to be related to differences among mother-infant dyads in maternal and infant characteristics, including mother's previous infant care experience (prairie voles, Microtus ochrogaster: Wang and Novak, 1992), physical condition (horses, Equus caballus: Cameron and Linklater, 2000), social status (red deer, Cervus elephus: Clutton-Brock, Albon, and Guinness, 1986), and offspring sex (red deer, Cervus elephus: Clutton-Brock, Albon, and Guinness, 1981; African elephant, Loxodonta africana: Lee and Moss, 1986). In addition to non-physiological factors, the neuroendocrine changes associated with pregnancy, parturition and lactation, have also been found to influence the patterning of mother-infant interactions and the timing of infant independence in several mammalian species.

In nonprimate mammals, ovarian steroid and peptide hormones associated with pregnancy, parturition and lactation (especially estrogens and prolactin) have long been known to be important for the onset and maintenance of postnatal maternal behavior (rodents: Bridges, 1990; Rosenblatt, 1990) (sheep: Dwyer, Gilbert, and Lawrence, 2004; Poindron and Levy, 1990) (rabbits: Gonzalez-Mariscal and Rosenblatt, 1996). Naturally occurring variation in maternal behavior in nonprimate mammals has been associated with differences in oxytocin receptor levels in the brain (rats: Champagne, Diorio, Sharma, and Meaney, 2001) and in plasma estradiol levels before birth (sheep: Dwyer et al., 2004).

Evidence from recent studies of human and nonhuman primates suggest that ovarian steroids, especially estrogens, may also be important in stimulating the expression of postnatal maternal behavior in primate mothers (Maestripieri and Zehr, 1998; Pryce, 1993). Less is known of the proximate physiological mechanisms, or neuroendocrine correlates, of *variability* in the mother-offspring relationship in primates than in nonprimate mammals. Research on this topic in primate mothers has produced conflicting results, with some studies finding positive (Dwyer et al., 2004; Pryce, Abbott, Hodges, and Martin, 1988) and others finding negative relationships between the quality of mother-infant interactions and concentrations of ovarian steroid hormones around the time of parturition (Bales, French, and Dietz, 2002; Fite and French, 2000; Fleming, Ruble, Krieger, and Wong, 1997; French, Koban, Rukstalis, Ramirez, Bardi, and Brent, 2004). Most prior studies were, however, confined to captive or laboratory populations of a few individuals. Captivity and provisioning can affect the expression of social behaviors (Groothuis and Vanmulekom, 1991; McPhee, 2004), modify neural processes and brain structures (Barnea and Nottebohm, 1994; Healy, Gwinner, and Krebs, 1996; Rosenzweig and Bennett, 1996), and influence the pattern of secretion of hormones (Baker, Gemmell, and Gemmell, 1998; Gardiner and Hall, 1997; Wingfield, Hegner, Dufty, and Ball, 1990); studies of wild populations are of particular value because they permit evaluations of the robustness of hormone-behavior relationships established in captivity in field settings (Costa and Sinervo, 2004; Fusani, Canoine, Goymann, Wikelski, and Hau, 2005).

In addition to proximate physiological factors, mother's prior infant care experience, social status, and infant gender have also been hypothesized to affect the patterning of mother-infant interactions in nonhuman primates (reviewed in Fairbanks 1996). Experience with previous infants has been reported to influence patterns of mother-infant interactions in several primate species (Berman, 1984; Fairbanks, 1988; Paul, Kuester, and Podzuweit, 1993; Schino, Damato, and Troisi, 1995). In most studies, older, more experienced mothers were found to be less protective than younger, less experienced mothers (Berman, 1984; Fairbanks, 1988; Gomendio, 1989; Hiraiwa, 1981; Hooley and Simpson, 1981; Schino et al., 1995) (but see Paul et al., 1993). The decreased maternal restraint associated with multiparity is often explained by the "experience hypothesis" (Fairbanks 1996). According to this hypothesis, experience with previous infants provides opportunities for mothers to enhance their parental skills, and increased exposure to infants makes mothers more competent in maternal care. Consequently, more experienced mothers may be more "laissez-faire" (Altmann, 1980) and more encouraging of infant independence because they are more efficient at infant care than less experienced mothers (Fairbanks 1996).

The social status of the mother has also been reported to affect the patterning of mother-infant interactions in at least three primate species, where low ranking mothers were found to be more protective of their infants than higher ranking mothers (Altmann, 1980; Digby, 1995; White and Hinde, 1975). The social risk factors normally associated with low dominance rank – higher levels of aggression – have also been related to greater protectiveness in two other populations (Hemelrijk and Dekogel, 1989; Simpson and Howe, 1986). These studies suggest that mothers may be more protective and less encouraging of infant independence when their infants are at greater risk from social aggression (Fairbanks 1996).

Sex differences in life histories and adult social behavior and ecology are widespread among mammals, including primates (Walters, 1987; Walters and Seyfarth, 1987). However, little is known of the time course, mechanisms and processes of physical and behavioral development of immature primates (Pereira, 1993). Sex differences in the social play of immatures have been observed in several species (Fagen, 1993; Maestripieri and Ross, 2004; Walters, 1987) and these differences have been related to differences in adult social behavior. In addition, sexual dimorphism in both social and foraging behavior of juvenile primates has been observed in a variety of species (Agostini and Visalberghi, 2005; Pereira, 1988; Strier, 1993; van Noordwijk, Hemelrijk, Herremans, and Sterck, 1993). These differences have been related to the divergent social and foraging skills of adult males and females and have been interpreted as reflecting juvenile primates' preparation for adulthood. However, it is unknown whether infant gender influences the patterning of social behavior even among very young infants who are dependent on their mothers as their primary caregiver and social partner.

We examine the effects of multiple (physiological and non-physiological) variables on the mother-offspring relationship during the first 8 weeks of infancy in 34 wild-feeding, free-ranging yellow baboon (*Papio cynocephalus*) mother-infant dyads in Amboseli, Kenya. Few studies have evaluated the influence of both types of variables on the mother-infant relationship, and only one prior study has done so in a wild animal population (Bales et al., 2002). Bales and colleagues (2002) focused their study on the golden lion tamarin (*Leontopithecus rosalia*), a cooperatively breeding mammal species in which most forms of offspring care can be provided by group members other than the mother. Our study focuses on a primate species in which mothers perform all forms of offspring care. We use contact and nursing behavior as measures of the mother-offspring relationship, and examine the extent to which perinatal ovarian steroids (excreted in feces), previous infant care experience, maternal dominance rank, and infant gender contribute to variation in the mother-infant relationship during a critical period of infant growth and development.

METHODS

Subjects and Data Considerations

Thirty-four mother-infant dyads living in five groups of wild yellow baboons (*Papio cynocephalus*) in the Amboseli basin, Kenya were studied from Sep 2002 to Nov 2003 by NN. Baboons are among the largest, most sexually dimorphic, omnivorous, and terrestrial of the monkeys. Yellow baboons are found in East Africa in semi-closed groups numbering from 10-200 members.

Subjects are part of a larger population of baboons that has been under continuous observation for over three decades (e.g. Alberts, Watts, and Altmann, 2003; Altmann, 1980; Altmann, 1998; Altmann and Altmann, 1970). The histories of each female in the population are known since birth from near-daily records of demographic events and reproductive cycles. All pregnant females who bore live young that survived the first two months of infancy were included in this study.

Fecal and focal sampling began on pregnant females two months prior to parturition and after birth, each mother-infant dyad was sampled throughout the first 8 postnatal weeks. Individual females and mother-infant dyads differed in the days on which they were sampled. Since such differences can confound analyses of individual differences during a rapid period of change in both behavior and hormones, we examined individual differences across females and across pairs using deviations from the average pattern for each point in time (measured in days or weeks) relative to parturition. We chose LOWESS (with a window of 0.5) because it is more "locally sensitive" to time-specific deviations from the average pattern (Altmann and Alberts, 2005; Moses, Gale, and

Altmann, 1992). All subsequent analyses, therefore, use deviations or residuals from the LOWESS-determined class average at each point in time relative to parturition.

Behavioral Measures

Each mother-infant pair was observed, on average, for 11.6 + 4.5 (SD) actual in-sight observation hours in 33.2 + 12.2 (SD), 20 min focal animal samples (Altmann, 1974) during the first 8 postnatal weeks. During each 20 min sample on a mother-infant pair, continuous records were kept on all changes in mother-infant contact, described as in or out of physical contact, and including the identity of the individual responsible for the change in contact state. In addition, all occurrences of social and/or agonistic interactions between (a) the mother and infant and (b) mother or infant and other members of their social group, including actor and recipient identities, were recorded during each focal sample. Within the focal samples, embedded point samples (Altmann 1974) were made every 5 min. on the activity of the focal female and her infant [feed (or nurse for the infant), rest, walk, etc.].

We use mother-infant contact and nursing as measures of the mother-infant relationship. Mother-infant contact was described by two measures: (1) the proportion of total changes in mother-infant contact or "transitions" made by the infant, and (2) the rate of transitions initiated by the infant. Time spent off the nipple was measured as the proportion of point samples in which the infant was not observed on the nipple.

Each pair's residual values for contact and nursing were measured as the pair's deviation from the class average for each of the 8 postnatal weeks, calculated as the pair's value for a given measure (e.g. the pair's rate of infant-initiated transitions for a given week) minus the class average for that measure (e.g. the average rate of infant-initiated transitions) for that week. Pairs with positive residuals have values above the class average, those with negative residuals have values below the class average for that week. For the contact measures, we omitted data from the first postnatal week because few changes in mother-infant contact occurred during this week. For each of the three measures of the mother-infant relationship, we use the mean of an individual pair's residuals as an informative measure of their behavior-for-infant age in weeks.

Biographic Measures

Data on maternal parity and dominance rank of subject mother-infant dyads were extracted from the long-term, electronic records of the Amboseli database, and infant sex was determined in the field within a few days following birth. Maternal age, parity and infant care experience are closely interrelated variables in this population. Parity, defined as a female's total number of pregnancies, regardless of outcome, and including the current offspring, was correlated with maternal age ($r^2=.91$, $n=34$, $p<.0005$). Our study included five primiparous females with no prior infant care experience and 29 multiparous females, with prior experience rearing 1-8 offspring each. For the six mothers with only one previous pregnancy, each had prior experience rearing offspring to at least 4.5 months of age. In our analyses, we use parity as a shorthand measure for mother's prior infant care experience.

Data on agonistic interactions collected during this study, along with data collected as part of regular monitoring of study groups, were used to assign relative ranks to each group member each month. Dominance ranks were determined by assigning wins and losses in dyadic agonistic encounters between group members (Alberts et al., 2003; Hausfater, 1975). Individuals were considered to have won encounters when their opponent gave only submissive gestures, while they gave only aggressive, or neutral (nonsubmisive) gestures (Alberts et al., 2003; Hausfater, 1975). A female's dominance rank among the adult females in her group the month her infant was conceived was considered her maternal dominance rank for that infant (Altmann 1980). Stability of dominance ranks throughout adulthood and even across generations has been documented for baboon and macaque females (Melnick and Pearl, 1987a; Pereira, 1995).

Fecal Hormone Sampling and Measurement

A total of 694 fecal samples were collected, giving an average of 1.3 fecal samples per female per week for each of the 8 weeks prior to and after parturition. Fecal samples were collected within minutes of deposit in a vial prefilled with 95% ethanol in a ratio of 2.5:1 ethanol to feces. Samples were stored in an evaporation cooler at ~15(daily minimum)-25(daily maximum)°C in the field camp before they were transported, every two weeks, to the University of Nairobi. There the ethanol was evaporated and the samples were lyophilized and stored in a -20°C freezer. Samples were then transported to Princeton University where each was sifted through fine mesh and 0.2 g of sample was extracted into 2 ml of 90% methanol. The methanol extracts were then subjected to solid phase extraction (Waters, Milford MA, WAT094226) (Khan, Altmann, Isani, and Yu, 2002; Lynch, Khan, Altmann, Njahira, and Rubenstein, 2003).

The concentration of total estrogens (E hereafter) and progesterone (P hereafter) in each fecal extract was assessed using I-125 radioimmunoassays. All samples were assayed in duplicate and mean concentrations were expressed as ng of hormone per g of dry fecal matter, to control for dietary differences between individuals and seasons (Wasser, Thomas, Nair, Guidry, Southers, Lucas, Wildt, and Monfort, 1993). Samples were assayed for estrogen metabolites using a total estrogens kit (ICN Diagnostics Division, Costa Mesa, California, USA, see Khan et al. 2002 for assay validation). The primary antibody in this kit has high cross-reactivities with the major estradiol metabolites present in baboon feces (Wasser et al. 1994). Samples were assayed for progesterone using the Direct Progesterone kit (Pantex, Santa Monica, CA). Though only a small portion of progestogens are excreted as progesterone in feces (Wasser, Monfort, Southers, and Wildt, 1994), the primary antibody in this kit cross-reacts 100% with progesterone (Lynch et al. 2003).

Endocrine data were divided into days relative to parturition, with the day before parturition considered day -1, the date of parturition considered day 0, and the day after parturition day 1. We generated separate pre- and postnatal LOWESS plots, and calculated each female's deviations from the class average for each hormone as the ratio of the female's E or P concentrations to the class average for that hormone that day. Females with residuals above 1.0 have values above the class average, those with residuals below 1.0 have values below the class average for that hormone that day. We excluded samples from days 0-3 from analyses of the postnatal period because, due to the 1-3 day lag time between steroid hormone secretion and excretion in feces (Wasser et al. 1994), values from these days were believed to reflect prenatal levels. These daily values were then divided into weeks relative to parturition, with the date of parturition considered the first day of "week 1", and the day before parturition considered the last day of "week -1", so as to produce a single value for each female each week. We then use the $\log_{10}$ of the mean of an individual female's residuals for the pre- and postnatal periods as informative measures of her relative E and P concentrations for each period.

Data Analysis

Our analysis strategy involved three steps. First, we evaluated the stability of mother-infant pair differences in all three measures of the mother-offspring relationship. Second, we evaluated the stability of individual mother's ovarian steroid concentrations over the perinatal period. We conducted these analyses of within-pair or within-individual stability using linear regression analyses on each pair's relative behavioral scores or each mother's relative hormonal scores across the perinatal weeks. We did this to determine whether these behavioral and hormonal measures represented stable individual or pair traits during the perinatal period, a time of rapid changes in both hormones and behavior. We then applied general linear model (GLM) and multiple regression procedures to evaluate (a) the sources of variability in perinatal E and P and (b) the sources of variability in the mother-infant relationship. To evaluate the sources of variability in perinatal E and P, we examined the effect of (1) the mother's parity, (2) maternal rank at conception, and (3) infant sex on the mean pre- and postpartum relative concentrations for E and P using GLM procedures. To evaluate the sources of variability in the mother-infant relationship, we examined the effect of (1) parity, (2) maternal rank, (3) infant sex, and (4) mean relative pre- and postnatal E or P concentrations on mother-infant contact and suckling behavior using GLM procedures. The effect of infant gender on the mother-infant relationship was further evaluated by conducting separate tests for each sex if dyads consisting of males and females differed with respect to the patterns observed in the pooled comparisons. If a model indicates that more than one variable has a significant or nearly significant effect on a measure of the mother-infant relationship, we used hierarchical multiple regression to control for the variable with the greatest effect, and then determined the additional unique contribution(s) of the other variable(s).

All statistical analyses were conducted using SPSS 12.0 (SPSS Inc. 2003). Relationships between explanatory variables were explored using Pearson's correlation coefficients. Values reported are means + SE. All analyses were two-tailed with $p<0.05$.

RESULTS

General Patterns

Infants became increasingly responsible for changes in mother-infant contact with age. The rate of change in contact initiated by infants increased steadily over the first 8 postnatal weeks while the rate of change in contact initiated by mothers varied little across this period (Fig 1A). Consequently, the proportion of infant-initiated transitions increased while the proportion of mother-initiated transitions declined over time (Fig. 1B). Similarly, infants spent increasing amounts of time off the nipple as they aged (Fig. 1C).

Both E and P concentrations remained consistently high across the last 8 weeks of pregnancy and declined precipitously after parturition (Fig. 2). By the second half of the first postnatal week, both E and P concentrations had returned to levels characteristic of non-pregnant females (see Beehner et al. (in press)) and remained at these levels to the end of the sampling period.

Individual and Pair Differences

Dyads differed in the patterning of mother-infant interactions and these differences were found to be stable across weeks, with most pairs showing considerable consistency in relative values for all three measures of the mother-infant relationship. Over 82% of the 34 pairs showed no significant time trend up or down in the relative rate of transitions initiated by the infant across weeks. In addition, over 88% of pairs showed no significant trend up or down in the relative proportion of infant-initiated changes in contact across weeks (n=5.9+1.0 SD relative values/pair for each measure). Finally, over 88% of pairs showed no significant trend up or down in the relative proportion of time off the nipple (n=6.8+1.2 SD relative values/pair). We infer from these findings that stable differences in the patterning of mother-infant interactions existed across dyads, with some pairs exhibiting consistently lower levels while others exhibited consistently higher levels of each behavior.

In addition, individuals differed in E and P concentrations and these differences were found to be stable across weeks, with most females showing considerable consistency in relative E and P concentrations. Over 70% of the 27 females with samples from at least 10 of the 16 perinatal weeks showed no significant time trend up or down in relative E or P concentrations over this period. We infer from these findings that stable differences in perinatal E and P concentrations existed across individuals, with some females characterized by consistently lower levels while others were characterized by consistently higher levels of each steroid. These results allow us to use (with confidence) average values for the mean pre- and postnatal period as informative measures of an individual female's relative E and P concentrations for each period. We then proceeded to apply regression and GLM procedures to evaluate the sources and consequences of variability in the mother-infant relationship and in perinatal E and P across dyads.

Predictors of Variability in Perinatal E and P

Females' mean relative concentrations of postpartum E, and both pre- and postnatal P were not predictable from infant sex, maternal rank or parity. Mean prepartum E was, however, predictable from maternal rank (F(1,30)=8.2, p=.007, Fig. 1), with higher ranking females characterized by higher mean prepartum E concentrations than lower ranking females. Though infant gender had no direct effects on prepartum E concentrations and the positive association between rank and prepartum E was observed in both dyads with male (r^2=.10, n=19, p=.19) and female (r^2=.35, n=15, p=.02) infants, the strongest (and only significant) effects were seen in dyads with female infants (Fig. 3).

Predictors of Variability in the Mother-Infant Relationship

Mother-infant contact

The two contact measures were correlated, with infants initiating higher rates of transitions in mother-infant contact overall also responsible for greater proportions of transitions overall (r^2_{34}=.30, p=.002). For simplicity, we use the rate of transitions initiated by infants as the measure of mother-infant contact interactions in subsequent analyses.

Mother-infant contact interactions were not predictable from perinatal E or P concentrations or by maternal rank. However, the rate of transitions initiated by infants was predictable from both parity (F(1, 28)=4.415, p=.045) and infant sex (F(1,28)=4.181, p=.050; Fig. 4). The higher the mother's parity number, and the more prior infant care experience she had, the more her infant initiated changes in mother-infant contact (Fig. 4). This pattern was found in both sexes, with male infants (n=19) initiating higher rates of transitions than female infants (n=15; Fig. 4). In multiple regression, parity alone explained 34% of the variance in the rate of infant-initiated transitions (F(1, 32)=16.105, p<.0005) and infant gender explained an additional 24% of the variance in transition rates (F(1, 31)=16.909, p<.0005). These results suggest that more experienced mothers and mothers of male infants may be more encouraging of infant independence than less experienced mothers and mothers of female infants.

Infant's time off the nipple

Mother-infant contact interactions and nursing behavior were weakly correlated, with infants initiating higher rates of transitions in mother-infant contact overall also spending more time off the nipple overall (r^2_{34}=.11, p=.061). This finding suggests that there was a general tendency for more active infants to be off the nipple more often than less active infants.

Though male and female infants differed significantly in relative rates of transitions (t(32)=2.4, p=.02), they did not differ significantly in the percent of time off the nipple (t(32)=.74, p=.47). When all 34 mother-infant dyads were considered, time off the nipple was not affected by infant sex, maternal parity or postnatal E or perinatal P concentrations. However, the percent of time infants spent off the nipple was nearly significantly influenced by prenatal E concentrations (F(1,28)=3.8, p=.061) and by maternal rank (F(1,28)=3.7, p=.065). Since maternal rank was more closely associated with perinatal E concentrations in mothers of female than in mothers of male infants (Fig. 3), we tested for the effects of rank and perinatal E on time off the nipple separately for each sex using multiple regression. In dyads with female infants, maternal rank and prenatal E concentrations together predicted infants' time off the nipple (F(2, 12)=6.8, p=.01), though neither rank (beta=-.34, p=.19) nor prenatal E (beta=.47, p=.08) alone made statistically significant contributions, with prenatal E having the larger effect of the two. In contrast, in dyads with male infants, infants' time off the nipple was not predictable from either maternal rank (beta=-.27, p=.29) or prenatal E (beta=.19, p=.44) alone, or with both factors in the model (F(2, 16)=1.3, p=.296).

These results indicate that though parity affected mother-infant contact interactions in both dyads with male and dyads with female infants, maternal rank and prenatal E concentrations predicted female infants' time off the nipple but had no detectable effects on male infants' time off the nipple.

DISCUSSION

Individual mother-infant dyads in the wild baboon population at Amboseli showed clear consistency in the patterning of within dyad interactions over the first two months of infancy. We inferred from this finding that stable differences in the mother-offspring relationship exist across dyads, and we proceeded to evaluate the sources of this variability, using biographic, social and endocrine factors as predictors. Several variables were found to affect the patterning of mother-infant interactions in our study population, with some more important for female than male offspring. Though rates of infant-initiated transitions were higher among male than female infants, offspring of more experienced mothers of both sexes initiated higher rates of transitions than those of less experienced mothers. However, maternal dominance rank and prenatal Es were predictive of time off the nipple for female infants, but had no effect on male infant's time off the nipple. These results can be interpreted to signify the greater influence of the mother's social world on the lives of female infants than on the lives of male infants and suggest the emergence of sex differences in the behavior of newborn infants that may become magnified during ontogeny.

Experience Effects on the Development of Infant Independence

In both dyads with male and female offspring, the more prior infant care experience mothers had, the more their infants initiated changes in mother-infant contact. Since age is related to prior infant care experience in this population, these results suggest that older mothers were less protective and more encouraging of infant independence than younger mothers. General life history theory predicts that, in species in which reproductive value declines with age, reproductive effort should increase with declining life expectancy (Clutton-Brock, 1984). In most reports of the cessation of reproduction in female mammals, there is little evidence of the midlife termination of reproduction observed in human females (Pavelka, Fedigan, and Zohar, 2002). Fertility is relatively stable throughout the adult lifespan, but declines abruptly as females approach their maximum expected life span for those few individuals surviving to this age [bighorn ewes, *Ovis canadensis*: (Berube, Festa-Bianchet, and Jorgenson, 1999); red deer, *Cervus elaphus*: (Fisher, McLeod, Mockett, Moore, and Krew, 1996); Japanese macaques, *Macaca fuscata*: (Fedigan and Pavelka, 2001; Pavelka and Fedigan, 1999); olive baboons, *Papio anubis*: (Packer, Tatar, and Collins, 1998); African lions, *Panthera leo* : (Packer et al., 1998)].

In baboons at Amboseli, maximum reported longevity for females in the wild is 26 to 27 years (Altmann and Alberts, 2003). Data on this population indicate that female mortality and birth rates are both relatively stable throughout much of adulthood, with mortality increasing gradually in the latter part of females' second decade of life, though birth rates remain stable until the beginning of the third decade of life for the few individuals who survive that long (Altmann and Alberts, 2003). In this study, mothers averaged 10.15+3.36 (mean+SD) years (range 5.29-17.76 years), with most (94%) mothers <16 years of age when their infants were born. Because none of the mothers in our study had approached the end of the average female reproductive lifespan, life history theory would not expect maternal investment (i.e. reproductive effort) to vary appreciably among this population of mothers.

However, the behavior of offspring suggests mothers did adjust their behavior towards infants in accordance with their own age and prior infant care experience. Our result is consistent with the supposition that older, more experienced mothers are more permissive and encouraging of infant independence because they are more competent and efficient at infant care than younger, less experienced mothers. Older mothers may target their infant care efforts more effectively (i.e. to those periods in which they are most critical for infant survival, growth and development) without investing more, and possibly investing less, in each offspring (Cameron, Linklater, Stafford, and Minot, 2000). Data consistent of this "targeted investment" hypothesis have been reported in horses (Cameron et al., 2000), and in several populations of captive and provisioned cercopithecine primates (Berman, 1984; Mitchell and Stevens, 1968; Schino et al., 1995) (but see Paul et al., 1993). The permissive rearing style of older mothers in our population may lead their infants to seek nutritional, locomotor, or social independence at an earlier age (Fairbanks, 1996), and this precociousness can have important life-history consequences for both mothers and offspring.

Infant Gender Effects on the Mother-Infant Relationship

Sex differences in infant-initiated changes in contact

Sex differences in adult social behavior and ecology are thought to originate in the perinatal period with infant exposure to sexually-differentiating hormonal events (Goy and McEwen, 1980) and social experiences (Meaney and Stewart, 1981). First, during fetal development, exposure of the developing brain to testosterone and other androgens causes the masculinizaiton and defeminization of the parts of the nervous system governing the expression of sexually dimorphic behaviors. Once permanently "organized", these sex differences can then be "activated" when needed by steroid hormones in adulthood (rodents: Grady, Phoenix, and Young, 1965; Phoenix, Goy, Gerall, and Young, 1959) (rhesus macaques: Goy and McEwen, 1980). The early social experiences of infants with conspecifics, including their own mothers, can also affect the development of sex differences in behavior (reviewed in (Meaney, Stewart, and Beatty, 1985)). Though sex differences in social play and mounting behavior appear to be widespread among older primate infants (Meaney et al., 1985), few studies have examined sex differences in the mother-infant relationship in the early postnatal period.

In this study, male infants were, on average, more active than female infants and initiated more changes in mother-infant contact than female infants. These data suggest that mothers of male infants may be more permissive and encouraging of infant independence than mothers of female infants, and provide one of the first demonstrations of the emergence of sex differences in the mother-infant relationship in a wild primate population. Our finding is consistent with those from several previous studies, conducted largely on laboratory or captive populations of macaques, of male infants exhibiting greater activity and enjoying greater freedom of movement than female infants (Jensen, Bobbitt, and Gordon, 1968; Mitchell, 1979; Mitchell and Brandt, 1970; Nakamichi, Cho, and Minami, 1990).

Consistent with these sex differences, males in several primate species have been reported to become independent of their mothers at an earlier age than females (chimpanzees, Nicolson, 1977) (pigtail macaques, Erwin, Anderson, and Bunger, 1975; Jensen, Bobbitt, and Gordon, 1967) (Japanese macaques, Itani, 1959) (bonnet macaques, Simonds, 1974) (rhesus macaques, Hinde, 1971), with some females maintaining close affiliative ties to their mothers long after sexual maturation (cercopithecine monkeys, Gouzoules and Gouzoules, 1987) (ringtailed lemurs, Nakamichi and Koyama, 1997).

Male baboons typically disperse from their natal groups as they near adult size and many continue to migrate between social groups throughout their lives (Alberts and Altmann, 1995). In contrast, female baboons remain in their natal group their entire lives, inheriting their mother's rank in the group's dominance hierarchy as juveniles (Walters, 1980). Our results suggest that, from a very early age, male infants are encouraged to explore the wider physical and social world beyond their mother's body, behavior which may help prepare them for their adult lives as migrants.

Effects of maternal rank and prenatal E on female infant's time off the nipple

Irrespective of infant sex, higher ranking mothers in our study had higher prenatal E concentrations. However, this pattern was stronger in mothers of female than male infants, and only in female infants was the combination of both high maternal dominance rank and high prenatal Es predictive of less suckling time. These results suggest that, from a very early age, the lives of female infants, but not those of male infants, are strongly influenced by their mother's social status.

Social aggression is a pervasive feature of life in baboon groups, even among females, who, like females in other female-philopatric cercopithecine primates, form stable dominance hierarchies that persist within and even between generations (Melnick and Pearl, 1987b; Walters, 1987). Because juvenile daughters often assume the rank immediately below those of their mothers in the group's dominance hierarchy, females' social experiences as immatures are expected to be strongly influenced by those of their mothers. Data from several primate populations (Digby, 1995; Hemelrijk and Dekogel, 1989; Simpson and Howe, 1986; White and Hinde, 1975), including baboons at Amboseli (Altmann, 1980), suggest that primate mothers are more protective and less encouraging of infant independence when their infants are at greater risk from social aggression. In this study, mothers were more restrictive and less permissive of female infants spending time off the nipple – and presumably out of body contact– the lower they ranked in the group's dominance hierarchy. This greater protectiveness may discourage female infants of low ranking mothers from venturing far from their mother's protection, where they are at greater risk of social aggression. In fact, one mechanism through which female offspring may "inherit" their mothers' rank is via aggression directed by other females towards offspring of lower-ranking females (Holekamp and Smale, 1991).

In addition to higher maternal dominance rank, higher prenatal concentrations of Es also predicted greater time off the nipple for female infants. The positive relationship between mothers' prenatal Es and infants' time off the nipple may be due to metabolic processes. In pregnant rats, estradiol decreases food intake and increases energy expenditure, causing body fat stores to decrease (Wade and Schneider, 1992). Reduced fat stores may then lead to reduced milk production (e.g. Crete and Huot, 1993) and subsequently reduced nursing time for mothers with higher prenatal concentrations of Es. However, this explanation is unsatisfying given that higher ranking mothers in our population had higher prenatal Es and prior studies of this and other populations have found that higher ranking females often have greater access to food resources than lower ranking females (Barton and Whiten, 1993; Post, Hausfater, and McCuskey, 1980; Saito, 1996; Sterck, Watts, and vanSchaik, 1997; Whitten, 1983).

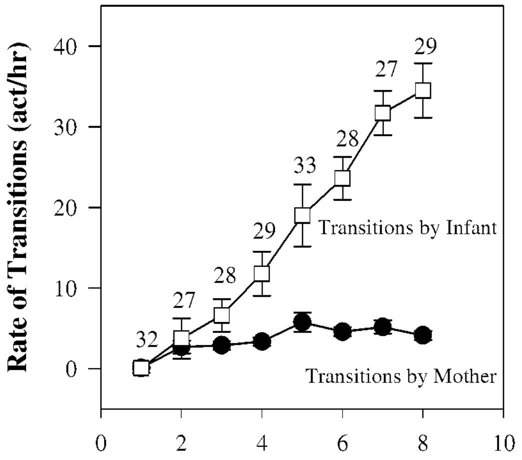
It remains possible, however, that though time spent on the nipple varied among pairs, overall milk or energy intake by infants did not. Variation in the suckling ability of infants and in milk composition may confound efforts to relate the amount of time spent suckling with milk or energy intake (Cameron, 1998). Unfortunately, techniques to more accurately measure milk transfer using radioactively labeled milk are not feasible for wild primate populations because they require capture and recapture of the mother and infant during a highly sensitive period of infant growth and development. Information on the mechanisms through which maternal dominance rank and prenatal Es may affect the patterning of mother-infant interactions therefore await further study.

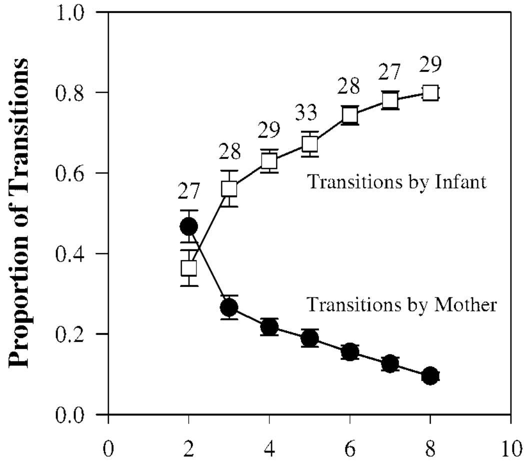
Recent empirical data from primate and nonprimate mammals suggest that perinatal concentrations of ovarian steroids, particularly Es, are important factors affecting variability in the mother-offspring relationship. For example, in self-report questionnaires, human mothers with higher prenatal concentrations of E expressed more negative mood states and felt less attached to their infants than mothers with lower prenatal Es (Fleming et al., 1997). Similarly, in captive baboons, mothers exhibiting poor or no infant care behaviors had higher concentrations of prenatal Es than "normal" mothers (French et al., 2004). In contrast, in sheep, mothers with higher prenatal Es groomed their infants more often than mothers with lower prenatal Es (Dwyer et al., 2004). And, in captive callitrichid primates, infant survivorship to 1 or 2 weeks was predictable from prenatal concentrations of Es, though in one study prenatal Es positively predicted infant survivorship (Pryce, 1988) while in another, the opposite pattern was observed (Fite and French, 2000).

The vast majority of prior studies of the effects of perinatal concentrations of Es on the mother-infant relationship have focused on captive or laboratory populations. Some have used indirect measures of offspring care in place of observations of behavior, making direct comparisons across studies are difficult. Because captivity and provisioning can affect the expression of social behaviors (Groothuis and Vanmulekom, 1991; McPhee, 2004), modify neural processes and brain structures (Barnea and Nottebohm, 1994; Healy et al., 1996; Rosenzweig and Bennett, 1996), and influence the pattern of secretion of hormones (Baker et al., 1998; Gardiner and Hall, 1997; Wingfield et al., 1990), studies of wild populations are of particular value because they permit evaluations of the robustness of hormone-behavior relationships established in captivity in field settings, where animals are exposed to a diversity of ecological and social stimuli often absent from captive settings (Costa and Sinervo, 2004; Fusani et al., 2005). Our study is the first to find evidence that variability in the patterning of mother-infant interactions in wild primates may be influenced by prenatal concentrations of Es, a finding previously only reported for captive primates (e.g. French et al., 2004; Pryce, 1988).

In summary, our results suggest that sex differences in the social behavior of infants emerge, in part, from infants' social interactions with their own mothers and from infants' experience of their mother's physical and social world.

Fig. 2.1. Change in mother-infant contact by week from birth. (A) Proportion of changes in mother-infant contact initated by the infant or by the mother by week from parturition, (B) Rate of changes in mother-infant contact initiated by the infant or by the mother by week from parturition, (C) Proportion of time on the nipple by week after parturition. Data are presented for the first 8 postnatal weeks for B and C. Because almost no transitions occurred during the first week, the proportion of transitions by infant or mother are only presented for weeks 2-8 (A). Numbers represent the number of individuals or mother-infant pairs with data each week.


Rate of Transitions (act/hr)
40
30
20
10
0
0
2
4
6
8
10
32
27
28
29
33
28
27
29
Transitions by Infant
Transitions by Mother


Proportion of Transitions
1.0
0.8
0.6
0.4
0.2
0.0
0
2
4
6
8
10
27
28
29
33
28
27
29
Transitions by Infant
Transitions by Mother

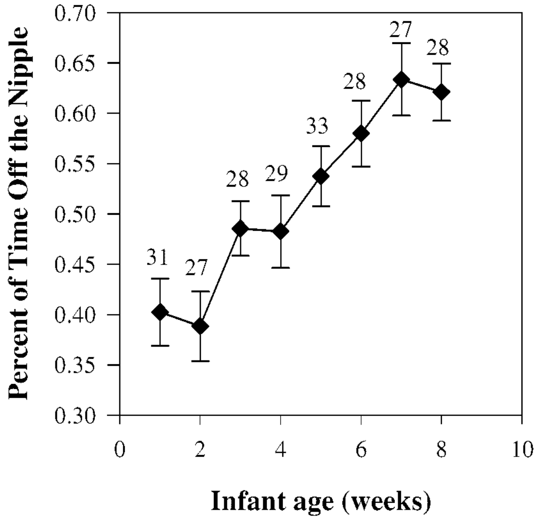

Percent of Time Off the Nipple
0.70
0.65
0.60
0.55
0.50
0.45
0.40
0.35
0.30
0
2
4
6
8
10
31
27
28
29
33
28
27
28
Infant age (weeks)

Fig. 2.2. Mean concentrations of total estrogens and progesterone (ng/g feces + SE) by week from parturition. Because of the 1-3 day lag time between steroid hormone secretion and excretion in feces (Wasser et al. 1993), values from the first postnatal week are divided into two periods, one encompassing days 0-3, presumed to reflect prenatal values, and one encompassing days 4-6.

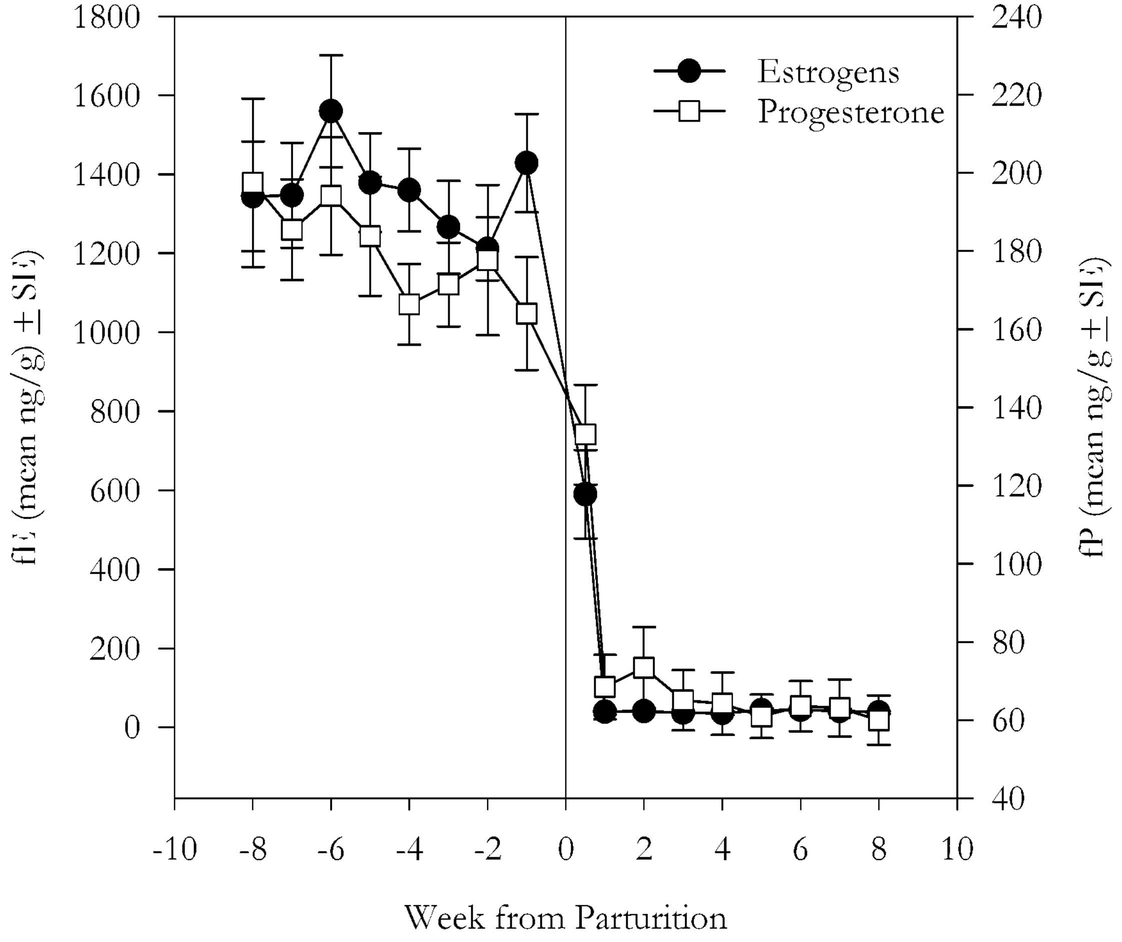


Fig. 2.3. The relationship between mean prenatal E concentrations and maternal rank for mothers with male (♂) and female (♀) infants. Each point represents a mother's rank at conception and the mother's mean relative E concentration during the last two months of pregnancy. The solid line represents the regression line for all 34 mother-infant dyads combined. The small dotted line represents the line for dyads with female infants (r2=.35, n=15) and the large dotted line represents the regression line for dyads with male infants (r2=.10, n=19).

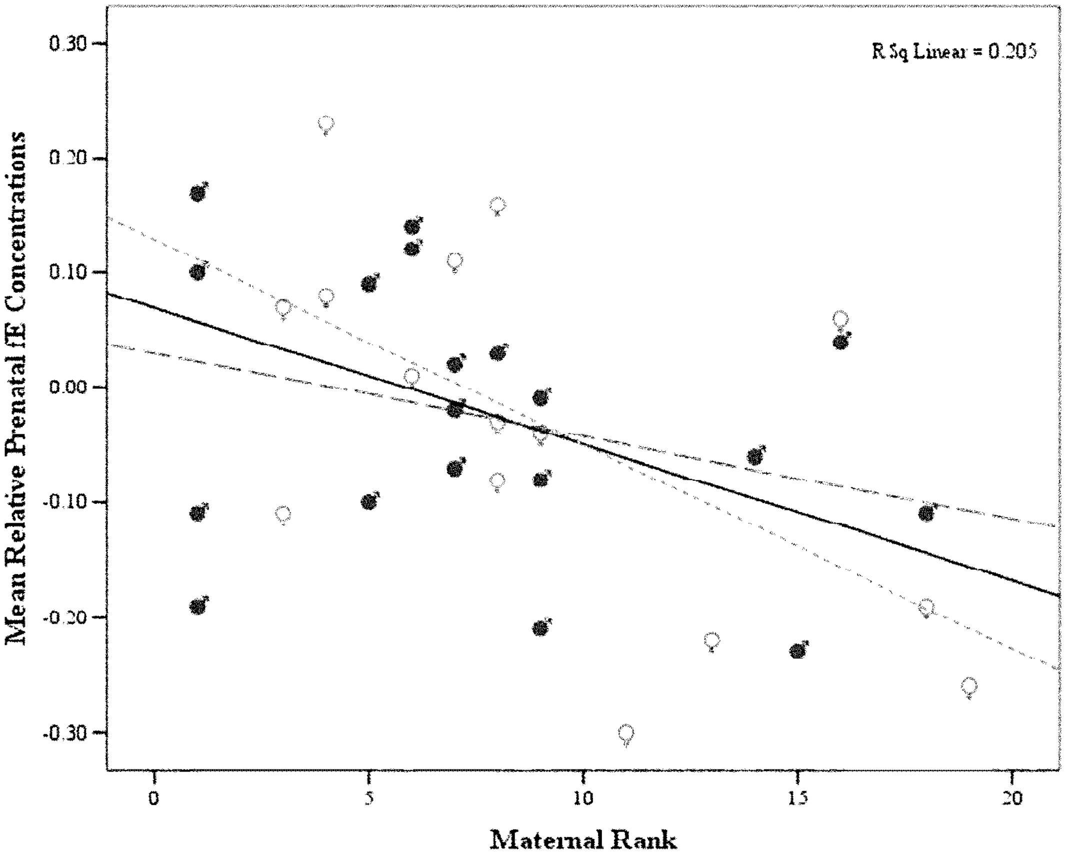
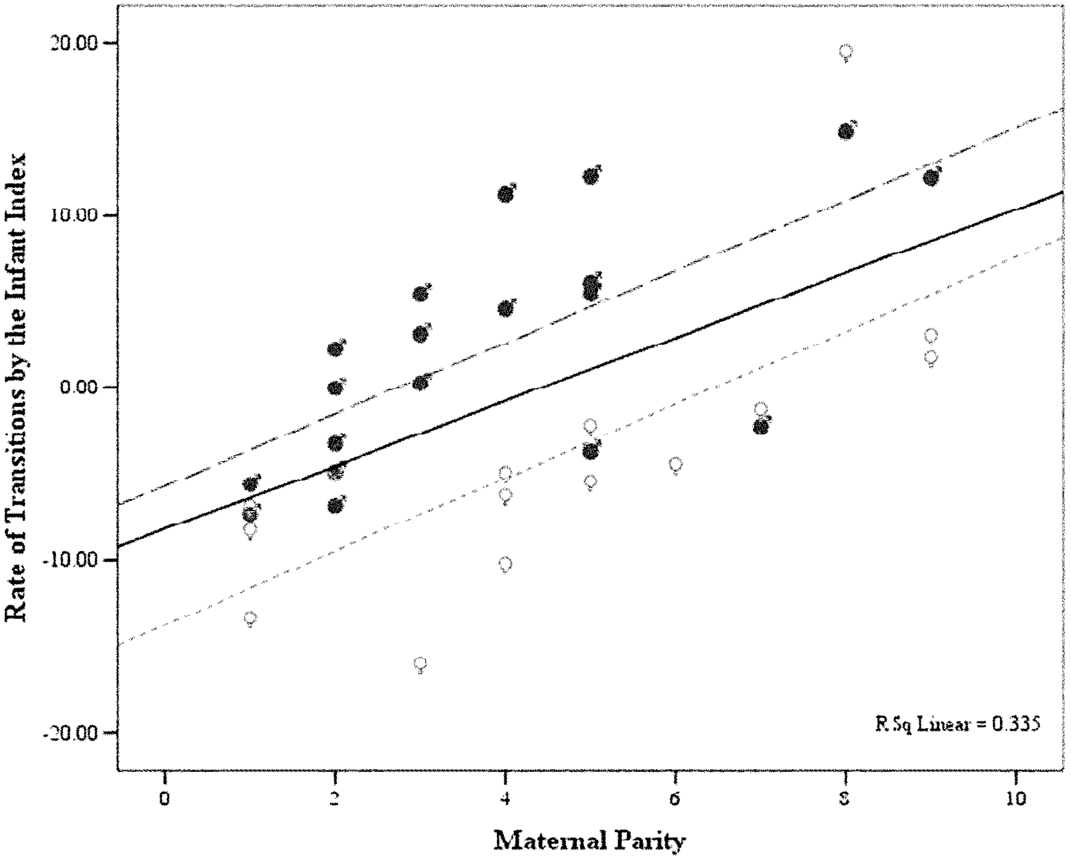


Fig. 2.4. The rate of infant-initiated transitions as a function of maternal parity for dyads with male (♂) and female (♀) infants. Each point represents a given mother-infant dyad's maternal parity and index score for the rate of infant-initiated transitions (see text). The solid line represents the regression line for all 34 mother-infant dyads combined. The small dotted line represents the line for dyads with female infants (n=15, r^2=.51) and the large dotted line represents the regression line for dyads with male infants (n=19, r^2=.47). Parity is associated with higher rates of infant-initiated transitions in both male and female infants. On average, male infants initiated higher rates of transitions than did female infants.



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CHAPTER THREE: "Friendships" Between New Mothers and Adult Males: Adaptive Benefits and Determinants in Wild Baboons (*Papio cynocephalus*)

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ABSTRACT

Close associations between adult males and anestrous females and their dependent offspring are rare in mammals, but are regularly observed in several primate species that live in multi-male, multi-female social groups. The existence of these relationships, called ‘friendships’, raises questions about their adaptive advantages for the male and female participants. Using data from genetic paternity analyses, patterns of behavior among parents, offspring, and other group members, and long-term (>30 years) demographic and reproductive records from a wild baboon population, we examine the patterning of male-female associations during the early postnatal period in four multi-male yellow baboon (*Papio cynocephalus*) groups in Amboseli, Kenya, and evaluate two hypotheses for why friendships might be adaptive for each sex. For females, we found strong evidence consistent with the female harassment hypothesis, that male friends provide protection to mothers and infants from harassment by other adult and immature females. In contrast, our results were inconsistent with the anti-infanticide hypothesis that has been suggested to account for the evolution of year-round male-female bonds in social animals, including primates. For males, we found some evidence consistent with the paternal care hypothesis, that friendships represent a form of parental investment in offspring by males. However, our results were not consistent with the mating effort hypothesis, that prior friendship increases a male’s chances of mating with a female in future reproductive cycles. We compare the results of our study with those from other populations, and examine why the benefits of friendships for each sex at Amboseli differ from those at other sites. Finally, we suggest a simple method for the identification of friendships using easily collectable data on proximity and grooming patterns which can be gathered as part of regular monitoring of social interactions within groups.

INTRODUCTION

The reproductive strategies adopted by male and female mammals differ markedly, and these differences are largely due to sexual dimorphism in offspring care patterns (Clutton-Brock and Parker 1992). While gestation and lactation predispose females to periods of extensive infant care during which they cannot produce additional offspring, mammalian males can sire offspring with multiple females virtually at once (Trivers 1972). Because their fitness is limited by their insemination success, males are expected to abandon females after fertilization in favor of other fertile females (Maynard Smith 1977). Indeed, in the vast majority of mammalian species, associations between adult males and females are confined largely to the brief period of female fertility (Clutton-Brock 1989), and consequently, most females care for their offspring alone (Woodroffe and Vincent 1994; van Schaik and Paul 1996). However, year-round associations between adult males and females have been reported in over two thirds of primate genera, compared to less than one sixth of genera in most other orders of mammals (Wilson 1975; van Schaik and Kappeler 1997). Among vertebrates, birds are most similar to primates in that stable male-female associations are typical of most species (Lack 1968).

Year-long associations between males and females in birds and mammals were originally believed to represent mating exclusivity in socially monogamous species or "nuclear families" of parents and offspring in multi-male, multi-female species (Morris 1967; Wittenberger and Tilson 1980; Gubernick 1994). However, this explanation fails to account for observed discrepancies between social and mating patterns and, in particular, for emerging evidence that male-female bonds in many species are often not associated with mating exclusivity: Over 10% of offspring in socially monogamous birds are, on average, sired by males other than the social father (Griffith et al. 2002; Westneat and Stewart 2003). In addition, highly specific associations, or 'friendships', between adult males and non-fertile or lactating females and their dependent offspring are regularly observed in several species of primates that live in multi-male, multi-female social groups in which females mate with multiple males during the fertile period [*Papio anubis*: (Ransom and Ransom 1971; Smuts 1985; Bercovitch 1991); *P. cynocephalus*: (Altmann 1980); *P. ursinus*: (Seyfarth 1978; Palombit et al. 1997); *Macaca fuscata*: (Takahata 1982); *M. mulatta*: (Chapais 1986b; Mason 1994); *M. sylvanus*: (Paul et al. 1996; Menard et al. 2001)]. These patterns raise intriguing questions about the adaptive costs and benefits of male-female social relationships in birds and primates for both the male and female participants.

In this study, we examine the predictors and benefits to males and females of 'friendships' between adult males and new mothers in a wild polygynandrous yellow baboon (*Papio cynocephalus*) population in Amboseli, Kenya. Using data from genetic paternity analyses, patterns of behavior among parents, offspring, and other group members, and the long-term (>30 years) demographic, and reproductive records of the Amboseli population, we examine the patterning of male-female associations during the early postnatal period and evaluate two hypotheses for why friendships might be adaptive for each sex.

Aggression is a pervasive feature of life in social groups (Aureli and de Waal 2000), and mothers and newborn infants are particularly vulnerable to social aggression (Nicolson 1987). By associating with an adult male, mothers may gain the male's protection for herself and her offspring from social aggression by other adult and immature females (the 'female harassment' hypothesis) (Altmann 1980). In many group-living primates, females other than the mother are often highly motivated to interact with newborn infants, but the reluctance of mothers to let other group members handle their newborn infants suggests some forms of handling may be harmful to infants (Nicolson 1987). Persistent aggressive infant handling or harassment and kidnapping are associated with greater risk of infant injury or mortality in some populations (Silk 1980; Kleindorfer and

Wasser 2004) and may represent a form of reproductive competition among females (Silk 1980; Wasser and Barash 1981). Mothers with young infants may reduce their risk of harassment by associating with male friends who may intervene on their behalf in agonistic interactions (Manson 1994), or who may, by their mere presence, provide the dyad protection from aggressive interactions, including intrusive infant handling, with other adult and immature females (Altmann 1980). Two predictions follow from this line of reasoning. First, immature and adult females should handle infants more frequently and more roughly than adult or immature males. Second, the number of acts of infant handling, particularly rough forms of handling, received by infants should be lower the more mothers associate with male friends.

Alternatively, mothers with newborn infants may associate with adult males to gain protection for their offspring from infanticide by other adult males (the 'anti-infanticide' hypothesis) (Hrdy 1979). Infant-killing or infanticide is the most serious danger posed by males towards infants (van Schaik and Janson 2000). Infanticide by males has now been regularly observed in lions (Pusey and Packer 1994), and in several species of rodents (reviewed in Blumstein 2000), and primates (Borries and Koenig 2000; Crockett and Janson 2000; Palombit et al. 2000; Steenbeek 2000), and is considered to be a sexually selected alternative male reproductive strategy by many researchers (van Schaik and Janson 2000). The sexual selection hypothesis states that by killing unrelated infants and effectively terminating the suppressive effects of suckling on postpartum fertility, males (a) accelerate the return to fertility of lactating females, thereby increasing the number of fertile females with whom they can potentially mate, and (b) remove potential competitors for their future offspring from the population (van Schaik and Janson 2000).

Infanticide has been suggested as the adaptive explanation for year-round male-female associations in many social animals (reviewed in Palombit 2000) and in gregarious primates universally (van Schaik and Kappeler 1997), but few direct tests of the anti-infanticide function of male-female bonds have been conducted (reviewed in Palombit 2000). Support for the anti-infanticide hypothesis comes from two well-studied primate systems. In Hanuman langurs, resident males were observed defending infants from potentially infanticidal attacks by immigrant males (Borries et al. 1999b), while in chacma baboons, playback experiments revealed that males responded more strongly to the screams of female friends than to those of other females, but only if the friend's infant was alive (Palombit et al. 1997). The 'friendship' between adult males and new mothers in several polygynandrous primate societies suggests that these strong male-female bonds serve to protect infants from infanticide. Although there are few reports of infanticide in the vast majority of primate societies in which friendships have been described (Maestripieri 2000), this pattern may be attributed to the success of friendships in deterring infant-killing in these populations.

A growing body of evidence suggests that infanticide is commonly associated with changes in male breeding status (Hausfater and Hrdy 1984; Parmigiani et al. 1994; van Schaik and Janson 2000). Male mating opportunities in many gregarious mammals are monopolized by one or several socially dominant animals (e.g. Clutton-Brock et al. 1988; Altmann et al. 1996; Creel et al. 1997; Engh et al. 2002). Among baboons at Amboseli, the alpha, or highest-ranking, male alone monopolizes, on average, 20% of all available female consort time (Alberts et al. 2003). Consequently, infanticide risk is expected to be high during periods of turnover in the alpha male position. Risk of infanticide is also expected to be high after the immigration of a new adult male into a group (Beehner et al. 2005). Immigrating males can be disruptive to both resident males and females, especially if they compete with resident males for high-ranking positions in the group (Alberts et al. 1992; Sapolsky 1993), or if they attack or attempt to attack females investing in another male's offspring, including mothers with young infants (Borries and Koenig 2000; Palombit et al. 2000). Risk of infanticide is therefore expected to increase (1) after the immigration of an adult male and (2) the shorter the tenure length of the highest-ranking male at rank one. It is during these periods of heightened infanticide risk that mothers with young infants are expected to seek the protection of male friends by associating more with them than during less turbulent times.

Males, in turn, may gain paternal care or mating benefits by associating with mothers and their dependent offspring. The 'paternal investment' hypothesis proposes that by associating preferentially with their own offspring, a male friend will help to improve the fitness of the offspring he has sired with the female (Bales 1980; Kleiman and Malcolm 1981; Parke and Suomi 1981; Smuts 1985; Taub 1990; Taub and Mehlman 1991). Thus, the first prediction of this hypothesis states that males will preferentially associate with females with whom they have sired infants.

Since females mate with multiple males during the fertile period (Alberts et al. 2003), male baboons at Amboseli may not be able to distinguish their own neonates from unrelated infants (but see Buchan et al. 2003). Males may therefore be confused about infants' true parentage, and direct care and affiliation towards infants in proportion to their certainty of paternity, based on prior mating success with mothers (Altmann et al. 1996), for that infant (Collins 1986; Burke et al. 1989; Dixon et al. 1994; Borries et al. 1999b). Thus, a secondary prediction of the paternal investment hypothesis is that males will associate more with females with whom they were more likely to have sired infants.

A growing body of evidence suggests, however, that animals can and do recognize paternal kin (Alberts 1999; Borries et al. 1999a; Borries et al. 1999b; Soltis et al. 2000; Widdig et al. 2001; Buchan et al. 2003; Smith et al. 2003). The behavior of males in several species suggests that males may be able to distinguish their own neonates from unrelated infants [birds (Moller and Birkhead 1993; Dixon et al. 1994; Weatherhead et al. 1994; Chuang-Dobbs et al. 2001), fish (Rios-Cardenas and Webster 2005), and primates (Borries et al. 1999b; Soltis et al. 2000)]. However, even if males in some species can recognize their own infants, other factors may influence whether they express their recognition. From a socioecological and life-historical perspective, males and females are limited in the amount of time and energy they can devote to reproduction, and the time and energy they devote to one offspring are time and energy they cannot devote to other offspring (Clutton-Brock 1991). Thus, a male's participation in a friendship bond with a particular female and her offspring may depend not only on the male's genetic relationship to the offspring, but also on the number of other offspring he has sired in the group. A father may therefore be more likely to associate with an offspring if he has fewer other immature offspring in the group.

Finally, fathers may associate more with some offspring than others because of the greater potential payoff for his investment in those offspring; that is, for a given amount of care, fathers are expected to be more likely to invest in those offspring who stand to gain the greatest possible benefit from their attention. Thus, we expect that paternal care and defense of offspring will become more important as the infant's risk of injury or mortality increases. We therefore expect fathers to associate more with infants the greater their risk of infanticide by males and the lower their mother ranks in the female dominance hierarchy. Though infants are rarely the recipient of direct aggression from females (Nicolson 1987), the social risks of low dominance rank for mothers (Walters and Seyfarth 1987) may indirectly affect infant health or survival (Silk 1980; Wasser 1983).

Alternatively, male care of infants (Price 1990; Buss 1994; Freeman-Gallant 1997) and friendship with mothers (Smuts 1985; Smuts and Gubernick 1992; Menard et al. 2001) may function to enhance a male's attractiveness as a future mating partner. This idea, called the 'mating effort' hypothesis, proposes that by demonstrating their willingness to invest in a female and her offspring, male friends can enhance their chances of being chosen by the female as a mating partner in future reproductive cycles (Seyfarth 1978; Smuts 1985; van Schaik and Paul 1996). However, matings achieved through prior affiliation and female choice may only be of secondary importance, compared with other mating tactics arising from direct male-male contest competition (Anderson

1983; Berenstain and Wade 1983; Noe and Sluijter 1990; Bercovitch 1991; Bulger 1993; Alberts et al. 2003). The mating effort hypothesis, therefore, does not expect friends to have greater mating success than non-friends. Instead, it predicts that males will have greater mating success with former friends than expected given their overall consorting activity (Smuts 1985). That is, males will achieve a greater share of their former friends available consort time (once they resume cycling) than they will achieve of all available female consort time (Smuts 1985).

Since fathers can potentially attain both mating and paternal care benefits through friendships with females and offspring, the mating effort and paternal care hypotheses are not mutually exclusive. However, the importance of mating effort may be clearer in those cases where males care for offspring they did not sire or were unlikely to have sired. It is, nonetheless, difficult to determine the relative importance of these two benefits to males in any one population, since the value of each benefit may change with male age and experience (Smuts 1985).

Predictions derived from the two hypotheses for why friendships might be adaptive for each sex, which are summarized in Table 1, were tested with data from 29 mother-infant dyads and their associated male friends inhabiting four multi-male baboon groups in our long-term study population in Amboseli, Kenya. In addition, we describe the patterning of male-female associations and examine the contributions of females towards the maintenance of friendships. Finally, we suggest a simple method for the identification of friendships using easily collectable data on proximity and grooming patterns which can be collected as part of regular monitoring of social interactions within groups.

METHODS

Subjects & Study Population

The subjects for this study are part of a larger population of wild baboons inhabiting the Amboseli basin, a semi-arid, short grass savannah ecosystem situated at the base of Mt. Kilimanjaro in East Africa. The population has been under continuous observation for over three decades (Altmann 1980; Altmann 1998; Alberts and Altmann 2003; Altmann and Alberts 2003, see www.princeton.edu/~baboon for a complete bibliography and the Baboon Project Monitoring Guide, which outlines data collection protocols for this population) and data on life history patterns are available for several hundred animals in a total of 8 completely wild-foraging groups. Baboons live in semiclosed matrilineal groups, which number from 10-200 members (Altmann and Altmann 1970). Males typically disperse from their natal groups as they near adult size and many continue to migrate between groups throughout their lives (Alberts and Altmann 1995). Females, in contrast, remain in their natal group their entire life, inheriting their mother's rank in the group's dominance hierarchy as juveniles (Walters 1980). Most matings occur within the context of mate-guarding episodes, called sexual consortships, during the follicular phase of the sexual cycle (Alberts et al. 2003). During this phase, females have prominent, swollen sex skins that increase in size until around the time of ovulation (Shaikh et al. 1982). Reproduction is non-seasonal, with births occurring throughout the year (Alberts and Altmann 2003), and mothers are anestrous for ~ 10 months after infant birth (Altmann et al. 1978). Finally, infancy lasts between one to two years (Altmann et al. 1988).

Subjects were observed by NN from Sep 2002 to Nov 2003 and included 29 mother-infant dyads and their associated male friends inhabiting the four multi-male study groups. All pregnant females who bore live young that survived the first two months of infancy were included in this study.

Behavioral Data

Observations began on pregnant females two months prior to parturition and continued for two months afterwards. Data on grooming and proximity were collected across the entire four month period, while data on parent-offspring interactions and infant handling patterns were made during the two postnatal months. During late pregnancy, females were observed, on average, for 10.9+0.9 actual in-sight observation hours in 31.3+2.5, 20 minute focal animal samples (Altmann 1974). Following birth, each mother-infant dyad was observed for 11.2 + 0.9 hours in 32.0 + 2.3, 20 min focal animal samples.

During each 20 min sample, continuous records were kept on all occurrences of infant social and agonistic interactions between the mother and other members of the social group, including actor and recipient identities, and times of onset and termination for each grooming bout. A grooming bout began when the animal came in manual or oral contact with another animal's fur and began picking through it, and ended when the animal ceased to pick through the other animal's fur. Within the focal samples, embedded point samples (Altmann 1974) were made every 5 minutes on the activity of the focal female and her infant, and on the identities of the female's nearest neighbor, her nearest adult neighbor, and her nearest adult male neighbor within 5 meters. Samples of mothers also served as samples on infants since infant baboons spent almost all of their time in bodily contact or in close proximity to mothers during the first two months of life (Altmann 1980). During samples of mother-infant dyads, continuous records were also kept on all occurrences of infant distress and all acts of infant handling. A bout of infant distress began with the first distress vocalization given by an infant and ended when the infant no longer exhibited signs of distress in relation to the original cause of distress. The following forms of infant handling behaviors were recorded during focal samples: touching, pulling, and contact breaking. A touch was recorded when one animal made manual contact with another animal in a nonaggressive manner. A pull was recorded when an animal tugged at the infant while it was in contact with the mother, and either the infant or the mother counteracted the force of the pull by holding the other member of the dyad tighter. Finally, an act of contact breaking was recorded when an animal succeeded in pulling the infant away from the mother's body. All data were recorded on a handheld data recorder (Psion Workabout, Psion Teklogix) and were transferred to Microsoft Excel XP and FoxPro 6.0 for further analysis.

We use data on proximity and grooming patterns between adult males and focal females to describe the patterning of male-female social relationships. Spatial proximity is often used as an indirect measure of social partner preference in mate choice tests in animals (e.g. Adkins-Regan 1999). First, we calculated the proportion of total point samples (or time) each female spent in close proximity (i.e. within 5m) to each adult male in her group and determined each female's most frequent adult male nearest neighbor. Grooming is the most common affiliative behavior among primates (Dunbar 1991) and is considered the 'glue' that binds individuals within social groups. We used data on the duration of all grooming bouts between focal females and adult males and (1) calculated the proportion of each females' total time budget grooming adult males, (2) calculated the proportion of each female's total grooming and total being groomed time accounted for by particular males and finally, (2) determined each female's most frequent adult male grooming and being groomed partner. For all proximity and grooming measures, we divided the data into pre- and postnatal periods, corresponding to the last eight weeks of pregnancy and the first eight weeks of lactation, respectively.

Next, we used data on infant distress cries and infant handling patterns to describe the social dangers faced by infants during the first eight weeks of life. First, we calculated the rate at which infants were handled by other group members by dividing the total number of acts of each type received by the infant by the total number of hours the mother-infant dyad was observed. Second, we calculated the hourly rate of interactions per potential partner by dividing the number of interactions of each type by the number of hours observed and the number of potential partners of each age/sex category present in the group during the two postnatal months. Finally, we calculated the rate at which infants gave distress cries by dividing the total number of distress bouts given by each infant by the number of hours the dyad was observed.

Demographic & Reproductive Data

The histories of all females present in the population during the study period are known since birth from near-daily records of demographic events and reproductive cycles. In addition, data on male life histories and male migration patterns are known for most males in the study population. Demographic and reproductive data used in this study were drawn from the long-term electronic records of the Amboseli Baboon Project (BABASE). For each mother-infant dyad, we determined (1) the mother's parity (the number of prior pregnancies, including the current infant), (2) the number of months since an unfamiliar adult male had emigrated into the group, and (3) the number of months that the highest-ranking male in the group during the infant's second month of life had held his number one position. Unfamiliar adult males were defined as any immigrant male who had not previously resided in the group.

The identity of male and female partners in all mating events and all mate-guarding episodes were recorded as part of regular monitoring of study groups. These data, along with all demographic and reproductive monitoring of study groups, continued to be collected even after the study period. Female reproductive condition was assigned based on post-hoc examinations of external signs recorded in the field, including highly visible sexual skin swellings that increase in size around the time of ovulation, menstruation, and changes in the female's paracollosal skin indicating pregnancy. In this study, we restricted our analyses to those consortships that occurred during the five days before the onset of deturgescence of the sex skin, because this is the period in which ovulation and conception are most likely to occur (Hendrickx and Kraemer 1969; Wildt et al. 1977; Shaikh et al. 1982). For each female, we determined the identities of all male consort partners during the cycle in which the infant was conceived, as well as the amount of the mother's consort time given to each partner. We refer to this period as 'the days of most likely conception of the infant'. Because insufficient sampling may cause bias in estimates of mating success (S. Alberts unpubl. data), we restricted some analyses to the subset of females (22 of 29) who were seen consorting for at least 5 hours total on the days of most likely conception of the infant. Measures for male mating success with mothers once these females resume cycling were adapted from Smuts (1985) and are described in the Data Analysis section.

Data on agonistic interactions collected during this study, along with data collected as part of regular monitoring of study groups, were used to assign relative ranks to each group member each month. Dominance ranks were determined by assigning wins and losses in dyadic agonistic encounters between group members (Hausfater 1975; Alberts et al. 2003). Individuals were considered to have won encounters when their opponent gave only submissive gestures, while they gave only aggressive, or neutral (nonsubmisive) gestures (Hausfater 1975; Alberts et al. 2003). A female's dominance rank among her group's adult females the month her infant was conceived was considered her maternal dominance rank for that infant (Altmann 1980). Stability of dominance ranks throughout adulthood and even across generations has been documented for baboon and macaque females (Melnick and Pearl 1987; Pereira 1995). In contrast, male dominance ranks can change throughout their lives, being highest when they are young adults and in their prime, and falling with age (Packer et al. 2000; Alberts et al. 2003). Instability in the male dominance hierarchy is, therefore, a common feature of baboon societies, and we tabulated the ranks of each adult male present in the groups during the study period.

Genetic Paternity Analyses

Paternal kinship is known for 340 individuals in our long-term study population, including 23 of the 29 infants included this study. Using male maturation dates and multilocus genotyping procedures, we assigned paternity by genotyping 504 individuals in the study population at multiple microsatellite loci (13.81+0.78 SD loci per individual), genotyping most animals at 14 loci (459 of 504, 91.1%) as described in Buchan et al. (2005). All loci were in Hardy-Weinberg equilibrium, with a mean of 11.07+2.62 SD alleles per locus. Mean observed heterozygosity across loci was 0.813+0.039. Males were considered potential fathers if they were present in the population and had enlarged testicles when the offspring was conceived. Males were assigned as fathers if they met one of two criteria: (1) They were the only male with no exclusions for a given offspring, considering maternal genotypes. (2) They had a single genetic mismatch with the offspring, considering maternal genotypes, and the paternity assignment was supported at the 95% confidence level by the maximum-likelihood method employed in CERVUS 2.0 (Marshall et al. 1998). To generate confidence levels with CERVUS, 10, 000 simulations were run with the following parameters: 70% of candidate parents (62) sampled, 98% of loci typed, and a typing error rate of 0.01. The typing error rate was set as the rate of mismatches between mother and offspring. (Buchan et al. 2005)

Data Analysis

We examined changes in females' proximity and grooming activity by comparing each female's proximity and grooming scores before and after birth using paired samples t-tests. We then identified a single male 'friend' for each mother-infant dyad, based on her proximity and grooming behavior with males, and a set of 'non-friends'. Non-friends consisted of all adult males who (1) were not the female's friend, and (2) were present in the study group during her offspring's first two months of life. Next, we examined the factors that contribute to variation in male friendships, by comparing friends to non-friends in (1) age, (2) dominance rank, (3) number of other immature offspring present in the group, and (4) prior mating success with the mother on the days of most likely conception of the infant using independent samples t-tests. Male age at infant birth was calculated from known or estimated male birthdates. Male dominance rank was calculated as the average of the male's ranks during the month the infant was born, and during each of the next two months, with rank one being the highest. The number of offspring sired by each male was drawn from the genetic records for the population. Immature offspring were all offspring, not including the current infant, who had been sired by the male and who had not attained sexual maturity (i.e. for girls, before the age of menarche; for boys, before the age of testicular enlargement) by the time the infant turned two months old. Prior mating success with mothers was defined as the male's proportion of the mother's total consort time during the cycle in which she conceived the infant.

To evaluate the ‘female harassment’ hypothesis, we treated the rate of rough infant handling as the response variable in a linear regression on the amount of time mothers spent in proximity to their male friend. We also compared the rate of rough handling received by infants whose mothers spent the most amount of time with male friends (i.e. mothers who ranked in the top quartile, or spent at least 28% of time in proximity to her male friend) to infants whose mothers spent less time with male friends.

To evaluate the anti-infanticide hypothesis, we treated the amount of time females spent in proximity to male friends as the response variable in a multiple regression on two measures of instability in male social relations: tenure of the highest-ranking male at rank one and the months since an adult male had emigrated into the group.

To evaluate the paternal investment hypothesis, we identified a set of ‘behavioral’ fathers (Buchan et al. 2003) for each infant, that is, all adult males who were observed consorting with the mother during the cycle in which she conceived the infant. We determined the proportion of friends who were ‘behavioral’ fathers, and, using independent samples t-tests, evaluated the extent to which prior mating success with mothers differed between fathers who were friends and those who were not. Next, we examined whether (1) the number of other immature offspring in the group, (2) the infant’s risk of infanticide (based on the number of months since an adult male had immigrated into the group) or (3) the mother-infant dyad’s risk of social aggression from females (based on maternal dominance rank), differed between fathers who were friends and those who were not, using independent samples t-tests.

Finally, to examine the mating effort hypothesis, we compared (1) each male’s consorting activity with their former friend with (2) what was expected given his overall consorting activity with all adult females in the group. To obtain each of these two values, we used measures which we adapted from Smuts (1985: 166). The first measure, which we call ‘the male’s share of the female’s consort time', is equal to the male's achieved proportion of the total consort hours that the female gave to all males on all her fertile days (from the day she resumed cycling to the day she conceived her next infant). The second measure, which we call 'the male's expected share of consort time', is equal to the male's achieved proportion of the total consort hours available in the group over the same time period. Each dyad in which the male's individual share of a female's consort time exceeded his expected share of consort time was assigned a plus, while dyads in which the male's individual share was the same as his expected share was assigned an equal, and all other dyads were assigned minuses. Pluses were interpreted to mean that the male consorted with the female on a greater percent of her consort hours than he did, on average, with other females. We then examined whether former affiliation increased a male's chances of consorting with a female more than expected given his consorting activity overall by comparing the performance of friend dyads with non-friend dyads using chi-square procedures.

All statistical analyses were conducted using SPSS 13.0 (SPSS Inc. 2003). Relationships between explanatory variables were explored using Pearson's correlation coefficients. Values reported are means + SE. All analyses were two-tailed with $p<0.05$.

RESULTS

Spatial Proximity, Grooming & Friendships

Variation in spatial proximity and grooming patterns between mothers and adult males indicated marked differences in male-female relationships and were used to define friendships. Females spent significantly more time in close proximity to adult males after (43+2%) compared to before parturition (21+2%) (paired samples t-test, p<.0005), and the greatest increase in proximity time with males was seen in the most frequent male nearest neighbor. Time in proximity to females' most frequent male neighbor nearly tripled from late pregnancy (8+1%) to the postnatal period (21+2%) (p<.0005). Most females exhibited consistency in their choice of male neighbors across the peripartum period; in more than half of all cases (15/29), female's most frequent male neighbor was the same individual before and after birth (Table II).

On average, females spent significantly less time grooming after than before parturition (Table III, p<.0005), although time spent grooming adult males did not change with infant birth (p=.930). Consequently, the percent of females' total grooming time accounted for by adult males increased significantly after parturition (p<.0005), and most of the increase was due to females' grooming one adult male (Table III). During late pregnancy, females' most frequent male grooming partner accounted for 14+3% of females' grooming time, and this value nearly doubled after infant birth (to 29+5%) (t-test, p=.001). In contrast, all other adult males combined accounted for less than 6% of females' grooming time across the peripartum period (Table III). Finally, in a third of all cases (8/25), females' most frequent male grooming partner was the same individual before and after birth (Table II).

Females spent significantly more time being groomed by other group members after the birth of their infants (Table III, p<.0005), although grooming by adult males accounted for only a fraction of one percent of females' time and this value changed little with infant birth.

Females exhibited consistency in their choice of male social partner. In two thirds (19/29) of all cases, the female's most frequent male nearest neighbor was also her most frequent male grooming partner (Table II). Because of the concordance between grooming and proximity partner preference in most dyads, in all subsequent analyses, we refer to a mother's most frequent male nearest neighbor as her male "friend". In addition, we use the amount of time spent in proximity to male friends as a measure of the strength of the male-female bond.

The Value of Friendships to Females

The female harassment hypothesis

Prediction 1. Females will handle infants more roughly and at higher rates than males. Adult and immature females were responsible for the vast majority of acts of infant handling, from touching, pulling to contact breaking (Fig. 1A). Touching was the most common form of infant handling, followed by pulling, while contact breaking was the least common (Fig. 1B). These behaviors can be roughly ranked from least to most intrusive, with touching consisting of mostly gentle contact. Pullings were more intrusive as the handler attempted to but was unsuccessful in breaking mother-infant contact (because either the mother or infant counteracted the force of the handler's pull). Finally, contact breaking was the most intrusive form of handling because it resulted in the termination of mother-infant contact entirely, though often for brief periods of time. Because pulling was similar in intrusiveness to contact breaking, we combined these two behaviors into a single measure which we call "rough handling" in subsequent analyses.

Comparisons of the number of handling acts committed per hour per potential partner of each age/sex class showed that (1) females of all ages were more active than males in handling infants, and (2) disparities in the frequency of handling by the different age/sex classes were consistent across handling behaviors (Fig. 1B). On average, infants were handled most often by adult females, followed by immature females and then adult males and, finally, least often by immature males (Fig. 1B).

Individual variation in the rate per hour at which infants were handled "roughly" by all group members was not associated with variation among dyads in maternal rank, parity, or infant sex (GLM, r^2_{adj}=-.057, p=0.69 for the entire model). However, the rate at which infants were handled roughly was associated with the rate at which infants gave distress vocalizations (Fig. 2, r^2=.386, p<.0005), an indication that the more intrusive forms of handling were stressful to infants.

Prediction 2. Infants whose mother associates more with male friends will receive less handling. The more time mothers spent in proximity to male friends, the lower the rate at which infants were handled roughly by other group members, a result that approached significance (r^2=.112, p=.072). In addition, and further consistent with the "female harassment" hypothesis, mother-infant dyads who spent the most amount of time with male friends (i.e. who ranked in the top quartile of time in proximity to male friends) experienced significantly lower rates of rough infant handling than those who did not (Fig. 3A, Table IV) (t-test, p=.011). Infants whose mothers spent the most time with male friends also exhibited significantly lower rates of distress vocalizations than those whose mothers did not (Fig. 3B, Table IV) (p=.025).

The anti-infanticide hypothesis

Prediction 1. Risk of infanticide will increase with increasing instability in male social relations. The immigration of unfamiliar adult males into study groups was associated with greater instability in the male dominance hierarchy; the number of months since an unfamiliar adult male had entered the group was correlated with the tenure length of the alpha male at rank one (r^2=0.26, p=.005). Although immigrant males were never observed attacking or attempting to attack infants during this study, evidence from other populations suggest that infanticide risk is highest during periods of immigrations or instability in the male dominance rank hierarchy (Hausfater and Hrdy 1984; Parmigiani et al. 1994; van Schaik and Janson 2000), and our results suggest that these two variables are strongly correlated.

Prediction 2. Females will seek protection from male friends during periods of enhanced infanticide risk. The amount of time a mother spent in proximity to her male friend was predicted by the number of months since an unfamiliar adult male had entered the group, and not by variance in the tenure of the highest-ranking male (r^2_{adj}=0.242, p=0.010 for the whole model, p=0.052 for the partial regression coefficient of the number of months since an adult male had immigrated into the group). Although the tenure of the highest-ranking male at rank one did make a significant unique contribution to the model, its effects were similar in direction to the first variable (Fig. 4). However, the effect of instability in male social relations on male-female associations was opposite to the one predicted by the "anti-infanticide" hypothesis: mothers with young infants spent *less* time in proximity to male friends the more recently an unfamiliar, and potentially infanticidal, adult male had emigrated into the group.

The Characteristics of Friendships

The 29 mothers in our sample included females of all dominance ranks, ages, and parities (Table V). The amount of time a mother spent in proximity to her male friend was not predictable from the sex of the infant, maternal rank or parity (GLM, r^2_{adj}=-.009, p=0.445 for the entire model). Thirty-four adult males were resident in the four groups during the study period, and of these, 16 males were friends with at least one female, giving a total of 29 friend dyads and 172 non-friend dyads. On average, friends were similar in age to non-friends, but occupied significantly higher rank positions during the period of friendship than non-friends (Table VI). In addition, friends tended to have more immature offspring in the group than non-friends, a result that approached significance (Table VI, p=0.06). Finally, friends (n=22 dyads) were more likely to have achieved more consort time with the mother during the cycle in which she conceived the infant than non-friends (n=122 dyads), a result that also approached significance (Table VI, p=0.09). In summary, male friends were generally 'more successful' than non-friends; that they exhibited a non-significant tendency to have had more mating success with mothers when they were likely to have conceived the infant suggests the possibility that friendships may function more as a form of paternal investment in the current offspring than male mating effort towards the next.

The Value of Friendships to Males

The paternal investment hypothesis

Prediction 1. Males will associate preferentially with their own offspring. Paternity was known for 78% (183/235) of all individuals present in the four groups during the study period, including 80% (91/114) of immature individuals (Table VII), 23 of whom were infants included in this study. Fathers were friends with mothers in nearly half (11/23) of all cases, while adult males other than fathers were friends with mothers in the other half of all cases (Table VIII).

Almost all friends who were not fathers (8/9 cases) had not been seen consorting with the mother when she was likely to have conceived the infant, while nearly all friends who were fathers (7/8 cases) had monopolized at least a third of the mother's available consort time during that period (Table VIII). This difference in prior consortship success with mothers between friends who were fathers and friends who were not fathers was statistically significant (Fishers Exact test, p=0.003) (Table VIII).

Prediction 1a. Fathers will associate more with mothers the more likely they are to have sired offspring with her. Thirteen adult males were identified as fathers of the 23 infants for whom paternity was known (Table IX). Because the five males who fathered multiple infants were not consistent in their pattern of affiliation with mothers and infants across different infants, we examined the determinants of affiliation for fathers using each father-mother dyad as a unit of analysis. The observation that more than twice as many (33% of 9) fathers who were not friends as fathers who were friends (13% of 8) were not seen consorting with the mother when she was most likely to have conceived the infant suggests that males may be adjusting their behavior towards infants in relation to their probability of paternity. Indeed, father-friends achieved a higher proportion of the mother's consort time (0.71+0.15) on the days of most likely conception of the infant than father-non-friends (0.43+0.15), though this difference was not significant (Table X). These results lend some support for the 'paternal investment' hypothesis.

Prediction 1b. Fathers will associate more with offspring the fewer other offspring they have in the group. Contrary to our expectations, father-friends did not differ significantly from father-not-friends in the number of other immature offspring in the group during the infant's first two postnatal months (Table X).

Prediction 1c. Fathers will associate more with offspring the greater its risk of injury or mortality. Also contrary to our expectations, the likelihood of friendship with fathers was not higher for mother-infant dyads at greater risk of infanticide by males or social aggression from group females; friendship with fathers was not related to the number of months since an adult male had emigrated into the group or to maternal dominance rank (Table X).

The likelihood of friendship with fathers was not influenced by mother's prior infant care experience (i.e. her parity number) or by the sex of the infant. Finally, fathers who were friends did not differ significantly from fathers who were not friends in age or dominance rank (Table X).

Prediction 2. Friendships will help improve the fitness of offspring. While friendships resulted in reduced rates of rough infant handling (Prediction 2 of female harassment hypothesis), the observation that (1) less than half of all friends were fathers and (2) friendships with fathers did not differ in intensity from friendships with non-fathers suggest that the value of friendships to infants did not vary with its relatedness to the male friend.

The mating effort hypothesis

Prediction 1. Males will have greater mating success with former friends in future reproductive cycles. On average, mothers resumed cycling 9.6+2.5 SD months after infant birth, and cycled for 4.8+3.0 SD months before conceiving their next infant. Friends of six females emigrated before their former friend resumed cycling, leaving 23 of the 29 study females with former friends in the group (Table XI). Two females were observed consorting for less than 5 hours total before conceiving their next offspring and were also not included in the analysis. Of the remaining 21 friend dyads, friends consorted with the female more often, as often as, or less than expected in 19% (n=4), 33% (n=7), and 48% (n=10), respectively, of all cases (Table XI). These results suggest the possibility that friendship in the past did not affect the probability that a male would form a consortship with that female in the future. Indeed, dyads involving previous friends (27% of 15) were equally as likely to consort with the female more often than expected than dyads involving non-friends (21% of 72) (Fishers' Exact, p=.732). On the other hand, dyads involving previous friends (33% of 15) were less likely to consort with the female less often than expected than dyads involving non-friends (56% of 72), though the difference was not statistically significant (chi-square with Yates correction, p=0.20). The previous two analyses were conducted on all friends and non-friends who were present in the group during all the days that former friends cycled before conceiving their next offspring. Since male friends of six of the 21 females emigrated before their previous friend conceived her next infant, this left only 15 females with their associated 15 former friends and 72 non-friends in the analysis. The results of our analyses, therefore, lend no support to the 'mating effort' hypothesis.

DISCUSSION

Defining Friendships

Measures of grooming and proximity between male-female pairs were used to differentiate pairs with particularly strong and persistent bonds from all other pairs. Grooming plays a key role in the formation and maintenance of social bonds in primates (Seyfarth 1983; Harcourt 1988; Dunbar 1991), and grooming intensity can be used as an indicator of the strength of affiliation between grooming partners. In addition, spatial arrangements within groups provide the broad outlines for social opportunities among group members, and consistent spatial patterning can provide an indirect measure of the 'value' of a relationship to an animal (Altmann 1980; Rowell and Olson 1983). Indeed, spatial proximity is often used an indicator of partner preference in mate choice tests, and females in at least one species have enhanced reproductive success and greater offspring viability and performance when paired with their 'preferred' male (Drickamer et al. 2000).

The striking overlap between females' most frequent male grooming and proximity partners in the vast majority of cases provided a basis for defining friendships. Because several females lacked grooming partners, we chose to define a friend as the female's most frequent male nearest neighbor, and used the amount of time spent in proximity to this male as an indicator of the strength of their relationship. Our criteria for friendships differs in several ways from previous methods of identifying male friends (see Smuts 1985; Palombit et al. 1997). Perhaps the most striking difference between our study and that of the two prior studies is that we did not collect data on the identity of the individual responsible for the onset and termination of proximity to various distances (from 0 to 15 m), and therefore could not compute the "composite proximity score" (Smuts 1985:46) which has been used previously to identify friendships. Data on approach and withdrawal are labor intensive to collect in the field and, as demonstrated by Smuts (1985)'s study, may not necessarily provide further resolution for differentiating friend from non-friend dyads in all cases. Although two thirds of the friend dyads in Smuts (1985)'s study were identified using the dyads' scores on proximity and grooming, a third of friend dyads were identified subjectively, based on prior anticipation of them qualifying as friend dyads even though their scores did not meet Smuts (1985)'s objective criteria for friendship. We recommend our method for identifying friendships to those researchers who wish to study patterns of male-female affiliation as part of regular monitoring of social interactions within groups or as part of a larger study of other topics.

Although we did not have the data to determine which sex was more responsible for the patterning of proximity, our analyses of grooming patterns suggest that females contributed more than males to at least one of the two sets of affiliative interactions (grooming and proximity) that constitute friendships: Females groomed males more often than they were groomed by them and devoted a greater share of their grooming time to adult males after infant birth. These patterns are consistent with those described in three well-studied primate systems where stable male-female bonds have been described. Female olive baboons at Gilgil (Smuts 1985), chacma baboons in the Okavango Delta (Palombit et al. 1997), and mountain gorillas at Karisoke (Harcourt 1979; Sicotte 1994; Watts 1996) all contribute more than their male partners to the formation and maintenance of their social bond. Thus, friendships at Amboseli did not differ qualitatively from those at other sites.

Value of Friendships to Females

The results of our study were consistent with the female harassment hypothesis. First, females of all ages at Amboseli handled infants more roughly and at higher rates than males. Similar patterns have been observed in other populations (Hiraiwa 1981; Nicolson 1987; Silk 1999). Second, infants whose mothers associated more often with males received less rough handling than infants whose mothers spent less time in proximity to male friends, and this was especially true for infants whose mothers had the strongest bonds with males. Infants who were handled roughly at higher rates gave more distress cries, suggesting that rough forms of infant handling may be harmful or stressful to infants. Indeed, aggressive handling of infants is associated with lower survival in two other primate populations (Silk 1980; Kleindorfer and Wasser 2004). Friendship with males may therefore help to reduce an infant's risk of injury or mortality. Mortality at Amboseli (Altmann and Alberts 2003) and other long-term study populations (Gerald 1995; Hill et al. 2001; Cheney et al. 2004) is highest during infancy. Taken together, these patterns suggest that mothers in other populations may also benefit from the protection of males from female harassment of offspring. Finally, our finding that variation in the rate at which infants were handled was not affected by infant sex, maternal parity or dominance rank suggests that infants of all backgrounds may benefit from male protection.

The anti-infanticide hypothesis was not well supported by our results. This hypothesis predicts that mothers should seek the protection of male friends during periods of enhanced infanticide risk. In a recent survey of reported cases of infanticide in wild populations, van Schaik (2000) found that 85% of reported cases of infanticide occur within the context of (1) an adult male rising in rank within a group or (2) the immigration of an adult male into a new social group. Although infanticide has rarely been observed in the baboons at Amboseli, even during periods of immigration or instability in the male dominance rank hierarchy (J. Altmann unpubl. data), in accordance with van Schaik (2000)'s findings, we defined infanticide risk in terms of instability in male social relations. However, contrary to the anti-infanticide hypothesis, mothers at Amboseli did not associate more often with male friends the more recently an adult male had immigrated into the group or the shorter the tenure of the highest-ranking male.

Although infanticide avoidance has been suggested to the adaptive reason for year-round male-female bonds in social animals (Hrdy 1979), to date, few tests of the anti-infanticide hypothesis have been conducted (reviewed in Palombit 2000). While some studies have found data consistent with this hypothesis (Watts 1989; Palombit et al. 1997; Borries et al. 1999b), others have produced more equivocal results (Wright 1995; Overdorff 1998). The results of this study suggest that friendships do not function to deter infanticide in the baboons at Amboseli. Instead of seeking protection from male friends during periods of enhanced instability in male social relations, new mothers at Amboseli appear to be avoiding males during these times of greater purported infanticide risk, possibly as a defense against becoming a focus of aggression during periods of enhanced male-male conflict (Smuts 1985). Taken together, the results of this study suggest that the benefits of friendships to females Amboseli and other primate populations where observed risk of infanticide is low or negligible more likely derive from male friends' protection of mothers and infants against harassment from other females.

Value of Friendships to Males

While some of the results of this study support some of the predictions derived from the paternal investment hypothesis, the data do not support other predictions derived from this hypothesis. Thus, while fathers did associate preferentially with their own offspring, they did so in only half of all cases. In addition, fathers were more likely to be friends with a mother the greater their likelihood of siring offspring with her. On average, fathers who were friends obtained 65% more of the mothers' consort time when she was most likely to have conceived the infant. Finally, fathers did not associate more with a given offspring the fewer other immature offspring they had in the group, nor did they associate more with offspring the greater the offspring's risk of injury or mortality from infanticide by males or social aggression by females.

The mating effort hypothesis was not well supported by the results of this study. The mating effort hypothesis predicts that prior friendship will enhance a male's chances of mating with a female in future reproductive cycles over and above what he would otherwise achieve. Enhanced male mating success with former friends has been reported in two populations (Smuts 1985; Menard et al. 2001), though in the majority of studies, males have not had greater mating success with former friends (Chapais 1983a; Chapais 1983b; Chapais 1986a; Hill 1990; Manson 1994; Paul 1999). In this study, friendship in the past did not affect the probability that a male would form a consortship with a female in the future. Nearly half of all males emigrated from the group before their former friend conceived her next offspring, and those males who stayed did not have greater success with their former friend than they would have achieved otherwise.

It is possible that the males who stayed did so to improve the survival prospects of offspring they had already sired in the group, rather than to achieve additional matings. Indeed, friends who were fathers (82% of 11 cases) were significantly more likely than friends who were not fathers (25% of 12 cases) to be present in the group during the mother's subsequent reproductive cycles (Fishers Exact test, p=0.012). Though we were unable to thoroughly test the mating effort hypothesis, because we were could not eliminate paternal care as a possible confounding factor, none of our results were consistent with the mating effort hypothesis.

In their review of the topic, van Schaik and Paul (1996) draw from a compelling body of evidence from studies of human and non-human primates to argue that male care for offspring rarely, if ever, reflects parenting effort. However, one recent study provides evidence that male care can represent paternal investment in offspring: Male baboons at Amboseli were found to selectively support their own juvenile offspring in agonistic disputes (Buchan et al. 2003). The results of this study, conducted on the same population, suggest that male baboons at Amboseli may exhibit paternal concern for neonatal offspring as well. Nearly one half of all friendship dyads consisted of a mother-father pair, and father-friends were more than twice as likely to remain in the group during the mother's future reproductive cycles than friends who were not fathers. Though it was beyond the scope of this study, future research may provide insight into the long-term benefits of fathers' residence in the group on offspring survival and fitness.

One final question remains: If friendships with females do not increase a male's chances of mating with the mother in future reproductive cycles, what other the possible benefits can accrue to friends who are not the infant's father? It is possible that, by associating with a new mother, males may gain additional matings with other females who observe his behavior (van Schaik and Paul

1996). Support for this idea comes from studies that have shown that (1) males are more attractive as mates when caring for offspring (Price 1990), including offspring sired by other males (Gori et al. 1996), or that (2) males are more affiliative towards infants when the mother was in sight than when she was not (Keddy-Hector et al. 1989). Alternatively, it is possible that by associating with a new mother, males benefit from the greater grooming activity the friendship provides. The fact that females invested more in friendships than males suggest that females may 'value' the association more, and may have more to gain from the friendship than males. Females may therefore trade grooming services for the opportunity to be in close proximity to males, in order to benefit from their active or passive protection against harassment by other females (Seyfarth and Cheney 1984; Barrett et al. 1999).

Finally, the observation that nearly all friends who were not genetic fathers were also not 'behavioral' dads suggests that friendships in this population do not arise from paternity confusion. This intriguing finding raises questions about the proximate mechanisms used by males in polygynandrous societies to identify their own neonates.

Fig. 3.1A. The proportion (mean+SE) of the total number of each handling behavior received by each infant from the four age sex classes. AdF=adult females, ImF=immature females, AdM=adult males, ImM=immature males. Numbers represent the number of infants included in the group mean. For 'breaking', data were only available for 28 infants since contact between one mother-infant dyad was never observed to be broken by another group member.

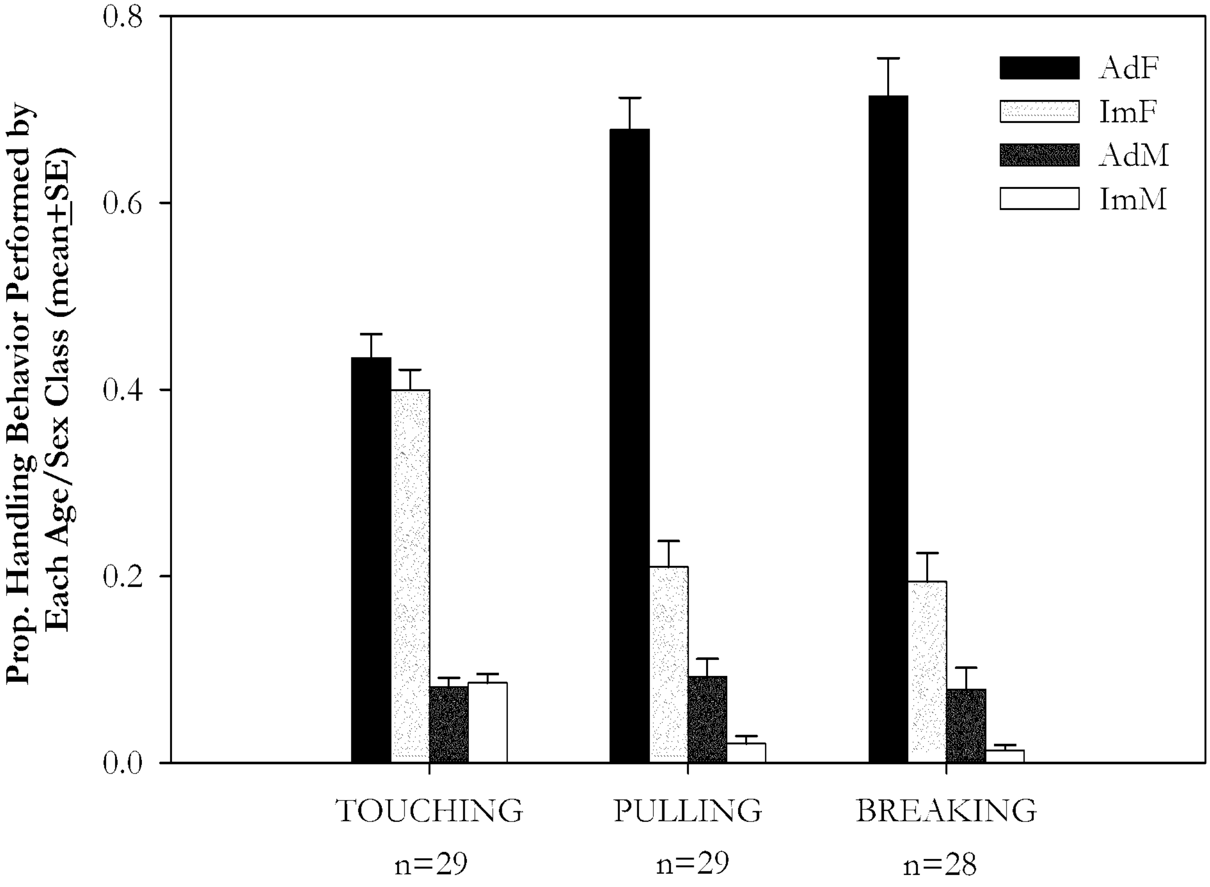

Fig. 3.1B. Mean (+SE) hourly rate of infant handling interactions per potential partner. This value was obtained by dividing the number of interactions of each type by the number of hours observed and the number of potential partners of each age/sex category present in the group. The rate of "rough" handling represents the sum of the rate of pulling and contact breaking. Letters and numbers indicate where values differ significantly among age sex classes (when symbols are not shared among classes) and where they do not (when symbols are shared) for a given handling behavior, based on repeated applications of paired-samples t-tests. Numbers below the interactions represent the sample size of infants.

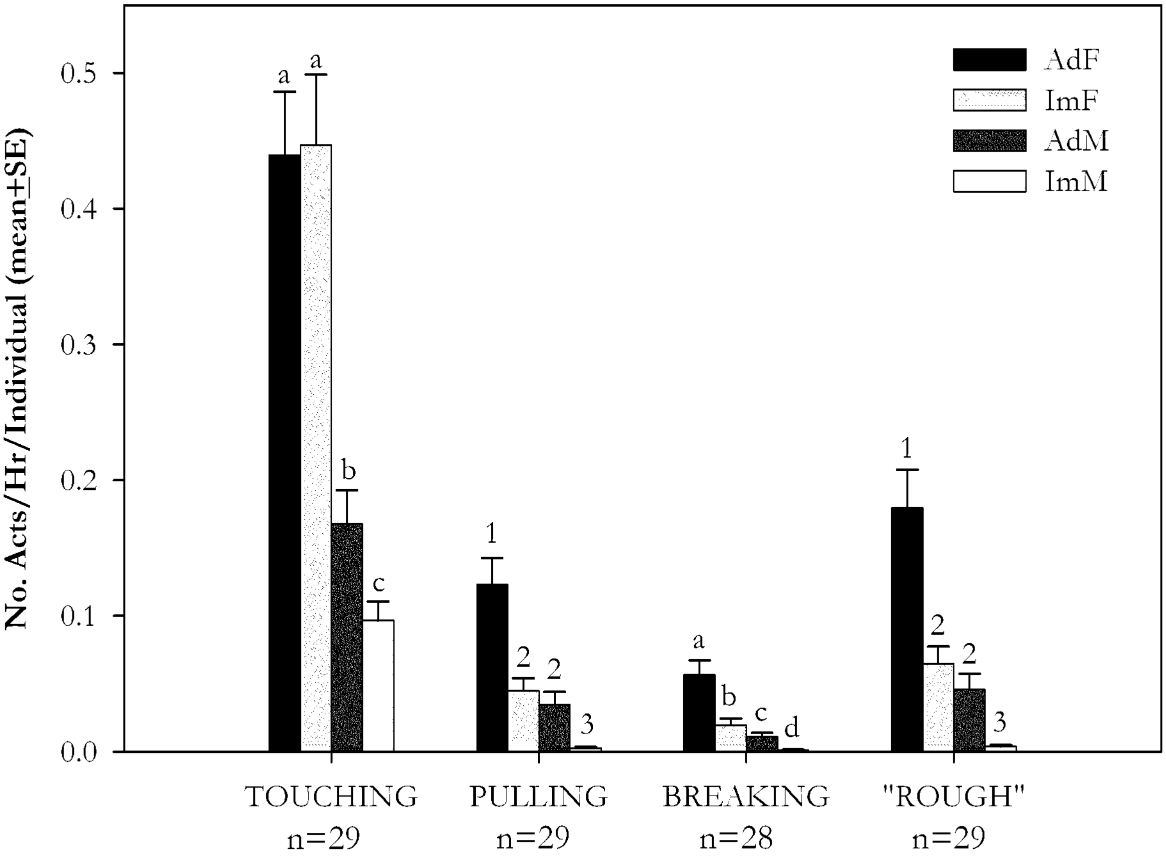

Fig. 3.2. The rate of infant distress vocalizations as a function of the rate of "rough" infant handling. Infants who received higher rates of "rough" handling exhibited significantly higher rates of distress cries, and this pattern was found in both male and female infants.

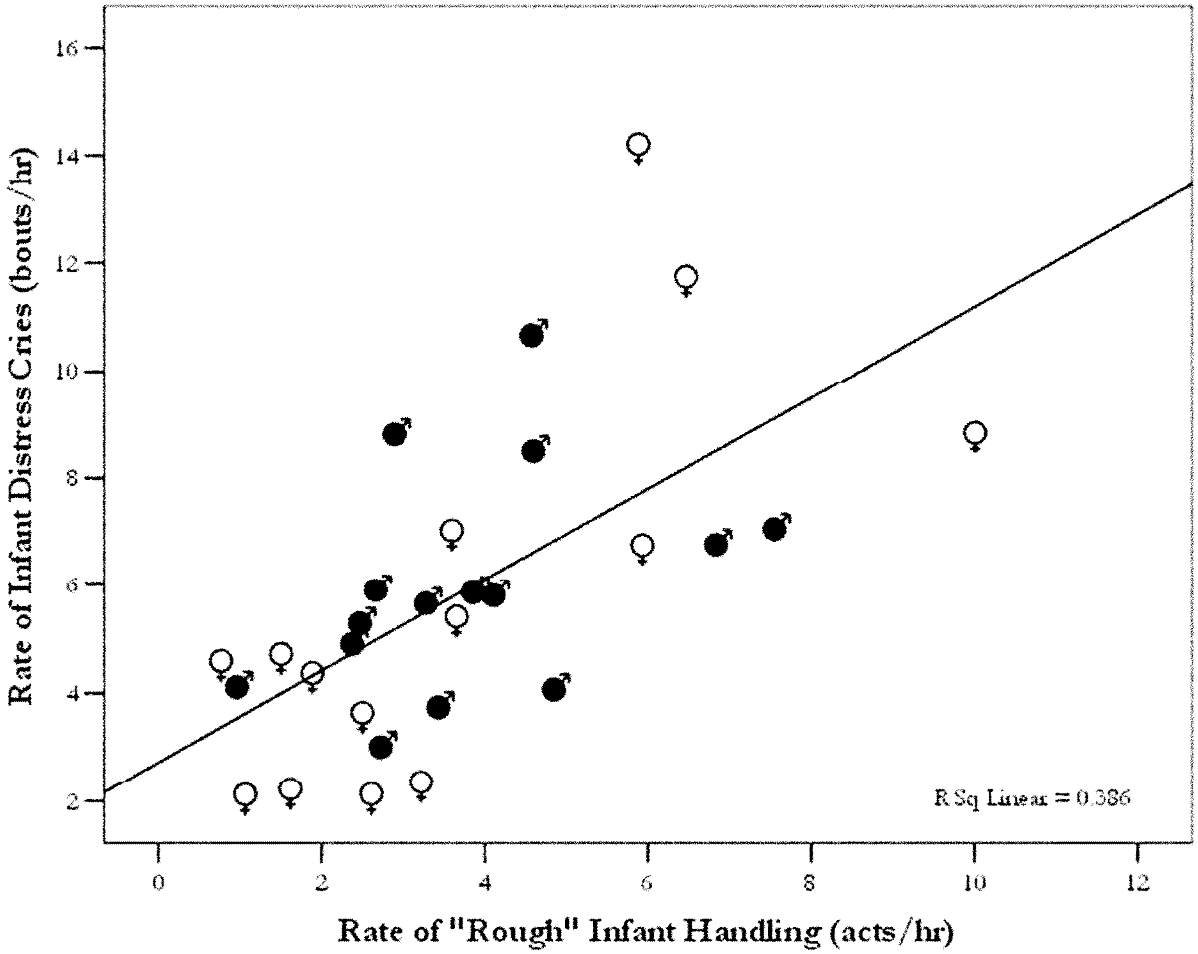

Fig. 3.3. Mean (+SE) rates of rough infant handling and distress cries in dyads that spent the most and those that spent less time in proximity to male friends. Infants whose mothers ranked in the top quartile (i.e. spent at least 28%) of time in proximity to male friends (A) experienced significantly lower rates of rough infant handling, and (B) gave significantly lower rates of distress vocalizations than infants whose mothers spent less time in proximity to male friends. *=difference is statistically significant at the p<0.05 level.

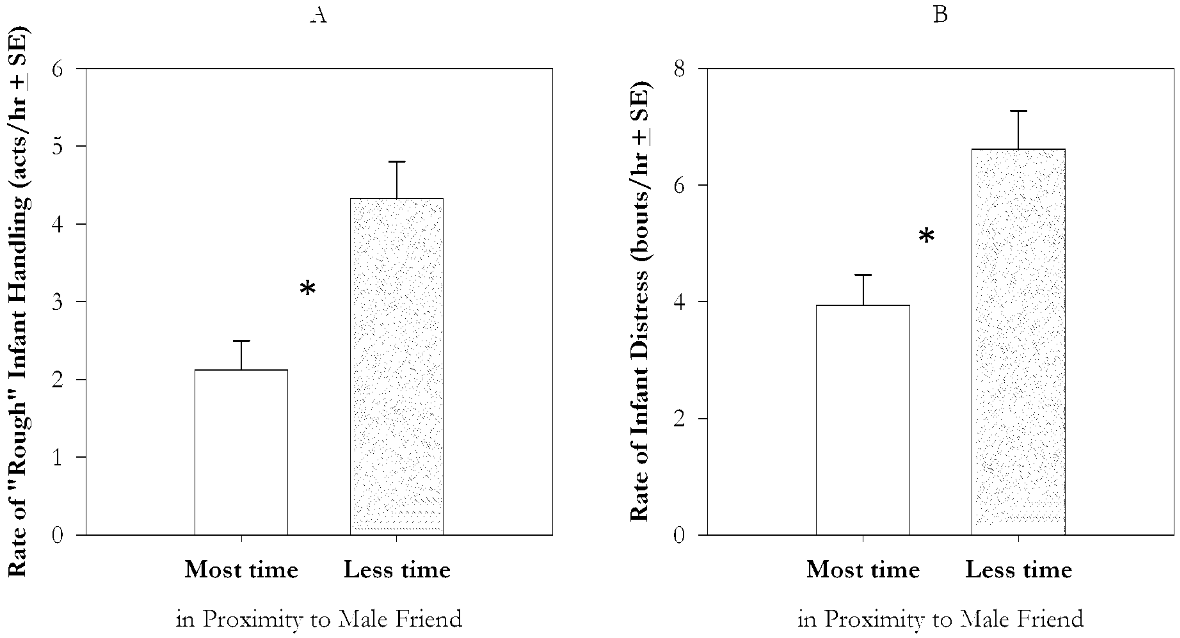

Fig. 3.4. The effect of instability in male social relations on the strength of male-female bonds. Mothers with young infants spent less time in proximity to male friends the more unstable male social relationships were within the group, i.e. the fewer the number of months since an unfamiliar adult male had emigrated into the group and the fewer the number of months since the alpha male has held his top ranking position (adjusted r^2=.242, df=28, p=.010). Of these two variables, months since an unfamiliar adult male entered the group made a larger unique contribution to the prediction of time spent in proximity to male friends (9%) than did number of months since the alpha made has retained his position (4%).

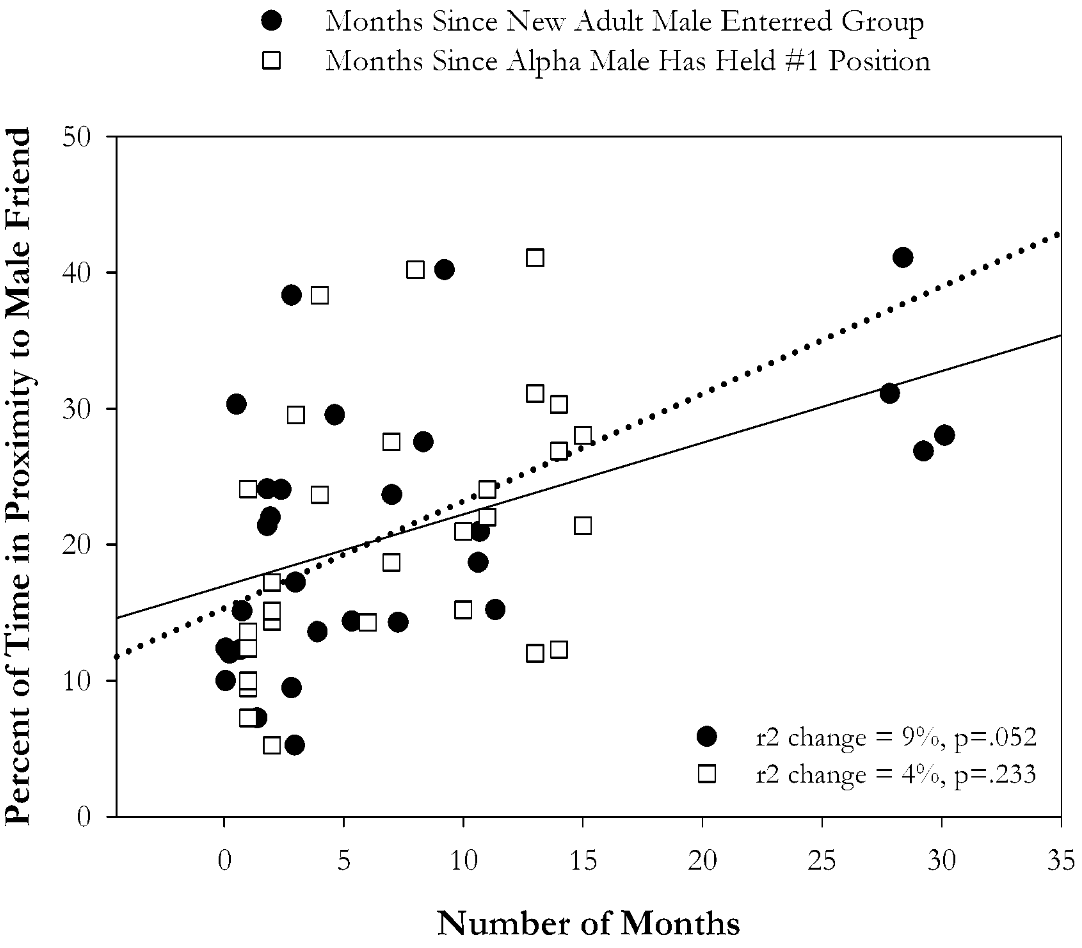

Table 3.I. Summary of predictions derived from hypotheses for why friendships might be adaptive for each sex.

Benefits to Females

Hypothesis 1: Friendships protect infants from harrassment from other females

1. Females will handle infants more roughly and at higher rates than males
2. Infants whose mothers associate more with male friends will receive fewer acts of handling than infants whose mothers associate less with male friends

Hypothesis 2: Friendships protect infants from infanticide by adult males

1. Risk of infanticide will increase with increasing instability in male social relations
2. Females will seek protection from male friends during periods of enhanced infanticide risk

Benefits to Males

Hypothesis 1: Friendships represent mating effort by males

1. Males will have greater mating success with former friends in future reproductive cycles than expected given their overall consorting activity

Hypothesis 2: Friendships represent paternal invesment in offspring

1. Males will associate preferentially with their own offspring
    - a. Fathers will associate more with mothers the more likely they are to have sired the offspring
    - b. Fathers will associate more with infants the fewer other immature offspring they have in the group
    - c. Fathers will associate more with offspring the greater its risk of injury or mortality
2. Friendships will help improve the fitness of offspring

Table 3.II. Identifying male friends from grooming and proximity data. Comparison of the identities of the mother's most frequent male grooming partner with that of her most frequent male proximity partner for the 29 focal mothers. If two names are given for Proximity Partner, females spent equal amounts of time in proximity to the both males, though only the amount of time spent in proximity to each male is given. Mothers were seen in proximity to adult males, but never grooming with them in 4 cases. Sorted by whether mothers' grooming partner was the same individual as her proximity partner (Y) or not (N).

Female	**Grooming Partner**	**Proximity Partner**	**Grooming = Proximity Partner?**	**Male Friend**
HUM2	REX	REX*	Y	REX
HYM1	REX	REX*	Y	REX
SER7	NYU	NYU	Y	NYU
DUN2	LIB*	LIB*	Y	LIB
VIV9	LIB	LIB	Y	LIB
CAI1	DEP*	DEP*/BLU	Y	DEP
DUX2	DEP*	DEP*	Y	DEP
LAZ5	DEA*	DEA*	Y	DEA
NAP4	HIB	HIB	Y	HIB
VEL7	MLO*	LOF/MLO*	Y	MLO
VET5	MLO	MLO	Y	MLO
VIO5	KER*	KER*	Y	KER
VOT3	MLO	MLO	Y	MLO
NOB3	HIB	HIB	Y	HIB
HON1	NYU*	NYU	Y	NYU
HAM5	EXO[a]	EXO*	Y	EXO
LAD4	ZIN	ZIN	Y	ZIN
LAV4	SHY[b]	BEA/SHY*	Y	SHY
VIN9	KER*	KER*	Y	KER
MYS4	-	ZIN	-	ZIN
KOL2	-	ROC	-	ROC
VOW1	-	KER*	-	KER
LAS5	-	AMA	-	AMA
WEN8	ALE	DEA	N	DEA
WEA8	AMA	BEA*	N	BEA
HOL3	REX	EXO*	N	EXO
LOL1	ZIN	IAG	N	IAG
WAD4	ZAI	HIB	N	HIB
LOC2	SHY	VAN*	N	VAN

* = male was female's most frequent (grooming or proximity) partner during both late pregnancy and the postanatal p

a = female was not observed grooming with adult males during postnatal period, but male was female's most frequent grooming partner during late pregnancy

b = male was not female's most frequent grooming partner during the postnatal period but was during late pregnancy

Table 3.III. Change in grooming patterns with adult males from late pregnancy to the early postnatal period for the 29 mothers.

	Prenatal (%)	**Postnatal (%)**	**trend**	**p^a**
Prop. total time grooming				
all group members	6.9±0.6	3.7±0.5	↓	<.0005**
all adult males	1.2±0.3	1.3±0.3		0.930
Prop. total grooming time grooming				
all adult males	15.5±4.0	34.8±5.1	↑	<.0005**
favorite male grooming partner	13.5±3.4	29.5±4.7	↑	0.001**
all other adult males combined	2.0±1.1	5.4±1.7	↑	0.027*
Prop. total time being groomed				
by all group members	3.6±0.4	8.5±0.6	↑	<.0005**
by adult males	0.3±0.1	0.3±0.1		0.906
Prop. total being groomed time being groomed				
by all adult males	7.0±3.0	3.4±0.7	↓	0.286
by favorite male being groomed partner	6.7±3.0	2.9±0.6	↓	0.234
by all other adult males combined	0.3±0.2	0.6±0.3	↓	0.527

* = difference is significant at $p \leq .05$

** = difference is significant at $p \leq .01$

^{a} = results of paired-samples t-tests

Table 3.IV. Comparison of mother-infant dyads that spent the most time in proximity to male friends to those dyads that did not. Dyads that ranked in the top quartile (>0.28) of time in proximity to male friends received lower rates of rough handling and exhibited lower rates of distress than all other dyads.

	Dyads in Top Quartile n=8	**Dyads Not in Top Quartile n=21**	**p**[a]
Infant handled roughly rate	2.1±0.4 acts/hr	4.3±0.5 acts/hr	p=0.011[×]
Infant distress rate	3.9±0.5 bouts/hr	6.6±0.7 bouts/hr	p=0.025[×]

[a] = result of independent samples t-tests

[×] = difference is statistically significant at $p \leq .05$

Table 3.V. The characteristics of friendships. The 29 mother-infant dyads included mothers and infants of all backgrounds. Male friends consisted of 16 of the 34 adult males resident in the four multi-male groups during the study period.

Mother	Group Identity	Infant Sex	Maternal Rank[a]	Maternal Parity[b]	Prop. of Time in Proximity to Friend (%)[c]	Friend	# Non-Friends[d]	Friend Age (yrs)[e]	Avg. Non-Friend Age (yrs)[e]	Total Consort Time (hrs)[f]	Prop. of Consort Time with Friend[g]	Prop. of Consort Time per Non-Friend[g]	Friend's Rank[h]
CAH	1.1	?	8	1	14.3	DEP	8	13.2	11.8	(-)	-	-	3
DUN2	1.22	?	1	2	28.0	LIB	3	10.3	12.1	10.5	1.00	0	1
DUX2	1.1	?	4	2	27.6	DEP	8	13.3	11.9	10.5	1.00	0	2
HAM5	1.1	?	19	5	12.3	EXO	7	13.5	12.1	8.1	0	0.14	6
HOL3	1.1	?	18	3	21.4	EXO	7	13.5	12.2	8.8	0.28	0.10	5
HON1	1.1	?	13	1	15.2	NYU	8	10.9	12.5	(-)	-	-	3
HUM2	1.1	?	16	2	30.3	REX	7	11.7	12.3	5.4	1.00	0	1
HYM1	1.1	?	16	1	40.2	REX	8	11.2	12.3	(-)	-	-	1
KOL2	2.2	?	14	2	9.5	ROC	8	18.3	12.4	5.1	0	0.13	4
LAD4	2.1	?	3	4	23.7	ZIN	5	16.1	12.0	5.3	0	0.20	3
LAS5	2.2	?	7	5	24.1	AMA	7	17	13.2	9.6	0	0.14	8
LAV4	2.2	?	18	4	5.3	SHY	7	15	12.1	10.6	0.18	0	7
LAZ5	2.2	?	9	5	17.2	DEA	7	8.8	13.0	16.9	0.37	0.03	2
LOC2	2.2	?	9	2	12.0	VAN	7	10.2	14.1	5.0	1.00	0	2
LOL1	2.1	?	8	1	24.1	IAG	6	13.6	12.4	3.6	0	0.17	4
MYS4	2.1	?	9	4	22.0	ZIN	6	15.7	12.0	9.1	1.00	0	2
NAP4	2.1	?	5	4	14.4	HIB	5	10	13.0	1.2	0	0.20	2
NOB3	2.1	?	6	3	13.6	HIB	6	9.9	13.1	5.7	0	0.17	1
SER7	1.1	?	1	7	21.0	NYU	8	10.9	12.5	4.2	1.00	0	3
VEL7	1.22	?	6	7	15.1	MLO	4	15.6	9.6	5.9	0	0.25	5
VET5	1.22	?	9	5	26.9	MLO	3	15.3	10.3	5.2	0	0.33	5
VIN9	1.22	?	8	9	41.1	KER	3	10.2	12.0	5.4	0	0.33	3
VIO5	1.22	?	7	5	31.1	KER	3	10.1	11.9	9.3	0	0.33	3
VIV9	1.22	?	11	9	38.3	LIB	6	10.7	10.0	5.8	1.00	0	6
VOT3	1.22	?	4	3	10.0	MLO	3	15.5	10.6	5.1	0	0.33	4
VOW1	1.22	?	7	1	12.4	KER	3	10.5	12.3	5.6	0	0.33	3
WAD4	2.1	?	1	4	18.7	HIB	4	10.5	13.2	8.0	0	0.18	2
WEA8	2.2	?	3	8	29.5	BEA	8	14.5	13.1	5.9	0	0.13	8
WEN8	2.2	?	6	8	7.3	DEA	7	8.2	14.4	9.6	0.32	0.10	1

a = female's ordinal rank number the month she conceived the infant (1 is highest)

b = total number of prior pregnancies, regardless of outcome, and including the current infant

c = proportion of mother's total time spent in proximity to the male friend X 100

d = total number of non-friend males in the group during the study period (see Methods for definition)

e = male age at the infant's birth in years (average value given for non-friends)

f = total number of hours mother was seen consorting with all adult males during the fertile period of the cycle in which she conceived the current infant. Three females, indicated by (-), were not seen co underlining, consorted for less than 5 hrs total and datafrom these 6 females were not used in analyses of prior consortship success with mothers

g = male's achieved proportion of mother's total consort time (average value given for non-friends)

h = male's average ordinal rank during the first two postnatal months (1 is highest) (average value given for non-friends)

i = total # of male's immature offspring (not including the infant if male is the father) present in the group during the infant's first two months of life (average value given for non-friends)

h = male friends who were also the offspring's genetic father are assigned a "Y", those who were not were assigned a "N", while infants for whom paternity has not been assigned are indicated by "-"

Table 3.VI. Results of comparisons of characteristics of all friend dyads with all non-friend dyads using independent samples t-tests.

	MALE FRIEND?		
	YES (n=29)	**NO** (n=172)	**p**
Male Age	12.6±0.5	12.4±0.2	0.731
Male Rank	3.5±0.4	4.9±0.2	0.001**
# of Other Immature Offspring	3.0±0.4	2.2±0.2	0.062
Prop. Mom's Consort Time[a]	0.3±0.1	0.1±0.0	0.091

a = analysis restricted to 22 females with 22 male friends and 122 non-friends (see Table V and Methods for explanation)

** = result is significant at $p<0.01$

Table 3.VII. The number and proportion of individuals present in the four groups during the study period for which paternity is or is not known. Adults include all individuals who have attained sexual maturity (menarche for females and testicular enlargement for males); "in transition" animals include all individuals who attained sexual maturity during the study period; and immatures include all other individuals.

	PATERNITY		
	Known	**Not Known**	**TOTAL**
Adults	79	29	108
	73%	27%	
In transition	13	0	13
	100%	0%	
Immatures	91	23	114
	80%	20%	
TOTAL	183	52	235
	78%	22%	

Table 3.VIII. Comparison of prior mating success with mothers between friends who were fathers (Y) and friends who were not fathers (N). Mothers who consorted with males for less than 5 hrs during the fertile phase of the cycle in which the infant was conceived (indicated by gray highlighting) were not included in the analyses.

Mother	Male Friend	Infant's Father	Male Friend = Father?	Total Consort Time (hrs)[a]	Friend's Prop. of Consort Time[b]	Father's Prop. of Consort Time[b]
DUN2	LIB	LIB	Y	10.5	1.00	1.00
DUX2	DEP	DEP	Y	10.5	1.00	1.00
MYS4	ZIN	ZIN	Y	9.1	1.00	1.00
VIV9	LIB	LIB	Y	5.8	1.00	1.00
HUM2	REX	REX	Y	5.4	1.00	1.00
LAZ5	DEA	DEA	Y	16.9	0.37	0.37
WEN8	DEA	DEA	Y	9.6	0.32	0.32
WEA8	BEA	BEA	Y	5.9	0	0
HOL3	EXO	REX	N	8.8	0.28	0.30
VIO5	KER	LIB	N	9.3	0	1.00
WAD4	HIB	KRA	N	8.0	0	0
VEL7	MLO	LOF	N	5.9	0	0
NOB3	HIB	IAG	N	5.7	0	0.25
VOW1	KER	LIB	N	5.6	0	1.00
VET5	MLO	LIB	N	5.2	0	1.00
KOL2	ROC	VAN	N	5.1	0	0.29
VOT3	MLO	KER	N	5.1	0	0
SER7	NYU	NYU	Y	4.2	1.00	1.00
LOL1	IAG	MOR	N	3.6	0	1.00
NAP4	HIB	ZIN	N	1.2	0	0
CAI1	DEP	DEP	Y	-	-	-
HYM1	REX	REX	Y	-	-	-
HON1	NYU	DEP	N	-	-	-

a = total number of hours mother was seen consorting with all adult males during the fertile period of the cycle in which she conceive

b = male's achieved proportion of mother's total consort time

Table 3.IX. Comparisons of fathers who were friends (Y) with fathers who were not friends (N) for the 23 mother-infant dyads for which paternal kinship was known.

Infant's Mother	Infant's Father	Friend = Father?	Prop. Time in Proximity to Dad[a]	Mom's Total Consort Time (hrs)[c]	Dad's Prop. of Mom's Consort Time[b]	Dad Age[d]	Dad Rank[e]	Dad's Other Immature Offspring	Maternal Rank[f]	Maternal Parity[g]	Infant Sex	Months Since New Adult ♂[h]
WEA8	BEA	Y	0.30	5.9	0.00	14.5	8	1	3	8	♀	4.62
LAZ5	DEA	Y	0.17	16.9	0.37	8.8	2	4	9	5	♂	2.98
WEN8	DEA	Y	0.07	9.6	0.32	8.2	1	3	6	8	♂	1.38
CAI1	DEP	Y	0.14	(-)	(-)	13.2	3	2	8	1	♀	7.28
DUX2	DEP	Y	0.28	10.5	1.00	13.3	2	2	4	2	♀	8.33
DUN2	LIB	Y	0.28	10.5	1.00	10.3	1	8	1	2	♂	30.13
VIV9	LIB	Y	0.38	5.8	1.00	10.7	6	10	11	9	♀	2.82
SER7	NYU	Y	0.21	4.2	1.00	10.9	3	3	1	7	♂	10.69
HUM2	REX	Y	0.30	5.4	1.00	11.7	1	6	16	2	♂	0.52
HYM1	REX	Y	0.40	(-)	(-)	11.2	1	4	16	1	♀	9.21
MYS4	ZIN	Y	0.22	9.1	1.00	15.7	2	4	9	4	♀	1.93
HON1	DEP	N	0.02	()	(-)	13.6	2	3	13	1	♀	11.34
NOB3	IAG	N	0.08	5.7	0.25	13.7	3	2	6	3	♂	3.90
VOT3	KER	N	0.03	5.1	0.00	10.5	3	3	4	3	♀	0.07
WAD4	KRA	N	0.08	8	0.00	8.3	1	1	1	4	♂	10.62
VET5	LIB	N	0.15	5.2	1.00	10.2	1	8	9	5	♂	29.25
VIO5	LIB	N	0.05	9.3	1.00	10.1	1	7	7	5	♀	27.84
VOW1	LIB	N	0.02	5.6	1.00	10.5	1	9	7	1	♂	0.07
VEL7	LOF	N	0.15	5.9	0.00	10.9	3	3	6	7	♀	0.75
LOL1	MOR	N	0.12	3.6	1.00	16.1	7	1	8	1	♂	2.39
HOL3	REX	N	0.14	8.8	0.30	11.8	1	6	18	3	♂	1.80
KOL2	VAN	N	0.01	5.1	0.29	10.5	2	5	14	2	♂	2.82
NAP4	ZIN	N	0.01	1.2	0.00	16	4	5	5	4	♂	5.34

a = proportion of mother's total time spent in proximity to father during the first two postnatal months

b = proportion of mother's total consort time during fertile period of conceptive cycle spent consorting with dad

c = total number of hours mother was seen consorting with all adult males during the fertile period of the cycle in which she conceived the current infant. Three females, indicated by (-), were not observed consorting, while another 3, indicated by underlining, consorted for less than 5 hrs total. Data from these 6 females were not used in analyses of prior consortship success with mothers

d = father's achieved proportion of mother's total consort time.

d = father's age at infant's birth

e = father's average ordinal rank during the first two postnatal months (1 is highest)

h = number of months from the day infants turned two months old since an unfamiliar adult male had emmigrated into the group

Table 3.X. Results of comparisons of fathers who were friends and fathers who were not friends, using independent samples t-tests.

	FATHER = MALE FRIEND?		
	YES (n=11)	NO (n=12)	P
Ratio :	5:6	8:4	0.41[a]
Months since new adult	7.3±2.5	8.0±3.0	0.85
Maternal			
Rank	7.6±1.6	8.2±1.4	0.80
Parity	4.5±0.9	3.3±0.5	0.28
Paternal			
Rank	2.7±0.7	2.4±0.5	0.72
Age	11.7±0.7	11.9±0.7	0.87
# other immature offspring	4.3±0.8	4.4±0.8	0.90
Prop. mom's consort time[b]	0.7±0.1	0.4±0.1	0.20

a = result of Fisher's Exact Test

b = analysis restricted to 8 father-friends and 9 father-not friends (see Table IX and Methods for explanation)

Table 3.XI. Male mating success of former friends in future reproductive cycles. Six friends were no longer present when mothers resumed cycling, and an additional 7 friends left the group before the female conceived her next offspring. Below, these 13 friend dyads are highlighted in grey.

Mother	Friend	Months until resumption of cycling[a]	Months spent cycling[b]	Prop. of months spent cycling male friend was present in group[c]	Total consort time (hrs) during months spent cycling	Friend achieve better (+), same (=) or worse (-)?[a]	Male Friend = Father?
DUX2	DEP	12.7	6.2	1.00	29.4	+	Y
HUM2	REX	10.5	6.3	1.00	11.5	+	Y
HYM1	REX	11.8	2.9	1.00	5.8	+	Y
WAD4	HIB	12.3	7.2	1.00	35.5	+	N
DUN2	LIB	8.7	7.4	1.00	28.6	=	Y
HAM5	EXO	11.1	0.8	1.00	10.9	=	-
HOL3	EXO	12.4	3.1	1.00	9.6	=	N
LAD4	ZIN	7.1	0.5	1.00	6.4	=	-
LAS5	AMA	9.6	6.1	1.00	15.2	=	-
LAZ5	DEA	10.2	2.1	1.00	12.6	=	Y
CAH	DEP	12.2	5.0	1.00	14.6	-	Y
MYS4	ZIN	11.2	3.4	1.00	8.0	-	Y
VET5	MLO	5.9	3.7	1.00	16.9	-	N
WEA8	BEA	7.8	3.8	1.00	5.5	-	Y
WEN8	DEA	6.4	4.3	1.00	23.5	-	Y
VIN9	KER	2.7	0.6	1.00	-		-
VOT3	MLO	10.1	3.9	0.94	16.3	-	N
NOB3	HIB	12.6	1.5	0.92	4.8		N
VIO5	KER	6.5	4.6	0.89	26.6	-	N
NAP4	HIB	12.0	0.9	0.83	5.7		N
VEL7	MLO	5.9	10.0	0.74	57.1	-	N
VIV9	LIB	10.2	12.2	0.74	33.2	-	Y
LAV4	SHY	11.2	9.3	0.66	25.8		-
HON1	NYU	11.4	3.9	0.00	17.9		N
KOL2	ROC	8.6	8.6	0.00	45.5		N
LOC2	VAN	9.8	8.2	0.00	44.8		-
LOL1	IAG	10.8	3.3	0.00	0.9		N
SER7	NYU	9.4	4.8	0.00	22.2		Y
VOW1	KER	8.7	4.1	0.00	14.6		N

a = length of period of postpartum amenorrhea (reproductive sterility) for mothers following the birth of the infant in months
b = months mothers cycled until the conception of their next infant
c = proportion of the total number of days from the day females resumed cycling to the day they conceived their next offspring that the male friend was resident in the group
d = the total number of hours the mother was seen consorting with an adult male during the fertile period of all subsequent cycles
e = designations are as follows: friends consorted with mothers more (+), as often as (=), or less than expected (-) (see Methods)

Table 3.XII. Comparison of future mating success of dyads consisting of friend with those consisting of non-friend males. Table gives the number and proportion of males in each class (friend, non-friend) who achieved greater than, the same as, or worse than expected success with the mother during all her future reproductive cycles, up to and including the cycle in which she conceived her next offspring (see Methods).

	Male's Mating Success with Former Friends Relative to All Other Females			
	BETTER[a]	SAME[b]	WORSE[d]	TOTAL
Friend dyads	4	6	5	15
	27%	40%	33%	
Non-friend dyads	15	19	41	75
	20%	25%	55%	

a = # and percent of males whose proportion of mother's total consort time was **greater than** their proportion of all available consort time in the group
b = # and percent of males whose proportion of mother's total consort time was **the same as** their proportion of all available consort time in the group
c = # and percent of males whose proportion of mother's total consort time was **less than** their proportion of all available consort time in the group

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CHAPTER FOUR: Birth Intervals in Wild Baboons: Influence of Life History Possibly Mediated Through Suckling Intensity and Postpartum Progesterone Concentrations

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ABSTRACT

Although the spacing between births is one of the most important determinants of female reproductive success in long-lived mammals, few studies have examined the factors that contribute to variation in this fitness variable. Using demographic and reproductive data from our longitudinal study of wild yellow baboons (*Papio cynocephalus*) in Amboseli, Kenya, in conjunction with detailed data on suckling patterns and fecal steroid hormone excretion in a subset of intensively studied mother-infant dyads from the larger study population, we examine the predictors and possible proximate causes of variation in interbirth intervals. Our results show that variation in postpartum fertility in Amboseli baboons was predicted by infant death, maternal dominance rank and prior infant care experience, but not by the sex of the current infant. They also show that variation in suckling patterns was predictable from maternal dominance rank and was associated with differences among (some) mothers in postpartum progesterone levels. In addition, our results suggest that differences among mothers in the duration of the period of postpartum amenorrhea were predictable from postpartum levels of progesterone. Our data provide intriguing evidence suggesting that the consistent effect of maternal rank on birth intervals in a wide variety of social mammals may be mediated by suckling behavior and a putative steroid hormone organizer of the hypothalamo-pituitary-ovarian axis responsible for normal ovarian cycling and fecund menstrual cycles. Herein, we propose a model to explain how the influence of maternal rank on birth intervals in this and other populations might be mediated through suckling behavior. Lastly, our results raise the concern that in studies of life history variables, small samples may not have sufficient power to detect significant relationships that exist in larger datasets.

INTRODUCTION

A female's fitness is affected by the duration of her reproductive lifespan, the frequency with which she produces offspring, and the fertility of her offspring (Clutton-Brock 1988). Variation in one or more of these fitness components can produce considerable variation in lifetime reproductive success among individuals in a population (King et al. 1991; Ribble 1992; Wauters and Dhondt 1995; Brommer et al. 1998; van Noordwijk and van Schaik 1999; Altmann and Alberts 2003a). The interval between successive births, or interbirth interval, varies widely among females in many mammal populations (Ribble 1992; Cote and Festa-Bianchet 2001; Altmann and Alberts 2003a). Variation in birth intervals between populations and social groups of the same species have been attributed to several demographic and ecological variables, including group size (e.g. Hill et al. 2000), rainfall patterns (e.g. Srivastava and Dunbar 1996), and ambient temperatures (e.g. Dunbar 1990).

Within social groups, variation in birth intervals among individuals has been attributed to several maternal and infant attributes, including infant mortality (e.g. Koyama et al. 1992; Polo et al. 2000), infant sex (e.g. Takahata et al. 1995; Monard et al. 1997), maternal parity (e.g. Silk 1990; Setchell et al. 2002), and maternal dominance rank (e.g. Holekamp et al. 1996; Altmann and Alberts 2003b). Of these factors, infant mortality (e.g. Suchindran and Adlakha 1984; Rao and Beaujot 1986; Koyama et al. 1992; Fedigan and Rose 1995; Hsu et al. 2001) and maternal dominance rank (e.g. Whitten 1983; Armitage 1986; van Noordwijk and van Schaik 1987; Creel et al. 1992; Dietz 1993; Holekamp et al. 1996; Creel et al. 1997; Pusey et al. 1997; Clutton-Brock et al. 2001; Altmann and Alberts 2003b) are most often associated with individual variation in postpartum fertility in social mammals. Still, the proximate pathways through which these factors may influence a mother's future reproduction are poorly understood, and the possibility that they may be related to the energetics of reproduction has been overlooked.

Females have limited physiological resources they can devote to reproduction, and expenditure on the current offspring can reduce a mother's ability to invest in future offspring (Trivers 1972; Pianka 1976). Individual differences in the patterning of mother-infant interactions, particularly those reflecting differences in energy expenditure by mothers, may affect the mother's future reproduction (e.g. Fairbanks 1996; Caldji et al. 1998; Francis et al. 1999; Liu et al. 2000).

Lactation is the major component of early infant care and represents the most energetically costly form of postnatal care for mammalian mothers (Prentice and Prentice 1988). In many mammalian species, lactation suppresses postpartum fertility (reviewed in McNeilly 1994), and experimental evidence suggests that the inhibitory effects of lactation on fertility may be mediated by the suckling stimulus itself (Loudon et al. 1983; Loudon 1987). The precise mechanism by which suckling inhibits fertility is not fully understood, but suckling has been repeatedly implicated in the inhibition of hormone secretion from the hypothalamo-pituitary-ovarian (HPO) axis in both cattle (Williams 1990) and humans (McNeilly et al. 1994), events essential for normal ovarian activity and fecund menstrual cycles in these and other species (Hauger et al. 1977; Sarkar and Fink 1979; Goodman and Karsch 1980; Rahe et al. 1980; Levine et al. 1982; Pohl et al. 1983; Skarin et al. 1983). Although suckling has been associated with depressed levels of several HPO peptide hormones (e.g. gonadotrophin releasing hormone [GnRH], and luteinizing hormone [LH] (Carruthers and Hafs 1980; Walters et al. 1982; Gordon et al. 1987; McNeilly 1994) , the interactions between suckling behavior and ovarian steroid hormones are less well understood (Williams et al. 1983; Wilson et al. 1988; Wilson 1992). Unlike peptide hormones, the measurement of steroid hormones can be done non-invasively in feces, without requiring capture or immobilization of animals (Whitten et al. 1998), and is of particular value during the highly sensitive period of motherhood and infancy.

Although suckling may be the primary regulator of the duration of postpartum infertility (Williams 1990; McNeilly 2001), few studies have explored the role of suckling stimuli or the hormone changes accompanying lactation as proximate mediators of the influence of dominance relationships on the duration of birth intervals. In this study, we evaluate the sources and possible proximate mechanisms mediating variation in the timing of females' postpartum reproduction in a population of wild yellow baboons (*Papio cynocephalus*) in the Amboseli basin, Kenya. We use demographic and reproductive data collected over three decades on eight different study groups to examine the influence of four major maternal and infant characteristics that have been linked to individual variation in postpartum fertility in many previous studies – infant survival, infant gender, maternal parity and dominance rank. We then explore the possible proximate pathways through which female dominance relationships – perhaps the single most reliable predictor of postpartum fertility among mothers of surviving infants in this and other mammal populations – may influence the timing of mothers' future reproduction. Here, we use data on suckling patterns and on the patterning of steroid hormone excretion in mothers, collected on a smaller subset of dyads from the larger study population, to examine whether differences in suckling frequency or intensity are predictable from differences among mothers in dominance rank and in postpartum concentrations of a putative steroid hormone organizer of the HPO axis (Helmond et al. 1980; Lagace et al. 1980; Ramirez et al. 1980; Williams et al. 1983), progesterone.

METHODS

Subjects & Study Population

The data for this study come from a population of wild baboons inhabiting the Amboseli basin, a semi-arid, short grass savannah ecosystem situated at the base of Mt. Kilimanjaro in East Africa. The population has been under continuous observation for over three decades (Altmann 1980; Altmann 1998; Alberts and Altmann 2003; Altmann and Alberts 2003a, see www.princeton.edu/~baboon for a complete bibliography and the Baboon Project Monitoring Guide, which outlines data collection protocols for this population) and data on life history patterns are available for several hundred animals living in a total of 8 completely wild-foraging groups.

Here, the subjects are divided into two samples, a longitudinal sample and a sample consisting of a subset of intensively studied mother-infant dyads from the larger study population. The longitudinal sample includes all births resulting in live born infants in eight different study groups that were monitored between Jan 1976 and Dec 2004. Two original study groups fissioned, resulting in four study groups, and one of these groups fissioned, yielding an additional two groups, for a total of eight study groups. Subjects for the sample of intensively studied dyads include 39 mother-infant pairs in five study groups that were observed from Sep 2002 to Nov 2003 by NN.

Demographic & Reproductive Data

The histories of most females in the population are known since birth from near-daily records of demographic events and reproductive cycles. Demographic and reproductive data were drawn from the long-term electronic records of the Amboseli Baboon Project (BABASE). For each birth, we determined (1) its parity (the number of prior pregnancies and including the current infant), (2) maternal dominance rank (the mother's ordinal rank number the month she conceived the infant), (3) infant sex, and (4) interbirth interval (the length of the interval from the birth of the infant to the birth of the next offspring). For baboons, as for many other mammals, the interval between subsequent births consists of three distinct phases: (1) a period of postpartum amenorrhea or reproductive sterility, (2) a period of reproductive cycling consisting of one or more estrus cycles, and (3) a period of gestation. We therefore also determined the length of each of the three phases of the interbirth interval for each birth. Finally, if the infant died during infancy (i.e. during the first two years of life), we noted the infant's age at death and determined when the death occurred relative to the timing of the mothers' future reproduction.

Female reproductive condition was assigned based post-hoc examinations of external signs recorded in the field, including highly visible sexual skin swellings that increase in size around the time of ovulation, menstruation, and changes in the female's paracallosal skin indicating pregnancy. Data collected during the protracted period of fissioning of one group (Alto's) were not included in our analyses because sampling during this period was less complete than during other periods in BABASE.

Behavioral Data

Data on suckling patterns during the first 8 postpartum weeks were collected on 34 dyads, following the early death of 5 of the original sample of 39 infants during the period of sampling. On average, each dyad was observed for 11.6 + 4.5 (SD) actual in-sight observation hours in 33.2 + 12.2

(SD), 20 min focal animal samples (Altmann 1974). During each 20 min sample on a mother-infant pair, continuous records were kept of all occurrences of all change in mother-infant contact and suckling patterns, including time of onset and time of termination for each contact and suckling bout. All data were recorded on a handheld data recorder (Psion Workabout, Psion Teklogix) and subsequently transferred to Microsoft Excel XP and Microsoft Visual FoxPro 6.0 for analysis.

We computed four measures of suckling activity for each mother-infant dyad. First, we computed indices representing the (1) relative mean hourly rate of suckling bouts for each dyad, and the (2) relative mean proportion of time each infant was observed on the nipple. We then used survival analysis to estimate the (3) mean bout duration and the (4) mean interval between successive suckling bouts (or interbout interval) for each dyad.

A suckling bout began and ended with the onset and termination of nipple contact, respectively. We initially used log survivorship analysis to determine whether a minimum criterion interval separating consecutive suckling bouts exists in our data (Fig. 4.1) (Martin and Bateson 1993). Not finding one (indicated by a 'break point' between a rapidly declining portion representing the short within-bout gaps and a slowly declining portion representing the long between-bout gaps), we include all suckling bouts as separate bouts in our analyses.

To obtain each dyad's suckling bout frequency relative to other dyads in the study, we first computed the hourly rate of sucking for each dyad by dividing the total number of suckling bouts by the total number of hours the mother-infant pair was observed each week. We then compared this value to the population average rate each week, and took the mean of the dyad's residuals or deviations from the group average rate across weeks as the dyad's relative suckling rate. Residuals were calculated by subtracting the population average hourly suckling rate from the dyad's rate each week. Dyads with positive residuals had higher suckling rates than the average dyad that week, while those with negative residuals had lower suckling rates than the average dyad that week. Finally, we computed the proportion of time each infant was observed on the nipple relative to other infants by taking the mean of the infant's residuals or deviations from the population average proportion for each of the 8 weeks of infancy. Here, infants with positive residuals spent more time on the nipple than the average infant that week, while those with negative residuals spent less time on the nipple than the average infant that week.

Because we could not record the time of onset or termination for some bouts, we used Kaplan-Mier failure time analyses, which make use of both uncensored and censored bouts and corrects for censoring, to provide an estimate of the mean bout duration and mean interbout interval for each dyad. Of the four suckling measures, interbout intervals have been most frequently implicated in the inhibition of postpartum ovulation (reviewed in Short 1984). For example, in experimental studies of cattle, mothers who were allowed to suckle for only 30 minutes each day had offspring that grew at normal rates but returned to estrous almost immediately, whereas mothers who were allowed to suckle throughout the day had significantly longer periods of lactational infertility (Short 1984).

Fecal Hormone Data

Fecal samples were collected from each mother during the first 8 postpartum weeks. A total of 308 fecal samples were collected from 34 mothers, yielding an average of 1.1 fecal samples per female per week. Samples were collected within minutes of deposit in a vial prefilled with 95% ethanol in a ratio of 2.5:1 ethanol to feces. Samples were stored in an evaporation cooler at ~15 (daily minimum) – 25 (daily maximum)°C in the field camp before they were transported, every two weeks, to the University of Nairobi. There the ethanol was evaporated and the samples were lyophilized and stored in a -20°C freezer. Samples were then transported to Princeton University where each was sifted through fine mesh and 0.2 g of sample was extracted into 2 ml of 90% methanol. The methanol extracts were then subjected to solid phase extraction (Waters, Milford MA, WAT094226) (Khan et al. 2002; Lynch et al. 2003).

The concentration of excreted progesterone in each fecal extract was assessed using I-125 radioimmunoassays. All samples were assayed in duplicate and mean concentrations were expressed as ng of hormone per g of dry fecal matter, to control for dietary differences between individuals and seasons (Wasser et al. 1993). We use reagents from a Pantex Progesterone I-125 kit to measure progesterone in baboon feces (assay development and validation in Lynch et al. 2003).

Individual females differed in the days relative to parturition on which they were sampled. Since such differences can confound analyses of individual differences during a rapid period of change in hormone concentrations (Altmann et al. 2004), we examined individual differences in excreted hormones across females using deviations from the group average for each point in time, measured in days after parturition. We chose LOWESS (with a window of 0.5) because it is more "locally sensitive" to time-specific deviations from the average pattern (Moses et al. 1992; Altmann and Alberts 2003a; Altmann and Alberts 2005). We calculated each sample's residual from the class average as the ratio of the sample's progesterone concentration to the population average progesterone level that day. Females with residuals above 1.0 have values above the group average that day, while those with residuals below 1.0 have values below the group average that day. We excluded samples from the first to the fourth days after birth (corresponding to days 0-3) because, due to the 1-3 day lag time between steroid hormone secretion and excretion in feces (Wasser et al. 1994), values from these days were believed to reflect prenatal levels. Daily residual values were then divided into weeks relative to parturition and a weekly mean progesterone value was calculated for each mother each week. Finally, a single mean progesterone value for the entire first 8 weeks of motherhood for each mother was computed by taking the $\log_{10}$ of the mean of the weekly means.

Data Analysis

In the analyses reported below, the mother-infant dyad is the unit of analysis. We restricted our analyses of the predictors of the length of the interbirth interval and its component phases to only those births that were succeeded by the birth of another live born infant, to eliminate any potential confounding effects of pregnancy failure on birth intervals. Births to females in the early years of populational sampling for which prior reproductive histories were not known were excluded from our analyses. Data on all variables of interest were available for 330 births to 110 adult females between Jan 1979 and May 2003 and are used in our analyses of the longitudinal population.

First, we examined the effect of infant loss on the timing of mothers' future reproduction by comparing the lengths of the interbirth interval and of each of the three phases of this interval between mothers whose infants had died and mothers of surviving infants, using Kaplan-Meier failure time analyses. Infant loss was characterized as occurring either before mothers had resumed cycling, or after they had resumed cycling but before they had conceived their next offspring.

We then evaluated whether maternal dominance rank, parity and infant sex predicted the length of the interbirth interval and each of the three phases of this interval for mothers of surviving infants, using general linear model procedures (GLM). For this particular analysis, the number of mother-infant dyads from the longitudinal sample (n=269) was nearly 10x the number from the sample of intensively studied dyads (n=28), 68% of whom were included in the first sample because of overlap in the period of study. Because our sample of intensively studied dyads was small, we used resampling procedures to examine the probability of obtaining the same patterns as in the larger populational sample given a smaller sample of mother-infant dyads. Using the Excel add-in (version 3.2), we randomly drew N samples (where N = 28, the number of mothers of surviving infants in our sample of intensively studied dyads) with replacement from the longitudinal data set of 269 births resulting in surviving infants. We then calculated the effects of parity and rank (the factors that had significant effects in the longitudinal dataset) on interbirth intervals for this randomly drawn group using multiple linear regression. This process was repeated 10, 000 times to generate a frequency distribution of the direction and magnitude of parity and rank effects on interbirth intervals which we used to determine the probability of detecting significant effects in a small sample of females.

Bivariate relationships between variables were explored using Pearson's correlation coefficients or linear regression analyses where appropriate. All statistical analyses were conducted using SPSS 13.0 (SPSS Inc. 2003). Values reported are mean+SE unless otherwise noted. All analyses were two-tailed with $p<.05$.

RESULTS

Longitudinal Sample

Effects of infant loss, maternal rank and parity on postpartum fertility

Infant loss shortened the length of the period of postpartum amenorrhea and the time spent cycling, and consequently, the interval to the birth of the next offspring (Table 4.I). Mothers whose infants died before they resumed cycling had shorter periods of postpartum amenorrhea (Fig. 4.2A, Table 4.I) and spent significantly less time cycling before conceiving their next offspring (Fig. 4.2B, Table 4.I) than mothers of surviving infants. However, gestation lengths did not differ significantly between the two groups of mothers (Table 4.I). Nonetheless, mothers whose infants infant died before they resumed menses had significantly shorter interbirth intervals than mothers of surviving infants (Fig. 4.2C, Table 4.I).

Among mothers whose infants died before they resumed cycling (n=61 infant deaths to 47 mothers), the age of infant death predicted the subsequent length of the period of postpartum amenorrhea and, consequently, the interval to the birth of the next offspring. Mothers whose infants died at an earlier age resumed cycling significantly sooner (Fig. 4.3A; $r^2=0.99$, $p<.0005$) and had significantly shorter interbirth intervals (Fig. 4.3B; $r^2=0.8$, $p<.0005$) than mothers whose infants died at a later age. Finally, mothers whose infants died after they had resumed cycling but before the conception of their next offspring (2.8+0.3 months, n=13) cycled for a significantly shorter period of time than mothers of surviving infants (4.4+0.2 months, n=256) (log-rank test, $p<.0005$).

Among mothers of surviving infants (n=269 births to 103 mothers), birth intervals were predicted strongly by maternal rank, weakly by parity, and not by the sex of the current offspring (Table 4.II). On average, higher ranking, multiparous females had the shortest interbirth intervals. The effect size for rank (=.123) was large, representing 12.3% of the variance in interbirth intervals explained by maternal rank, while the effect size for parity (=.040) was small (following criteria for determining effect size in Cohen 1988).

The effect of rank on interbirth intervals (Fig. 4.4A) stemmed from its main effect on the length of the period of postpartum amenorrhea (Fig. 4.4B). On average, higher ranking mothers resumed cycling significantly faster than lower ranking mothers (Table 4. III, Fig. 4.4A), and the magnitude of this effect (=.166) was large.

The effect of parity on birth intervals was only apparent after separating first-time from multiparous mothers and stemmed from the effects of parity class on the length of the period of reproductive cycling and gestation (Fig. 4.5). On average, multiparous mothers spent significantly less time cycling (Table 4.IV) and had significantly shorter periods of gestation than primiparous mothers (Table 4.V, Fig. 4.4), although the magnitude of these effects (0.068 and 0.020, respectively) were small.

Sample of Intensively Studied Dyads

Effect of sample size

In the original sample of intensively studied dyads (n=39), infant loss shortened the length of the period of postpartum amenorrhea, the period of reproductive cycling, and the overall interbirth interval. These findings were consistent with those above from the longitudinal dataset. However, among mothers whose infants were alive when they resumed cycling (n=28), we identified no significant predictors of the length of the interbirth interval.

We suspect that the lack of significance in this sample is due to small sample size. In fact, rank had no significant effect on birth intervals in 54% of the 10, 000 randomly drawn samples of 28 births in our resampling analysis, while parity had no significant effect on birth intervals in 84% of the 10, 000 randomly drawn samples of 28 births. That is, the results of our resampling analyses suggests that given a sample size of 28 births, our sample of intensively studied dyads had 46% power to detect an effect of rank and 16% power to detect an effect of parity.

Suckling patterns

Suckling activity changed dramatically across the first 8 weeks of infancy (Fig. 4.6). Infants spent decreasing amounts of time on the nipple as they grew older (Fig. 4.6A), and this change was accompanied by more frequent suckling (Fig. 4.6B) and shorter suckling bouts (Fig. 4.6C). Because 26.4+1.3% (SD, n=34) of all suckling bouts were censored, we could not obtain estimates of bout lengths for some dyads some weeks. Thus, the populational means graphed in Fig. 4.6C are almost certainly underestimates of the true bout lengths. The interval between successive suckling bouts also decreased as infants grew older (Fig. 4.6D), though here the pattern of decrease was somewhat erratic.

Interbout interval was correlated with both the percent of time infants were observed on the nipple and with suckling bout frequency. Dyads with longer intervals between successive nursing bouts spent significantly less time on the nipple (r^2=-.41, p<.0005) (Fig. 4.7A) and had significantly fewer bouts per unit time (r^2=-.47, p<.0005) (Fig. 4.7B) than dyads with shorter intervals between bouts.

Rank effects on suckling, progesterone, and postpartum fertility

Maternal rank predicted individual variation among infants in two suckling measures: the interbout interval and the percent of time infants spent on the nipple. Infants of higher ranking mothers had longer intervals between successive suckling bouts (r^2=-.22, p=.006) (Fig. 4.8A) and spent less time on the nipple (r^2=.21, p=.006) (Fig. 4.8B) than infants of lower ranking mothers. These effects were present in both male and female infants, though the magnitude of the effect of rank on suckling patterns was greater in female than male infants (Fig. 4.8).

Less suckling among infants was, in turn, associated with higher levels of maternal progesterone in some, but not all, mothers. Among dyads with female infants (n=15), mothers whose infants spent less time suckling (r^2=-.30, p=.07) (Fig. 4.9A) and exhibited longer interbout intervals (r^2=.36, p=.04) (Fig. 4.9B) had higher progesterone concentrations.

Fecal progesterone levels were also predicted by maternal rank, but the effect of rank on postpartum progesterone was found only in mothers of female (r^2 =.28, p=.04), and not mothers of male (r^2=.01, p=.69), infants. On average, higher ranking mothers of female infants exhibited significantly higher concentrations of postpartum progesterone than lower ranking mothers.

Among mothers of surviving infants, the mean length of the period of postpartum amenorrhea was 10.0+2.1SD months (range 6.8-12.7 months, n=28). Individual variation in the length of the period of postpartum amenorrhea was predicted by maternal progesterone levels during the first two months of motherhood. On average, mothers with higher levels of postpartum progesterone had shorter periods of postpartum amenorrhea ($r^2=.312, p=.002$) and the magnitude and direction of this effect was similar in dyads of male and dyads of female infants (Fig. 4.10).

DISCUSSION

Although the spacing between births is one of the primary determinants of female reproductive success in long-lived mammals (Clutton-Brock 1988), few studies have examined the factors that contribute to variation in this fitness variable (Silk 1990; Fedigan and Rose 1995; Kelly et al. 1998; Polo et al. 2000). Our results show that variation in postpartum fertility in Amboseli baboons was predicted by infant death, maternal dominance rank and prior infant care experience, but not by the sex of the current infant. They also show that variation in suckling patterns was predictable from maternal dominance rank and was associated with differences among (some) mothers in postpartum progesterone levels. In addition, our results suggest that differences among mothers in the duration of the period of postpartum amenorrhea may be predictable from postpartum levels of progesterone. Lastly, our results raise the concern that in studies of life history variables, small samples may not have sufficient power to detect significant relationships that exist in larger datasets.

Effect of Infant Mortality on Postpartum Fertility

Infant mortality shortened the length of the interbirth interval and the duration of the first and second phases of this interval. In addition, mothers whose infants died younger resumed cycling faster and had shorter interbirth intervals than mothers whose infants died at a later age. These results are consistent with previously published reports of shorter birth intervals following the death of infants across a range of other mammals (e.g. Suchindran and Adlakha 1984; Rao and Beaujot 1986; Koyama et al. 1992; Fedigan and Rose 1995; Hsu et al. 2001). Infant death terminates the period of investment in the current offspring, and maternal resources no longer monopolized by the former offspring can subsequently be directed towards the production and care of other offspring. Lactation may mediate this process since nipple stimulation during suckling episodes is terminated with infant death, and the suckling stimulus may be the primary factor responsible for disrupting the pulsatile pattern of release of hormones from the HPO axis required for ovulation to occur (Tay et al. 1992; Ordog et al. 1998).

How Maternal Rank May Influence Postpartum Fertility

The results of our analyses of the longitudinal dataset suggest that, of the three mother-infant attributes we measured, maternal dominance rank made the single greatest contribution to variation in birth intervals among mothers of surviving infants. This finding is consistent with previously published reports for this and many other mammal populations. Indeed, rank effects on female reproductive parameters, including age at sexual maturity and reproductive rate, have now been documented in many mammal societies where group life is organized by dominance rank relationships (e.g. Whitten 1983; Armitage 1986; van Noordwijk and van Schaik 1987; Creel et al. 1992; Dietz 1993; Holekamp et al. 1996; Creel et al. 1997; Pusey et al. 1997; Clutton-Brock et al. 2001; Altmann and Alberts 2003b).

The proximate pathways through which dominance relationships influence birth intervals are poorly understood (Harcourt 1987; Harcourt 1989; Smuts and Nicolson 1989; Creel et al. 1992;

Creel et al. 1997), but may be related to the energetics of motherhood and reproduction. Here, we propose a model to explain how the influence of maternal rank on birth intervals in this and other populations might be mediated through suckling behavior (Fig. 4.11). We suggest that rather than influence reproduction directly, rank differences in nutritional condition among lactating mothers may lead to differences in suckling behaviors among infants which will, in turn, affect the timing of mothers' future reproduction.

High female rank is associated with foraging success in many animal populations (e.g. Post et al. 1980; Whitten 1983; van Noordwijk and van Schaik 1987; Barton and Whiten 1993; Robichaud et al. 1996; Harwood et al. 2003; Vogel 2005), including some where high rank is known to confer a reproductive advantage on females (e.g. Whitten 1983; van Noordwijk and van Schaik 1999; Altmann and Alberts 2003a). In Amboseli, low ranking individuals of both sexes are more likely to be interrupted during feeding bouts than high ranking animals (Post et al. 1980). This reduced feeding efficiency may result in poorer nutrition for low ranking mothers.

Reproduction in female mammals is responsive to the availability of metabolizable energy (Wade et al. 1996), and differences in maternal nutritional condition can affect the timing of postpartum reproduction. Nutritional condition can influence postpartum fertility directly by influencing mothers' ability to resume reproductive activity, or indirectly by affecting the milk supply and the suckling behavior of offspring (Loudon 1987; Aguirre et al. 1998).

Studies of humans and other animals suggest that while nutritional condition can affect postpartum fertility directly, these effects are typically small (Glasier and McNeilly 1990; Duquette and Millar 1995; Ylonen et al. 2003) unless under conditions of severe food limitation (Denhartog and Vankempen 1980; Woodside 1991; Ramachandran 1992). However, the direct and indirect effects of maternal nutritional condition on postpartum fertility can be difficult to disentangle

(Glasier and McNeilly 1990), but quantification of suckling patterns may provide insight into the factor that is more relevant in a particular situation.

In the few studies that have quantified milk production and composition, mothers in poor physical condition were found to produce less milk per unit time than mothers in better physical condition (Loudon et al. 1983; Brown et al. 1986; Landete-Castillejos et al. 2005). In addition, some poor quality mothers produce poorer quality milk (lower in both micro and macronutrients) than mothers in better physical condition (Brown et al. 1986). In response, offspring of poor quality mothers in these populations suckled more frequently or intensively (Loudon et al. 1983; Lunn 1985), possibly to overcome their mother's deficient milk supply and obtain adequate nutrition for their growing needs.

Greater suckling activity can, in turn, lengthen the interval between births, possibly by increasing the inhibitory effects of nipple stimulation on the hormones of the HPO axis (Delvoye et al. 1978; McNeilly 1994). Greater suckling activity is associated with disruptions in the pulsatile patterns of secretion of several HPO hormones, including GnRH and LH (Gordon et al. 1987; McNeilly 1994), and these disruptions are believed to be of primary importance in the regulation of postpartum fertility (Short 1993; McNeilly 2001). Progesterone has been implicated as an organizer of the HPO axis (Helmond et al. 1980; Lagace et al. 1980; Ramirez et al. 1980; Williams et al. 1983), and, in a study of rhesus macaques, lower levels of postpartum progesterone were associated with prolonged lactational infertility in younger mothers (Wilson et al. 1988; Wilson 1992). Furthermore, research on cattle suggests that experimental increases of progesterone in postpartum cows may improve luteal functioning once females resume cyclic activity (Williams et al. 1983).

Greater suckling activity is associated with longer intervals between births in many animal populations, including humans (e.g. Konner and Worthman 1980; Howie and McNeilly 1982), by delaying the resumption of postpartum ovulation (e.g. Bongaarts and Potter 1983; Stewart 1988), and the conception of the next offspring (e.g. Gomendio 1989b; Ziegler et al. 1990; Margulis et al. 1993). That the neural stimulus of suckling itself is responsible for postpartum infertility has been demonstrated in two species. Experiments with sheep (Kann and Martinet 1975) and wallabies (Renfree 1979) have shown that if the teat is surgically denervated, lactation continues normally and infants growth proceeds normally but the suppressive effects of suckling on postpartum fertility is lost.

At present, data from other populations are needed to fully evaluate the hypothesis that suckling activity may mediate the effects of maternal rank on interbirth intervals, but the results of our study provide some evidence consistent with this hypothesis. Our results show that suckling intensity and frequency were predictable from maternal rank and associated with variation among (some) mothers in postpartum progesterone during the first two months of motherhood. They also show that maternal progesterone levels predicted variation in the length of the period of reproductive sterility. Our results suggest that mother-infant dyads consisting of female infants may be more sensitive to the effects of rank on the mother's future reproduction than mothers of male infants, a finding consistent with the future life experiences of each sex. Because female baboons remain in their group of birth their entire lives, 'inheriting' their mother's rank as juveniles, while males disperse from their natal group and attain their rank via fighting ability, the lives of females as infants are more closely tied to those of their mothers. In summary, our data provide intriguing evidence consistent with the hypothesis that rank-related, suckling-mediated reductions in postpartum progesterone may be predictive of the subsequent length of lactational infertility in some primate mothers. Future studies will be of particular value in elucidating the specific pathways through which lactation may mediate the effects of maternal rank on the mother's future reproduction, a phenomenon that has been found in a wide variety of mammal societies but has, as yet, never been fully explained.

Effects of Parity, Infant Sex, and Sample Size

In our analyses, experienced mothers cycled for a shorter period of time before conceiving their next infant and had shorter gestation lengths than inexperienced mothers, though these effects only resulted in small improvements in birth intervals. Because age and prior experience are highly correlated, the greater reproductive efficiency of more experienced mothers may also be due in part to their increased age. Increasing age and parity are associated with fewer cycles to conception (Wasser et al. 1998) and with shorter interbirth intervals in other primates, including humans (Fedigan and Rose 1995; Strassmann and Warner 1998). Moreover, first-time mothers have longer intervals to the birth of their next offspring compared to multiparous mothers in some primate species (Gomendio 1989a; Silk 1990; Setchell and Wickings 2004). Reproductive performance is known to improve with age and experience in many species of birds (Clutton-Brock 1988; Newton 1989). Several hypotheses have been proposed to explain this pattern, though few studies have rigorously evaluated them (Forslund and Part 1995). One set of hypotheses, the "age-related improvements of competence" hypotheses (Forslund and Part 1995), seem particularly applicable to long-lived mammals, such as baboons. These hypotheses posit that individuals improve in certain skills that have positive effects on their reproduction with age and prior experience, including foraging ability and the production and care of young (Forslund and Part 1995). Mothers with prior infant care experience at Amboseli reproduced more efficiently than first-time mothers, possibly as a result of enhanced reproductive competence with age and experience.

In Amboseli, suckling patterns and birth intervals following the birth of surviving infants did not differ significantly between the sexes, suggesting that patterns of maternal expenditure did not differ markedly between male and female offspring. Where the benefits of maternal investment differ between male and female offspring, mothers are expected to bias care in favor of the sex that would benefit the most from the additional investment (Trivers and Willard 1973). In baboons, where females are philopatric and daughters typically inherit their rank from their mothers, this bias is expected to result in rank-related adjustments in birth sex ratios, with low ranking mothers favoring sons and high ranking mothers favoring daughters (Clark 1978; Silk 1983). However, in a recent survey of 36 wild baboon populations, Silk & colleagues found no evidence that baboon mothers facultatively adjust birth sex ratios in an adaptive, uniform manner (Silk et al. 2005). Thus the results of both Silk et al.'s (2005) analysis across populations and our intensive study at Amboseli suggest that offspring sex does not predict variation in maternal investment patterns in baboons.

Finally, the results of our resampling analyses suggest that we did not have an adequate sample size to detect the effects of maternal rank and prior infant care experience on birth spacing in our small dataset that were evident in the longitudinal population. These results highlight the relevance of power analyses in studies of the predictors of life history variability in long-lived mammals.

Fig. 4.1. Log-survivorship curve for intervals between suckling bouts. Data were pooled across all dyads.

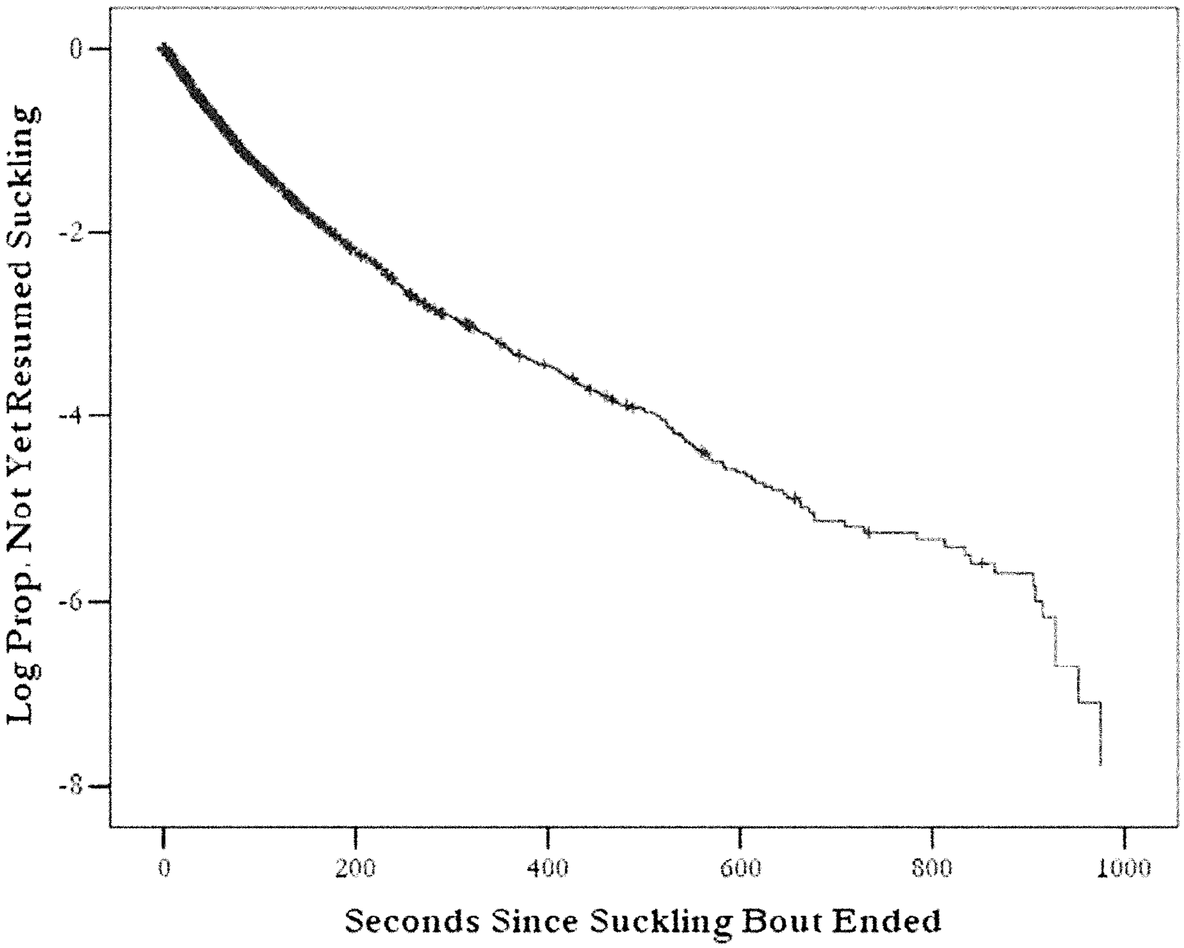


Fig. 4.2A. Effect of infant loss on the length of the period of postpartum amenorrhea. Months from birth to the resumption of menses for mothers whose infants died before they resumed cycling (dashed line) and mothers of surviving infants (solid line).

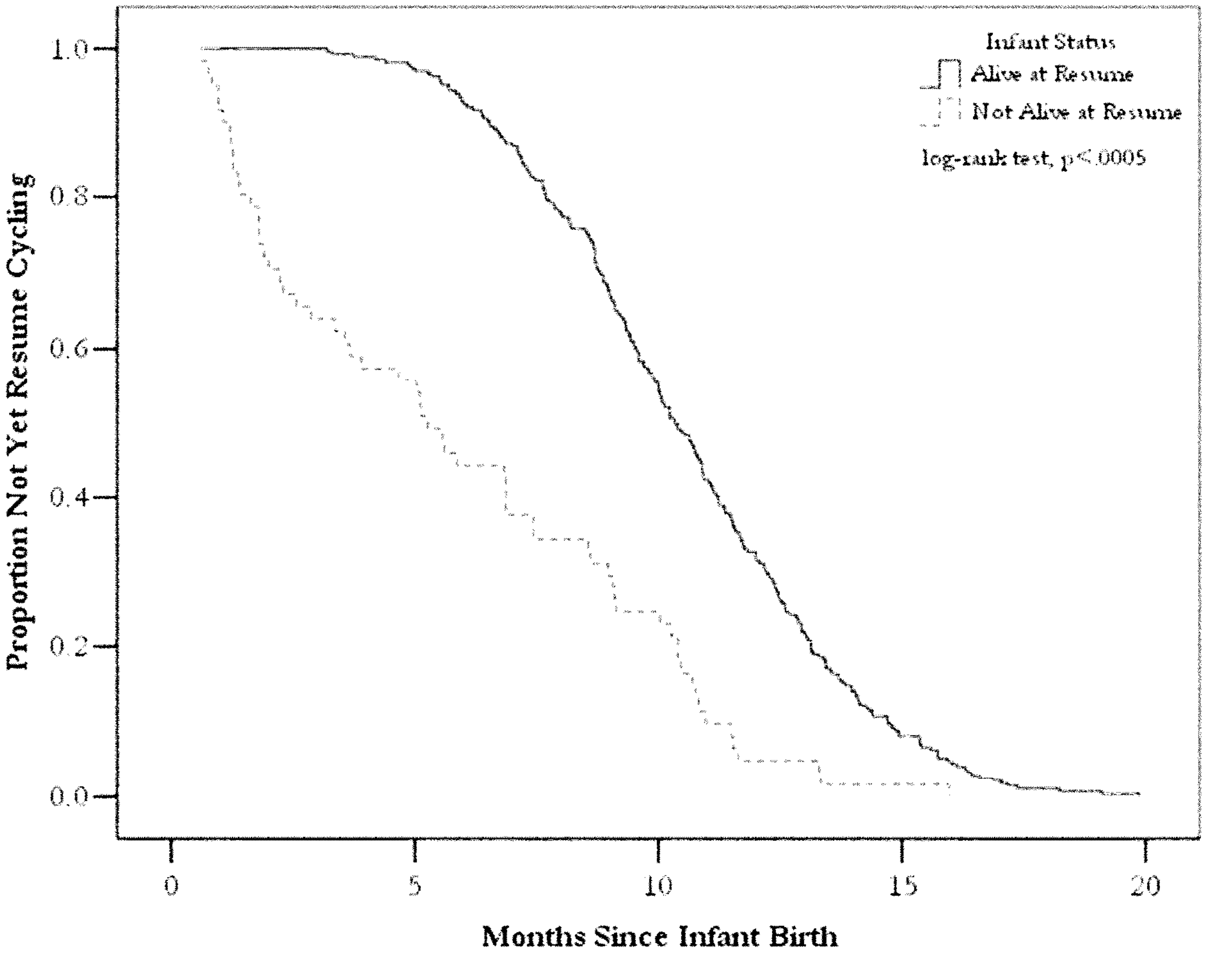


Fig. 4.2B. Effect of infant loss on the length of the period of reproductive cycling. Months from the resumption of menses to the conception of the next offspring for mothers whose infants died before they resumed cycling (dashed line) and mothers of surviving infants (solid line).

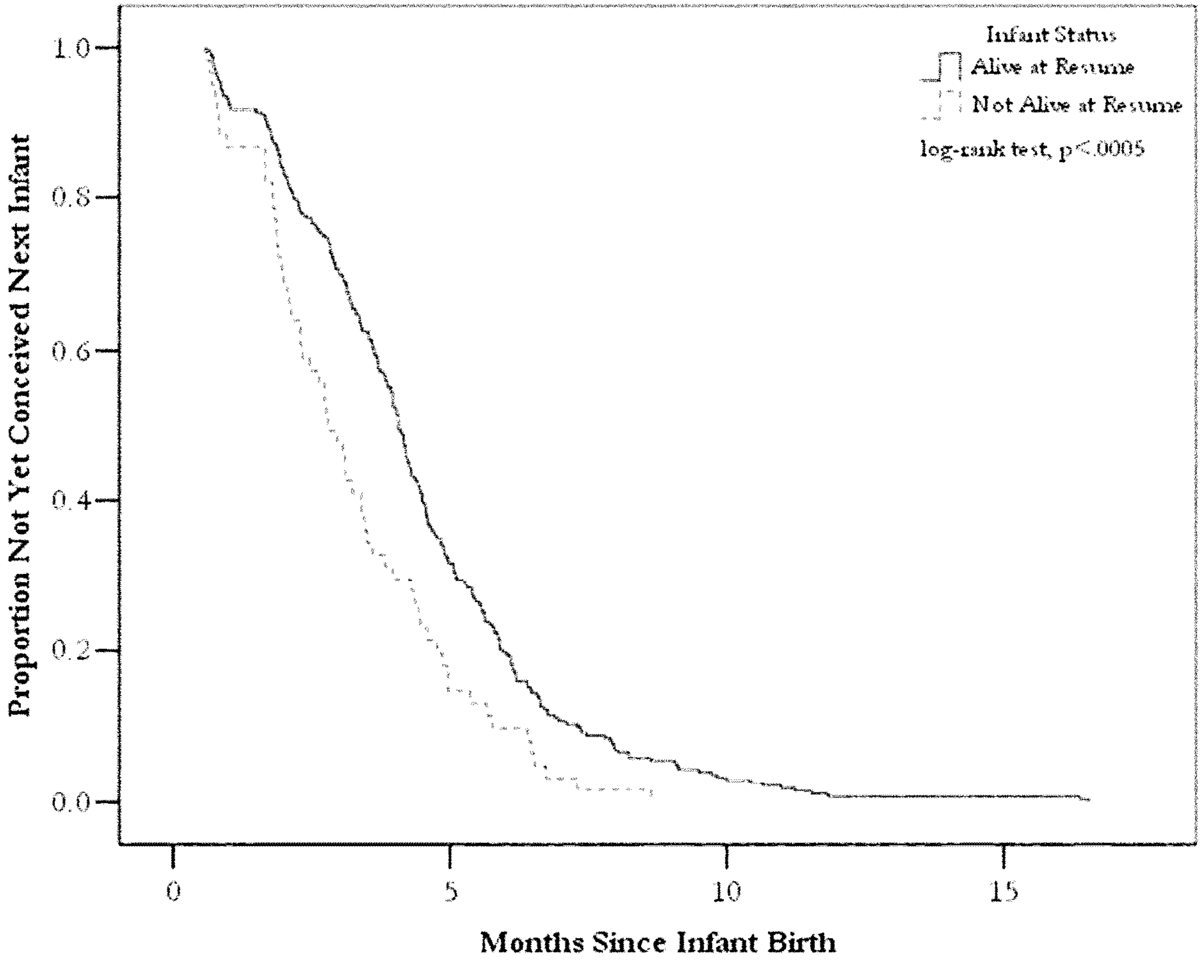


Fig. 4.2C. Effect of infant loss on the length of the interbirth interval. Months from infant birth to the birth of the next offspring for mothers whose infants died before they resumed cycling (dashed line) and mothers of surviving infants (solid line).

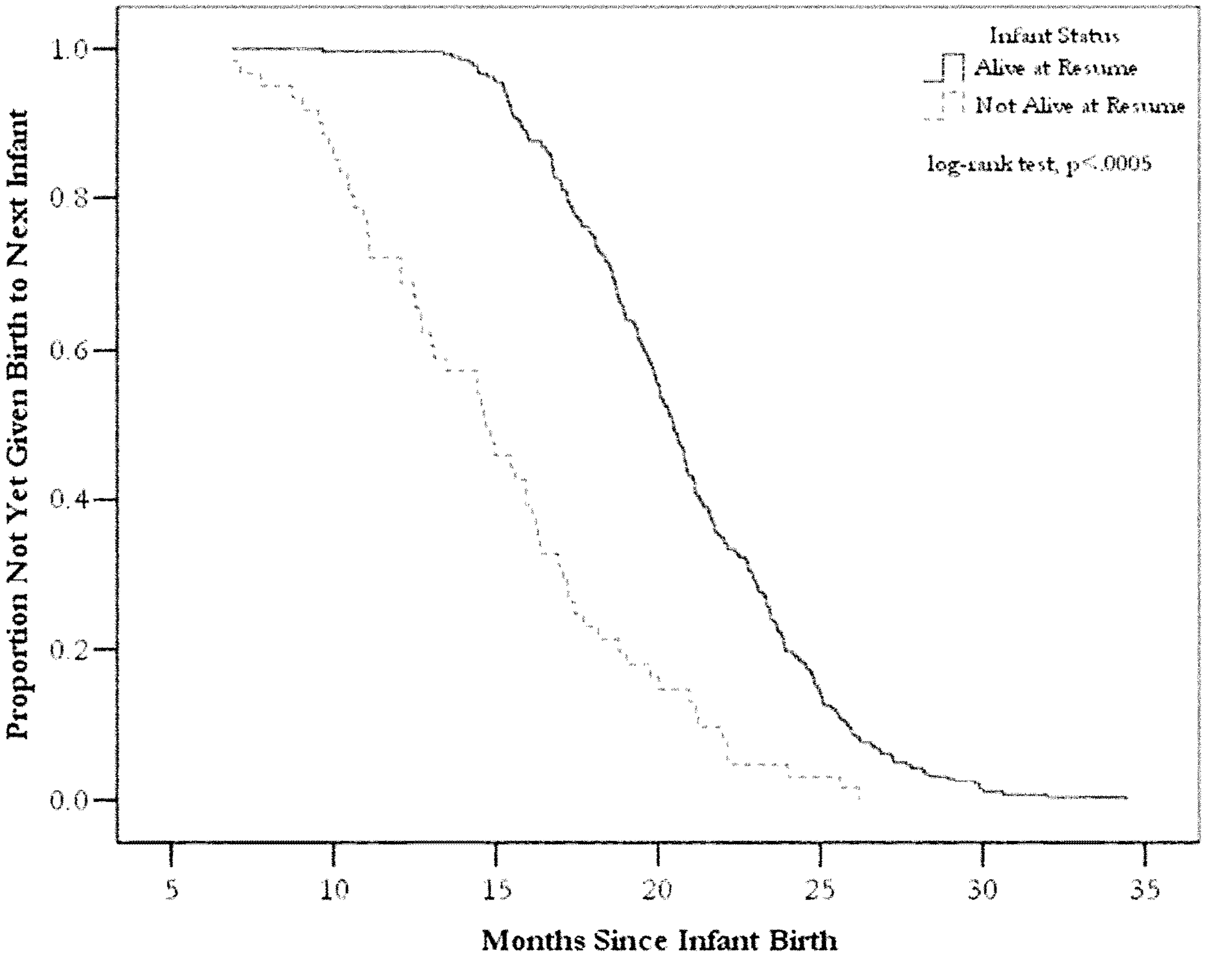


Fig. 4.3A. Age of infant death predicted the length of the period of postpartum amenorrhea. Mothers whose infants died at an earlier age resumed cycling sooner than mothers whose infants died at a later age.

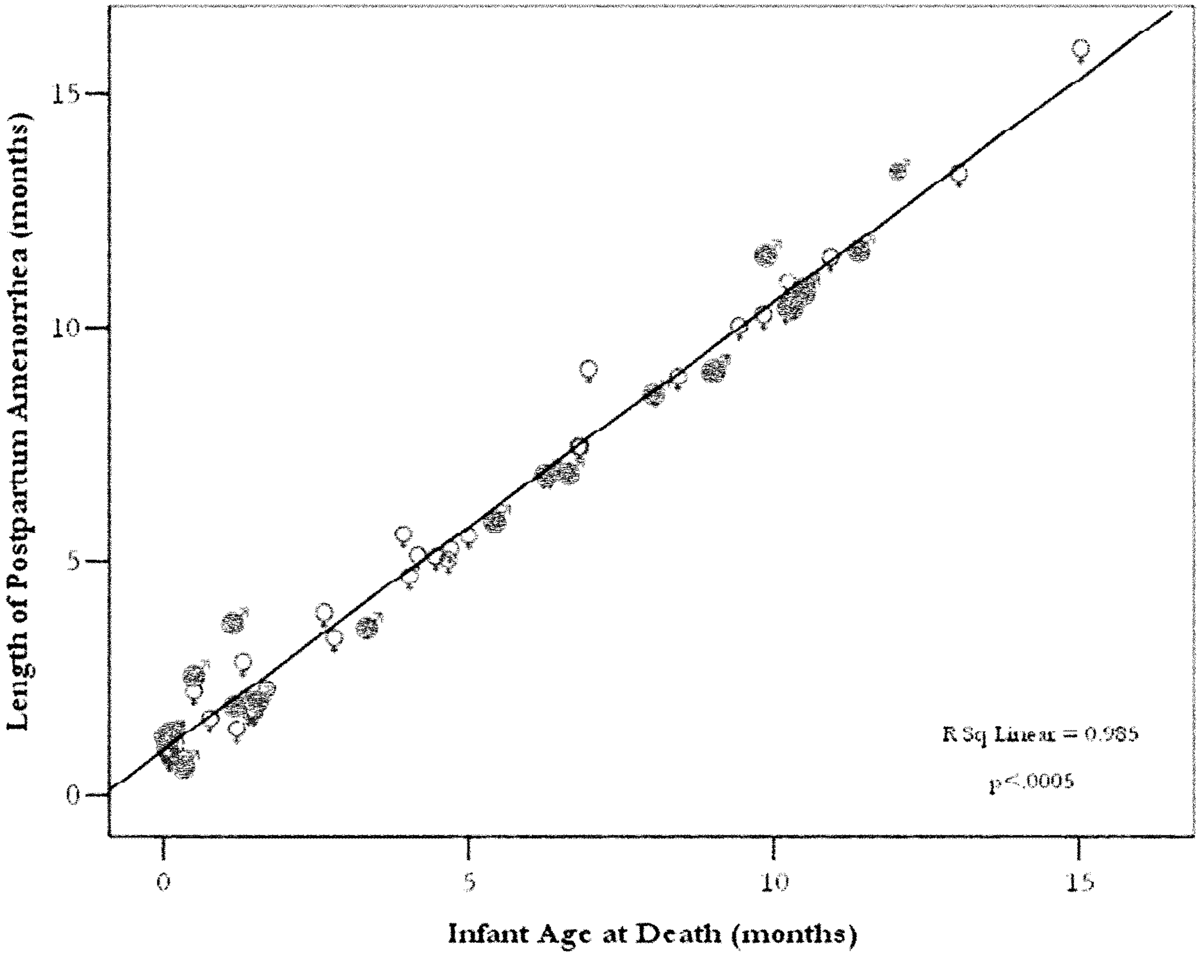


Fig. 4.3B. Age of infant death predicted the subsequent length of the interbirth interval. Mothers whose infants died at an earlier age had shorter interbirth intervals than mothers whose infants died at a later age.

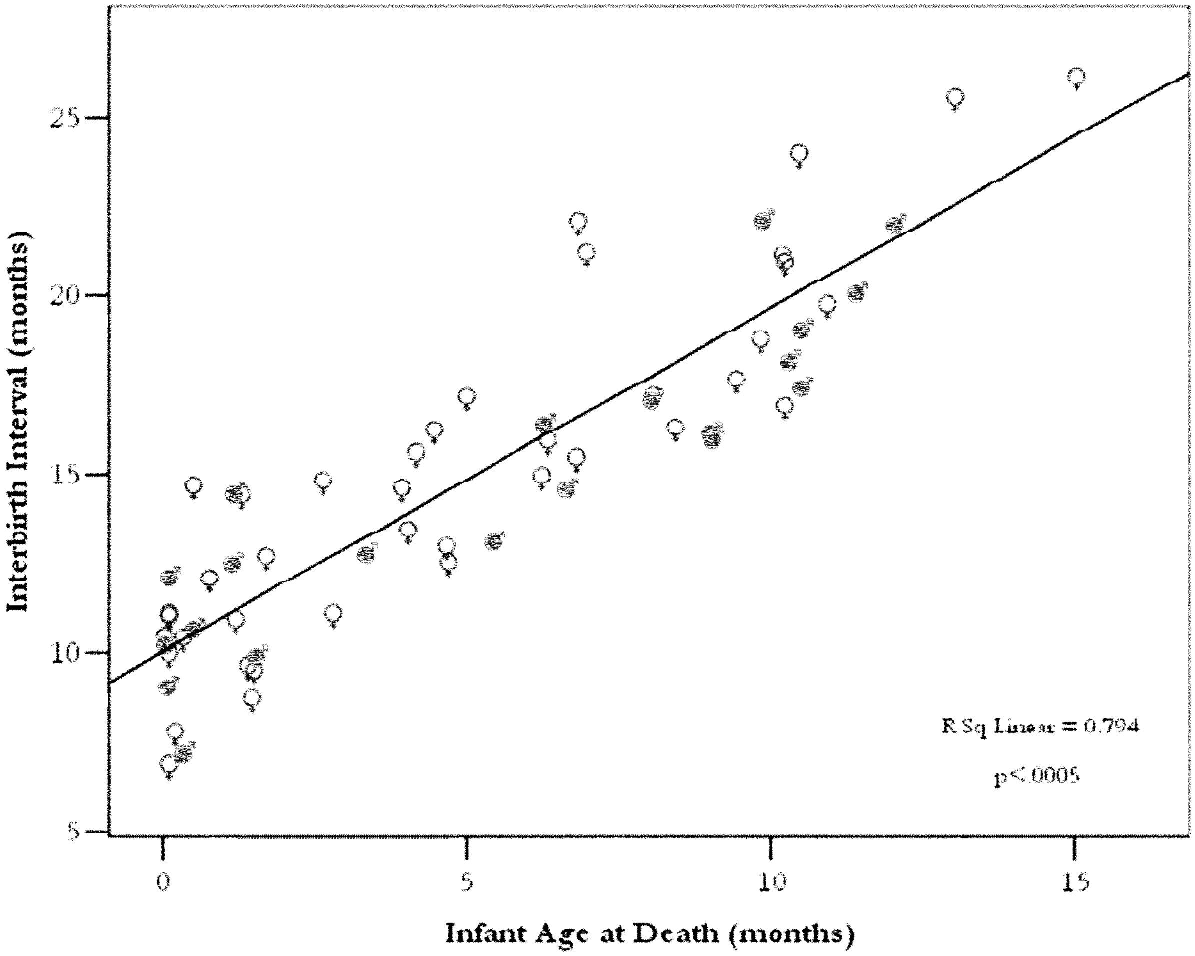


Fig. 4.4A. The effect of maternal dominance rank on the length of the interbirth interval among mothers of surviving infants in the longitudinal population. Higher ranking mothers had shorter interbirth intervals than lower ranking mothers (r2adj=0.149, p<.0005 for the whole model, p<.0005 for the partial regression coefficient of maternal rank) and the magnitude of this effect was large.

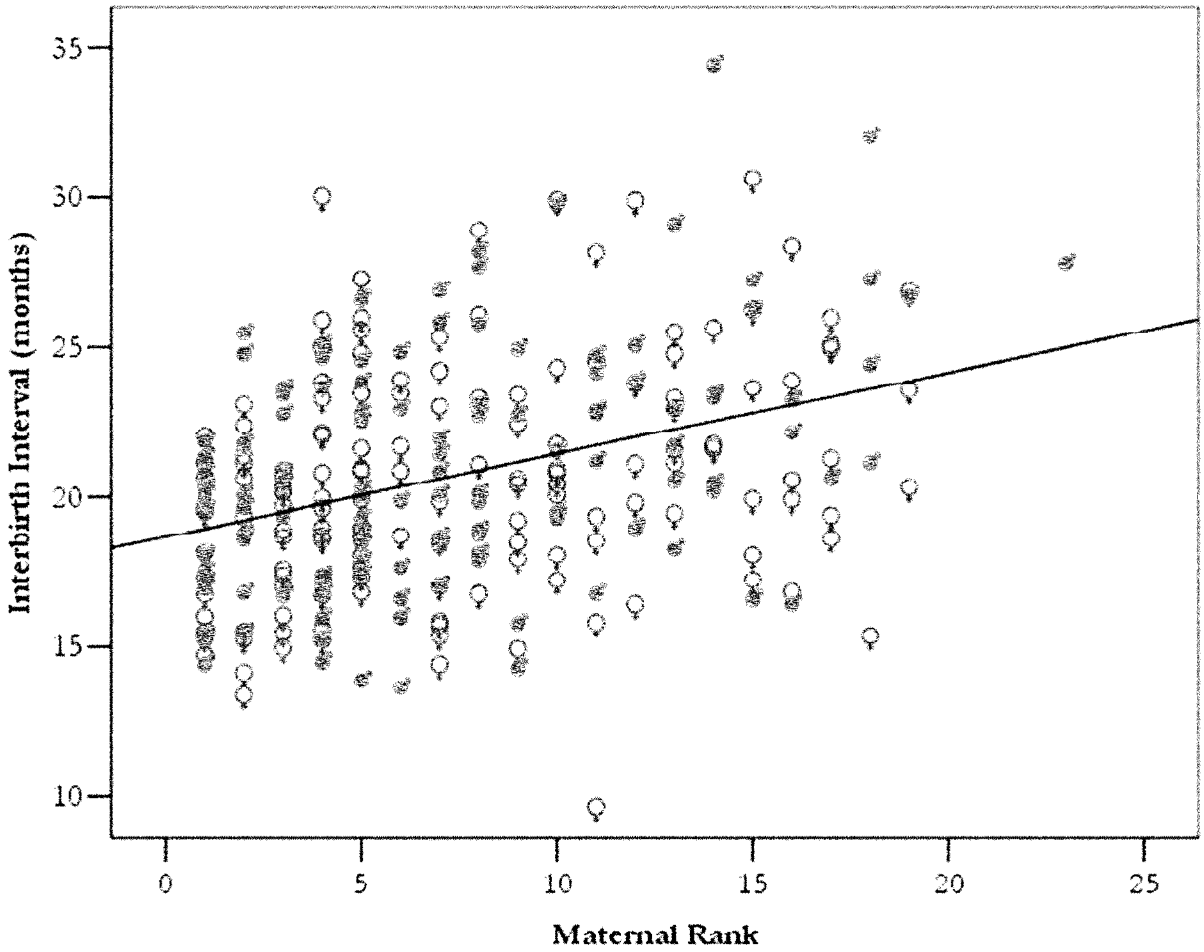


Fig. 4.4B. The effect of maternal dominance rank on the length of the period of postpartum amenorrhea among mothers of surviving infants in the longitudinal population. Higher ranking mothers had shorter periods of postpartum amenorrhea than lower ranking mothers (r2adj=0.152, p<.0005 for the whole model, p<.0005 for the partial regression coefficient of maternal rank).

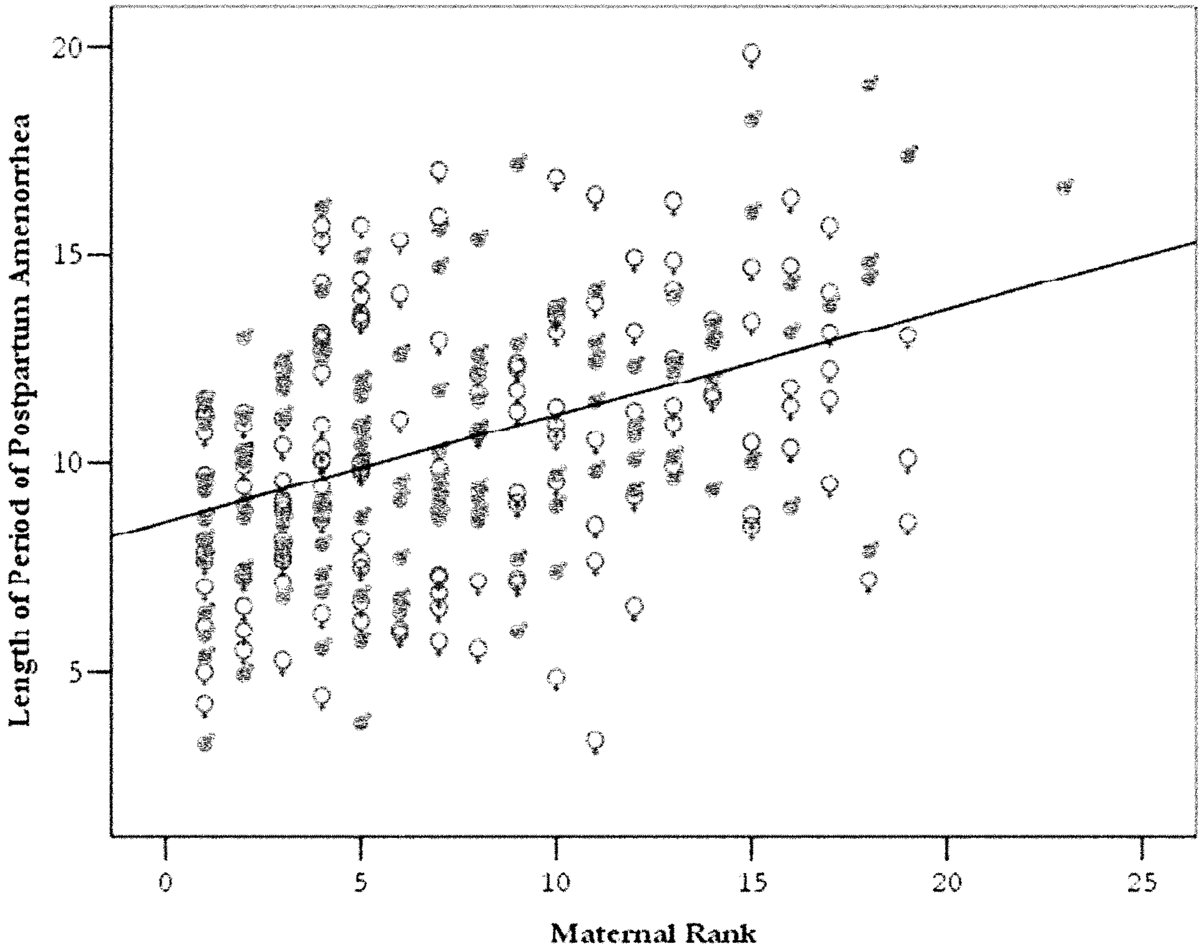


Fig. 4.5. The effect of prior infant care experience on the interbirth interval and each of the three phases of this interval. Primi=primiparous or first-time mothers, multi=multiparous mothers, ppa=the length of the period of postpartum amenorrhea, cyc=the length of the period of cycling, ges=gestation length, and ibi=the interbirth interval. The star indicates the existence of statistically significant differences between the two classes of mothers.

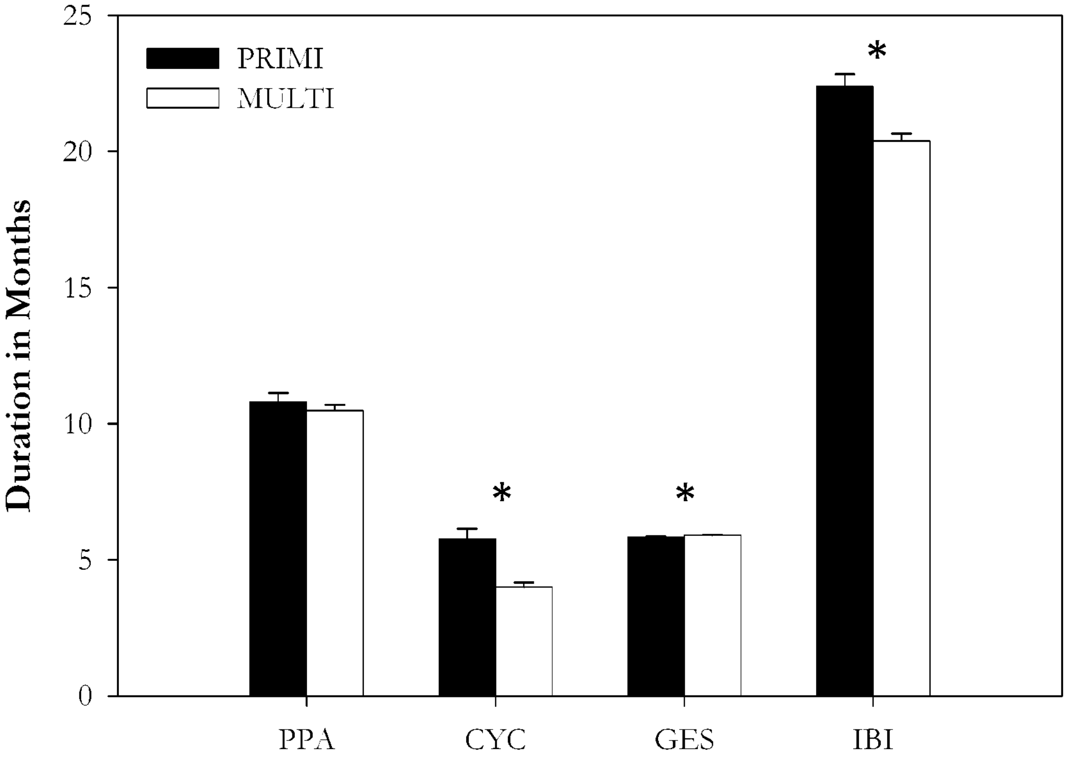


Fig. 4.6. Change in suckling patterns across first 8 weeks of infancy. Numbers above weeks indicate the number of dyads contributing data to the group mean. See Methods for definitions of suckling measures.

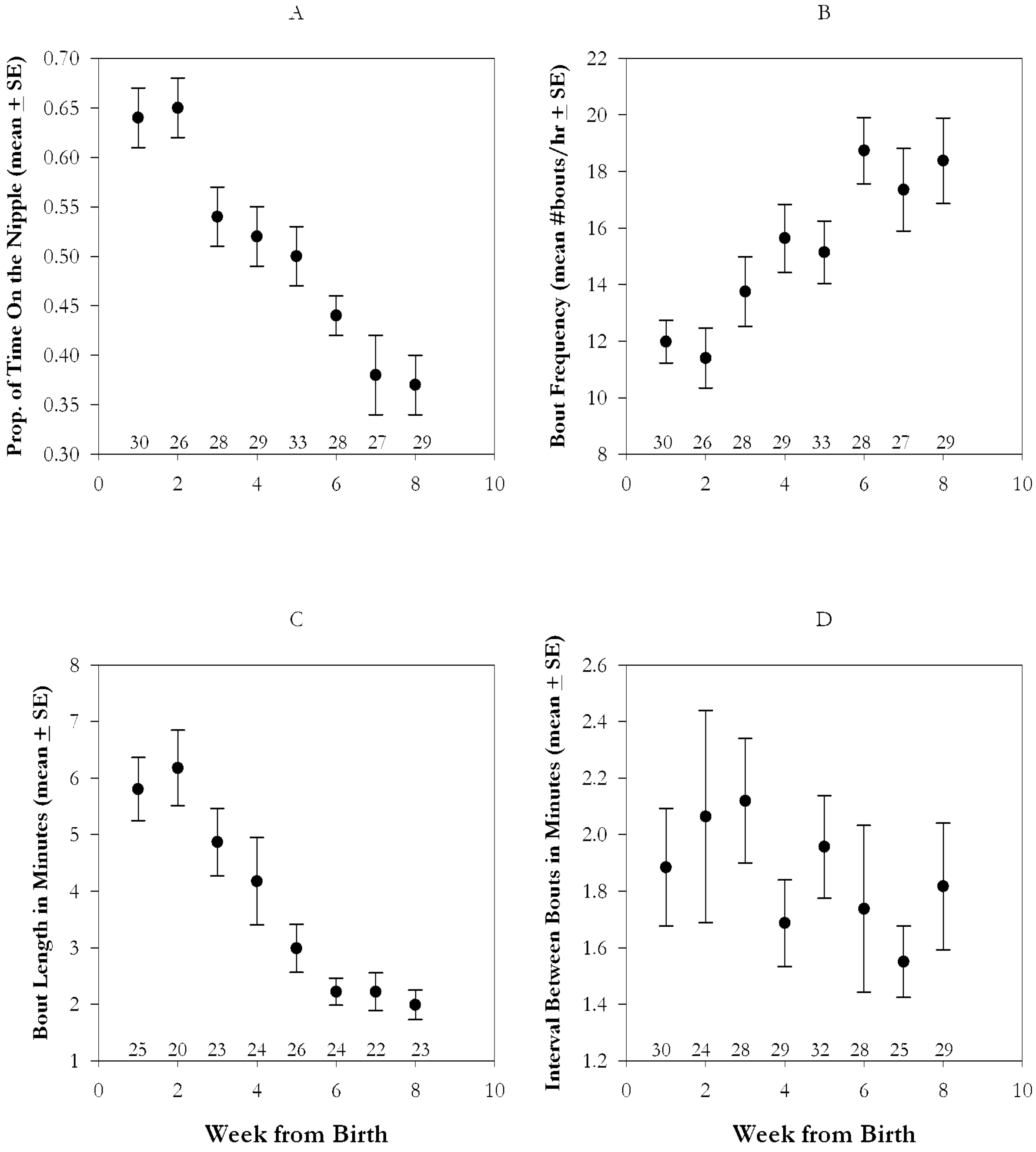
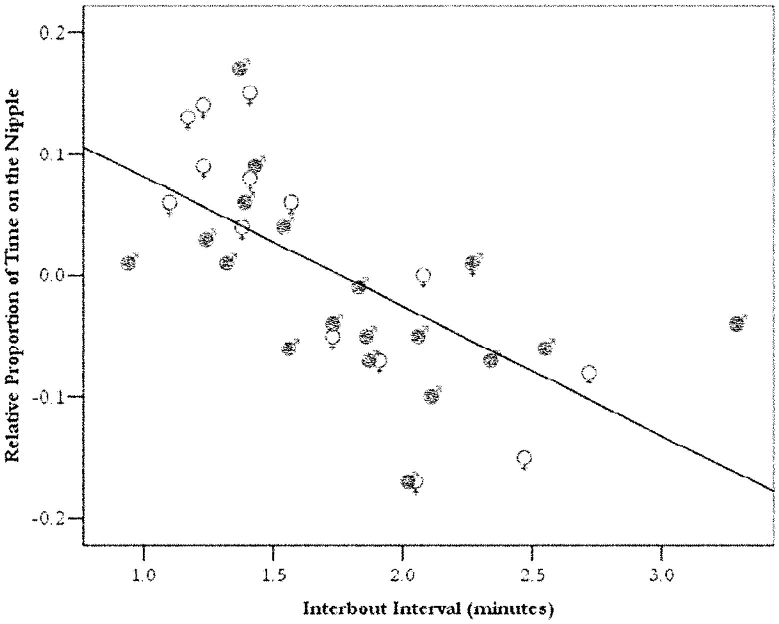


Fig. 4.7. Correlations between a given dyad's interbout interval and (A) its relative proportion of time on the nipple, and (B) its suckling bout frequency. Dyads with longer intervals between successive suckling bouts spent relatively less time on the nipple and had relatively fewer bouts per unit time than dyads with shorter intervals between bouts.

A



B

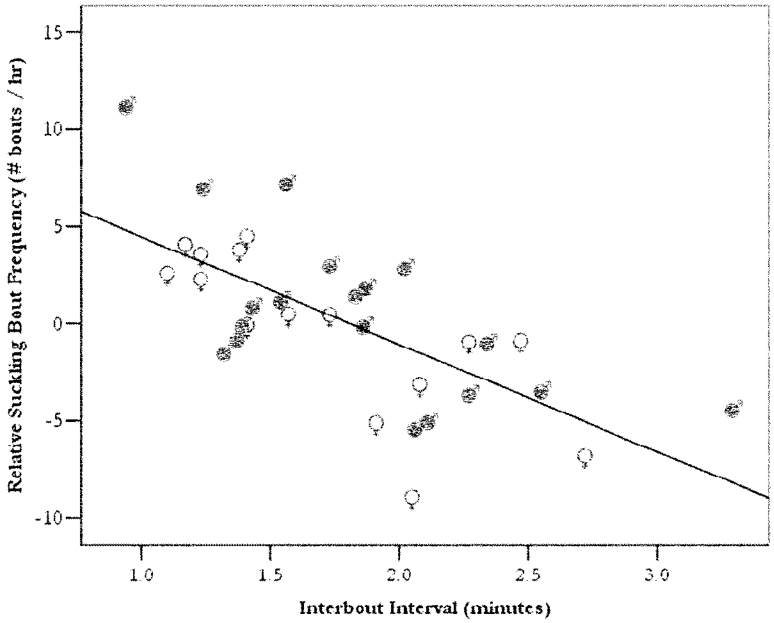


Fig. 4.8A. Maternal rank effects on the amount of time infants spent on the nipple. Higher ranking dyads spent, overall, less time on the nipple (for infant age) than lower ranking dyads (overall r2= 0.210, slope=.008, p=.006; ♀ r2= 0.245, slope=.010 p=.060; ♂ r2= 0.158, slope=.006, p=.092).

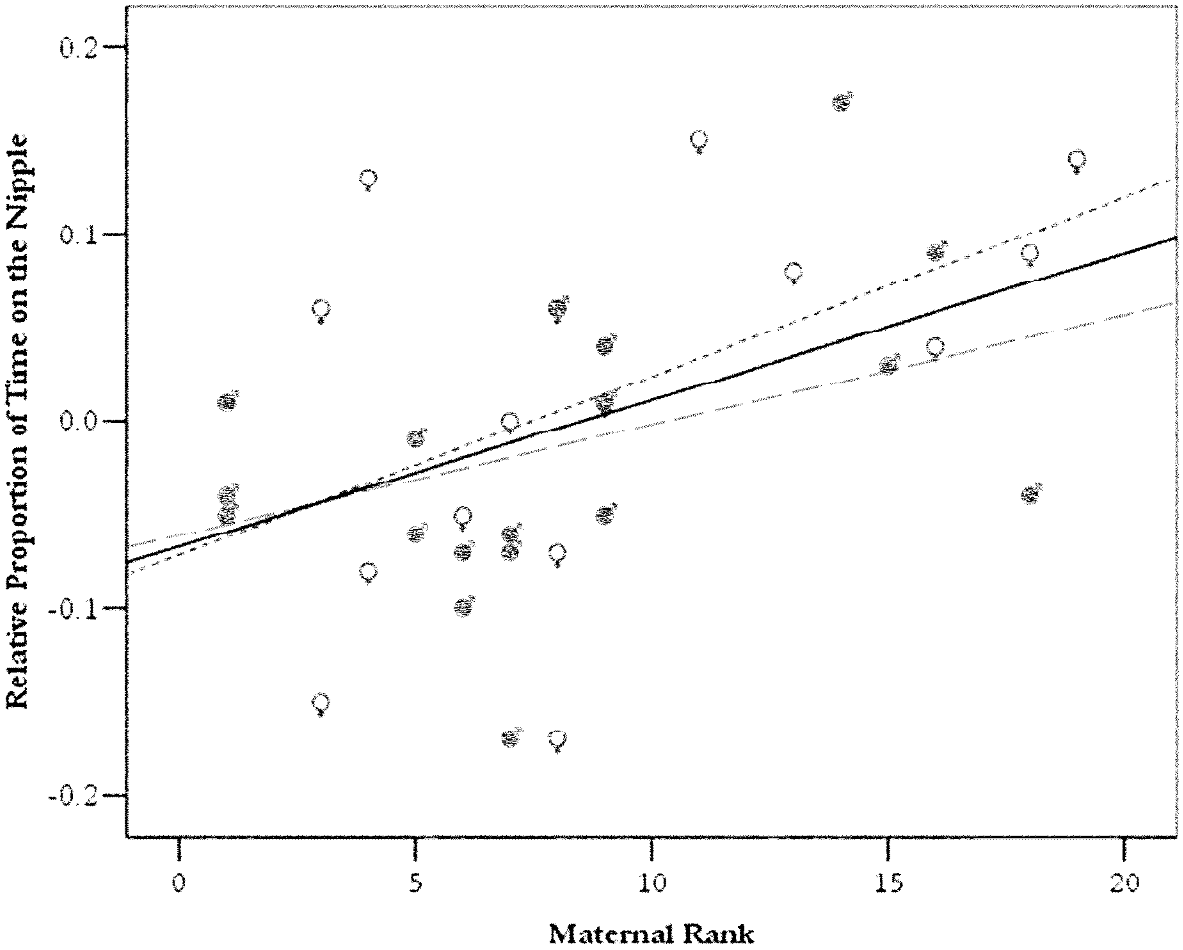


Fig. 4.8B. Maternal rank effects on interbout intervals. Higher ranking dyads had longer intervals between successive suckling bouts than lower ranking dyads (overall r2= 0.215, slope=-.047p=.006; ♀ r2= 0.285, slope=-.052, p=.040; ♂ r2= 0.159, slope=-.043, p=.091).

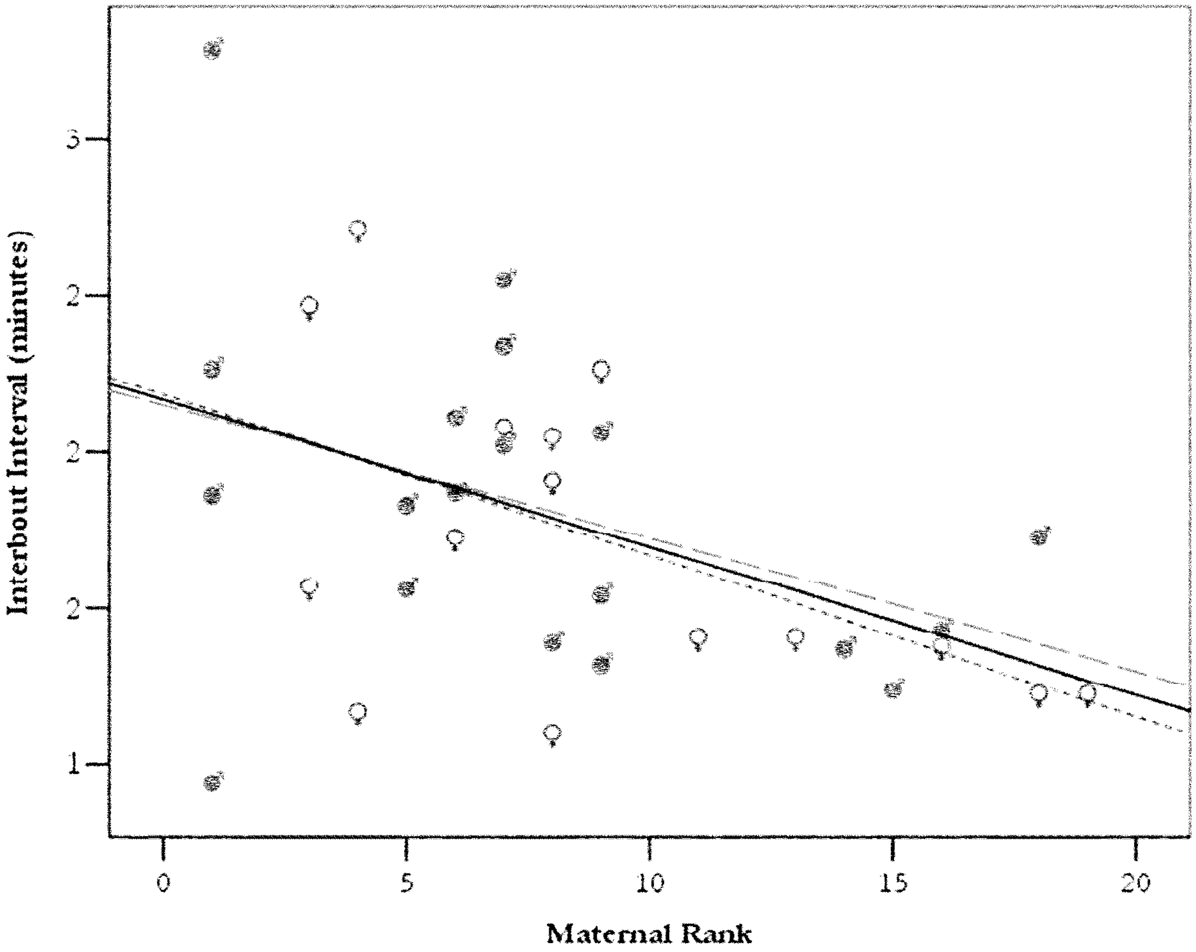


Fig. 4.9A. Relationships between the amount of time infants were on the nipple and maternal postpartum progesterone concentrations. Less time spent on the nipple (for infant age) was associated with relatively higher progesterone concentrations (for infant age). While the direction of this effect was similar for dyads of both sexes, the effects was significant only for dyads with female infants (overall r2= 0.094, slope=-.169, p=.078; ♀ r2= 0.263, slope=-.298, p=.051; ♂ r2= 0.016, slope=-.063, p=.611).

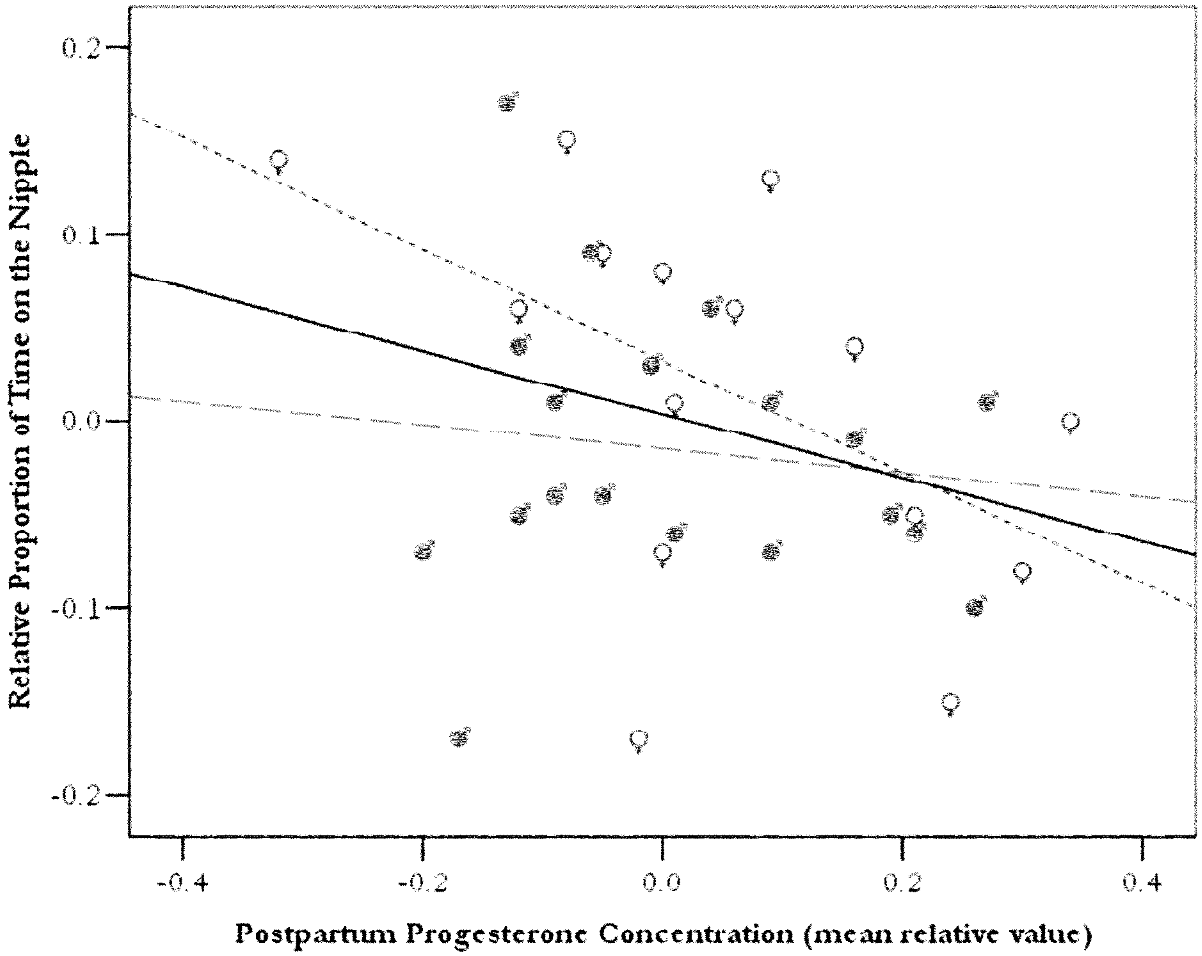


Fig. 4.9B. Relationships between interbout intervals and maternal postpartum progesterone concentrations. Longer intervals between successive suckling bouts were associated with relatively higher progesterone concentrations (for infant age). While the direction of this effect was similar for dyads of both sexes, the effects was significant only for dyads with female infants (overall r2= 0.065, slope=.844, p=.145; ♀ r2= 0.308, slope=1.62, p=.032; ♂ r2= 0.001, slope=.134, p=.883).

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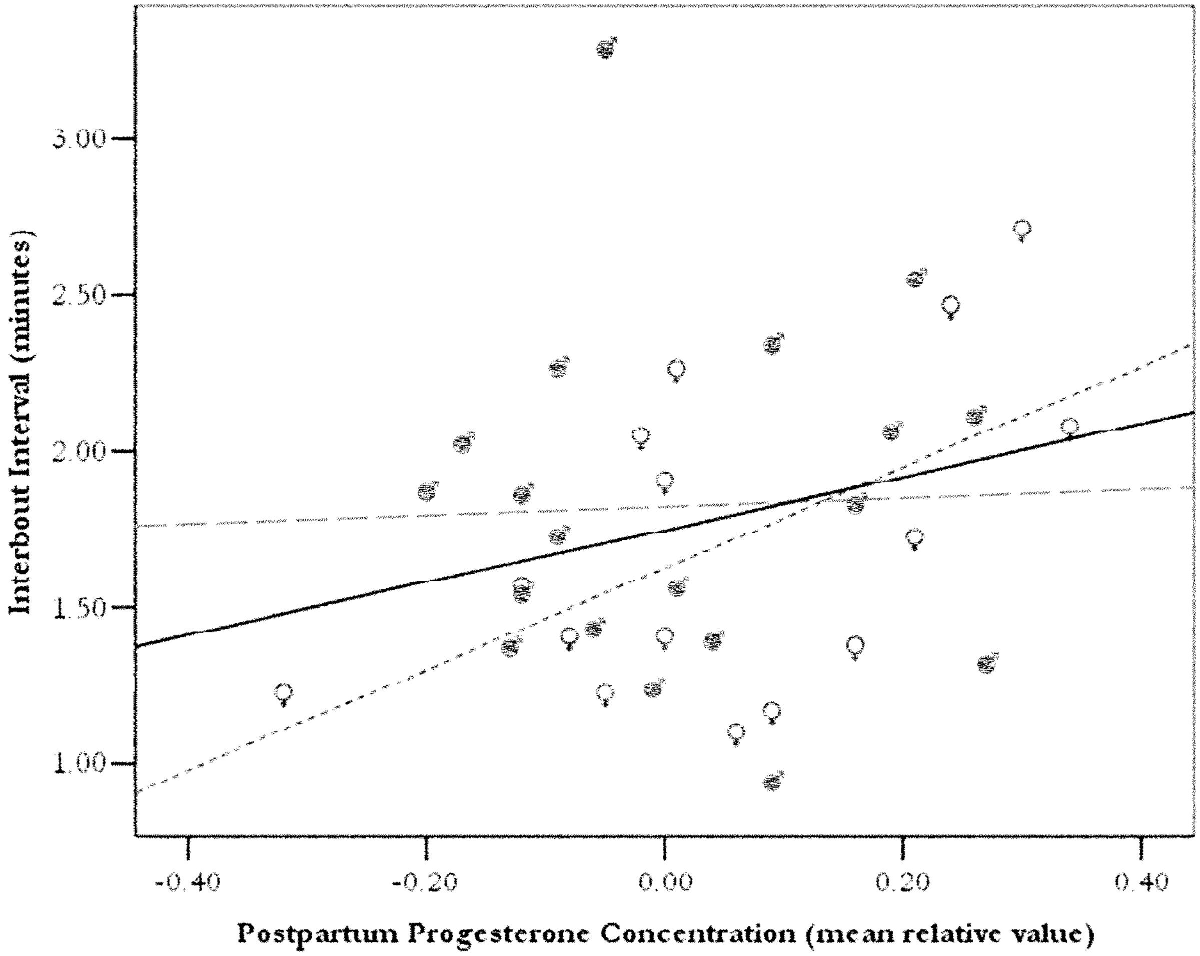

Fig. 4.10. Effect of postpartum maternal progesterone concentrations on the length of the period of postpartum amenorrhea. Mothers with relatively higher postpartum progesterone concentrations (for infant age) exhibited shorter periods of postpartum amenorrhea and the magnitude and direction of this effect were similar in dyads of both sexes (overall model r^2=.312, slope=-7.26, p=.002; ♀ r^2=.461, slope=-8.16, p=.022, after removal of the one female outlier [Dux2] in the upper-right hand quadrant; ♂ r^2 =.212, slope=-6.48, p=.073).

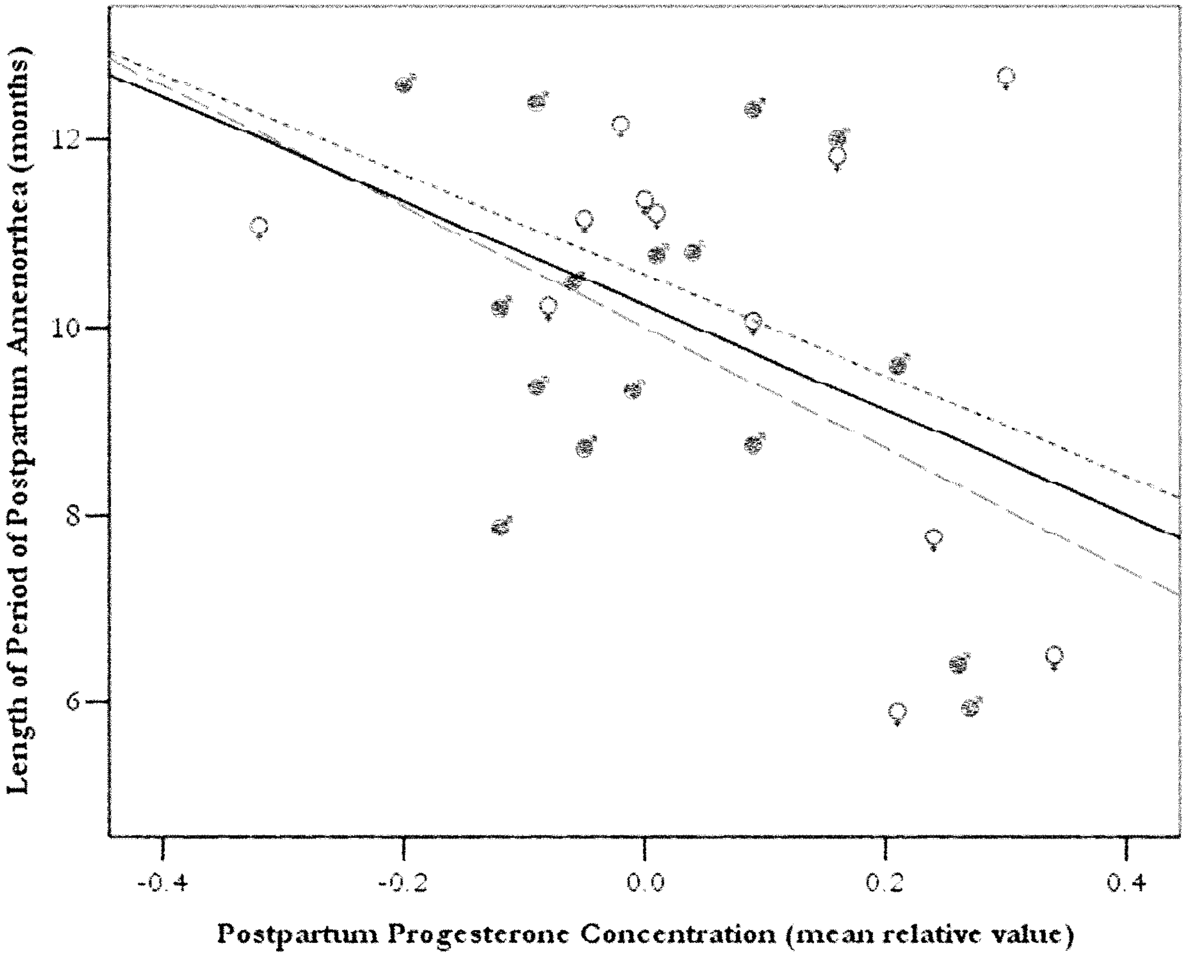

Fig. 4.11. Schematic representation of the proposed pathways through which suckling behavior may mediate the effects of maternal dominance rank on interbirth intervals. The solid lines represent bivariate relationships between variables that have been demonstrated for a variety of animals. The middle portion represents the possible pathways through which rank can influence a mother's future reproduction, and the dotted lines represent relationships between variables that were found in this study. ♀ represents significant relationships found only in mothers of female infants.

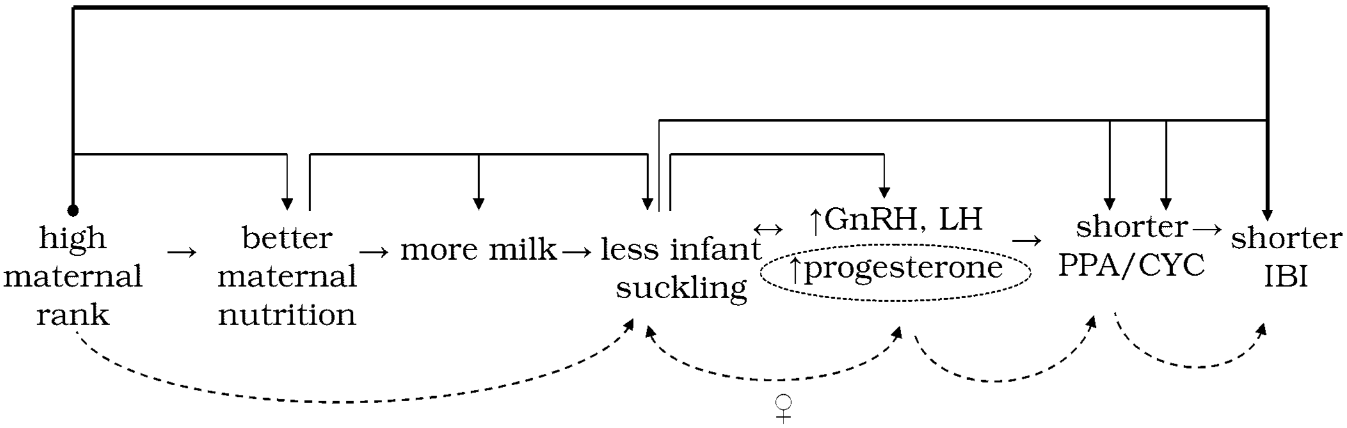

Table 4.I. Effect of infant death on mothers' future reproduction. P values represent differences between mothers whose infants died before they resumed cycling and mothers of surviving infants compared by Kaplan Meier survival analysis (log-rank tests; significant level = 0.05). Units are months since infant birth.

	Mothers whose infants died	**Mothers of surviving infants**	**p**
	n=61 births to 47 mothers	*n=269 births to 103 mothers*	
Postpartum amenorrhea	5.9±0.5	10.5±0.2	p<.0005
Time spent cycling	3.2±0.2	4.4±0.2	p<.0005
Gestation period	5.9±0.0	5.9±0.0	ns
Interbirth Interval	15.0±0.6	20.8±0.2	p<.0005

Table 4.II. General linear model of interval to the birth of the next offspring on three predictor variables for 269 births. P values less < 0.05 are in bold. There was no interaction effect between maternal parity class and infant sex.

Source	**R^2_{adj}**	**df**	**Mean square**	**F**	**P**
Overall model	0.149				
Model		4	165.974	12.741	**<.0005**
Error		264	13.027		
Total		269			
Predictor variables		**df**	**Effect size[c]**		**p**
Maternal parity[a]		1	0.123		**<.0005**
Maternal rank[b]		1	0.005		0.258
Infant sex		1	0.040		**0.001**
Parity*Sex		1	0.001		0.544

a = first-time mothers are compared to all other multiparous mothers

b = mother's ordinal rank number the month the current infant was conceived, with one the highest

c = partial eta squared

Table 4.III. General linear model of the length of the period of postpartum amenorrhea on three predictor variables for 269 births. P values less < 0.05 are in bold. There was no interaction effect between maternal parity class and infant sex.

Source	**R^2_{adj}**	**df**	**Mean square**	**F**	**P**
Overall model	0.156				
Model		4	110.001	13.42	**<.0005**
Error		264	8.197		
Total		269			
Predictor variables		**df**	**Effect size**[c]		**p**
Maternal parity[a]		1	0.000		0.766
Maternal rank[b]		1	0.166		**<.0005**
Infant sex		1	0.001		0.638
Parity*Sex		1	0.000		0.935

a = first-time mothers are compared to all other multiparous mothers

b = mother's ordinal rank number the month the current infant was conceived, with one the highest

c = partial eta squared

Table 4.IV. General linear model of time spent cycling on three predictor variables for 269 births. P values less < 0.05 are in bold. There was no interaction effect between maternal parity class and infant sex.

Source	**R^2_{adj}**	**df**	**Mean square**	**F**	**P**
Overall model	0.071				
Model		4	35.133	6.097	0.210
Error		264	5.762		
Total		269			
Predictor variables		**df**	**Effect size**[c]		**p**
Maternal parity[a]		1	0.081		**<.0005**
Maternal rank[b]		1	0.001		0.600
Infant sex		1	0.004		0.309
Parity*Sex		1	0.003		0.398

a = first-time mothers are compared to all other multiparous mothers

b = mother's ordinal rank number the month the current infant was conceived, with one the highest

c = partial eta squared

Table 4.V. General linear model of gestation length on three predictor variables for 269 births. P values less < 0.05 are in bold. There was no interaction effect between maternal parity class and infant sex.

Source	**R^2_{adj}**	**df**	**Mean square**	**F**	**P**
Overall model	0.021				
Model		4	0.113	2.404	0.527
Error		264	0.047		
Total		269			
Predictor variables		**df**	**Effect size[c]**		**p**
Maternal parity[a]		1	0.020		**0.021**
Maternal rank[b]		1	0.000		0.742
Infant sex		1	0.007		0.169
Parity*Sex		1	0.000		0.731

a = first-time mothers are compared to all other multiparous mothers

b = mother's ordinal rank number the month the current infant was conceived, with one the highest

c = partial eta squared

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GENERAL DISCUSSION

At least three major themes emerge from our study of the causes and consequences of variation in the mother-infant relationship in yellow baboons at Amboseli: (1) individual consistency in behavioral and hormonal measures, (2) relationships between hormones and mother-infant behaviors in wild populations, and (3) sex differences in the mother-infant relationship. Below, we discuss each of these themes and the contributions made by our study to each area of research.

Individual Consistency in Behavioral and Hormonal Measures

Natural selection is one of the primary forces driving biological evolution. Individual consistency in a trait and variability among individuals in the trait are essential for selection to take place (Brodie 1993; Brodie et al. 1995). Without both, there can be no predictable covariance between traits and their fitnesses, and selection cannot occur (Brodie 1993). Since within-individual variation in a trait can limit the potential of that trait to evolve (Brodie and Russell 1999), individual consistency or repeatability of traits must be measured as a first step towards understanding trait evolution in a population (Hayes and Jenkins 1997; Holmes and Sherry 1997). Variation between individuals has long been a topic of research among biologists (Hayes and Jenkins 1997), but only recently have studies begun to focus their attention on variation within individuals.

Emerging evidence suggests that individual consistency in behavioral (e.g. garter snakes: Brodie 1993; bighorn ewes: Reale et al. 2000) and hormonal measures (e.g. human males: Hurwitz et al. 2004; human females: van Rooij et al. 2005) occurs across a variety of animals, including humans. Moreover, individual consistency in the interactions between some behavioral and hormonal measures has now been documented in several populations, including male rats (Marquez et al. 2005; Marquez et al. 2006), heifer calves (Van Reenen et al. 2005), sows (Spinka et al. 2000), and capuchin monkeys (Byrne and Suomi 2002). Individual consistency or repeatability of behavioral and physiological traits across time is useful for understanding how the measurement of these traits is representative of an individual (Boake 1989). Moreover, they provide insight into the stability of traits across environmental conditions.

In this study, we found evidence of within individual consistency in several hormones across the peripartum period and in several behavioral measures across the early postnatal period during a single breeding event. Baboon females at Amboseli exhibited individual stability in the pattern of excretion of glucocorticoids and the ovarian steroids, estrogens and progesterone, across late pregnancy and the early postpartum period. In addition, mothers exhibited consistency in their responsiveness to infant distress cries over the first two months of infancy. Moreover, mother-infant dyads showed significant consistency in suckling patterns and in the rate at which infants initiated changes in mother-infant contact across the first eight postnatal weeks.

We believe ours is the first study to document within individual stability in hormonal and behavioral measures within a single breeding event in wild primate mother-infant dyads, and one of the first studies to do so in an animal population. Although repeated sampling and measurement of both behavior and hormones can be difficult in studies conducted in the wild, we believe such undertakings are essential for ensuring that what is referred to as an individual's behavior or hormones in studies of the interactions between hormones and behavior actually reflects the individual and not measurement error.

Relationships Among Hormones and Mother-Infant Behaviors in Wild Populations

Most of our understanding of the proximate causes and fitness consequences of variation in the mother-infant relationship comes from studies of laboratory rats. Naturally occurring variation in the behavior of rat mothers is mediated by a complex suite of hormones (Bridges 1996). In addition, individual variation in rat mothering has been shown to affect the development of individual differences in stress reactivity in the offspring (Fleming et al. 1999; Meaney 2001) and in offspring behavior towards pups as adults (Francis et al. 1999). Moreover, maternally-mediated nongenomic mechanisms for the intergenerational transmission of individual differences in maternal behavior (Champagne et al. 2001) and in stress reactivity (Weaver et al. 2004) have also been identified in the rat.

Such a mechanism of nongenomic transmission of phenotypic variability from generation to generation via the behavior of the mother, referred to as "maternal effects", can have important fitness consequences for offspring performance (Mousseau and Fox 1998). Maternal effects occur when the phenotype of the mother or the environment she experiences, causes phenotypic effects in her offspring that are unrelated to the offspring's genotype (Mousseau and Fox 1998). Maternal effects have only recently been widely recognized as important forces in the evolution of behavior (Bernardo 1996; Mousseau and Fox 1998) and adaptations involving maternal effects are unique in that the genes underlying their expression are contained within the maternal generation while the phenotypic variation on which natural selection may act is expressed by the offspring.

This study contributes to our understanding of the causes and consequences of variation in mother-infant interactions in mammalian taxa, and helps address the disproportionate attention given to mother-infant relationships in the rat and other laboratory animals. Because captivity and provisioning can affect the expression of social behaviors (Groothuis and Vanmulekom 1991;

McPhee 2004), modify neural processes and brain structures (Barnea and Nottebohm 1994; Healy et al. 1996; Rosenzweig and Bennett 1996), and influence the pattern of secretion of hormones (Wingfield et al. 1990; Gardiner and Hall 1997; Baker et al. 1998), studies of wild populations are of particular value because they permit evaluations of the robustness of hormone-behavior relationships established in captivity in field settings, where animals are exposed to a diversity of ecological and social stimuli often absent from captive settings (Costa and Sinervo 2004; Fusani et al. 2005).

In this study, we found evidence that late pregnancy glucocorticoids (GCs) in wild baboon mothers predict greater maternal responsiveness to infant distress cries after birth. This effect is understandable from an adaptive standpoint: GCs typically mobilize energy reserves in response to stressors and are believed to help animals cope with and survive these stressors, but elevations in GCs can also occur in anticipation of a challenge if these challenges are predictable in their occurrence and variability in response to these challenges has potential fitness consequences (Sapolsky et al. 2000). We also found evidence that both higher maternal dominance rank and higher prepartum concentrations of the ovarian steroids estrogens predicted lower suckling time for female infants, but not male infants. In addition, during the postnatal period, high maternal rank was associated with both higher concentrations of progesterone and reduced suckling activity for dyads with female, but not male, infants. Furthermore, we found evidence that higher postpartum progesterone was itself associated with reduced suckling intensity and shorter periods of postpartum amenorrhea for mothers of female, but not male, infants. These results suggest that rank-related, suckling-induced elevations in postpartum progesterone may be predictive of shorter periods of postpartum infertility for mothers of female, but not male, infants. Taken collectively, the findings from our study suggest that a variety of hormones have an important influence on the mother-infant relationship, and account for some of the variability across dyads in the nature of these relationships in wild baboons. Moreover, they suggest that, from a very early age, the lives of female infants, but not those of male infants, are strongly influenced by their mother's social world.

Sex Differences in the Mother-Infant Relationship

Sex differences in life histories and adult social behavior and ecology are widespread among animals, including primates (Beatty 1979; Gurney and Konishi 1980; Clutton-Brock et al. 1982; Clutton-Brock et al. 1987; Walters 1987; Segovia and Guillamon 1993; Isaac 2005). However, little is known of the time course, mechanisms and processes of physical and behavioral development of immature animals (Pereira 1993). Sex differences in the social play of immature primates have been observed in several species (Walters 1987; Maestripieri and Ross 2004) (Walters 1987, Fagen 1993, Maestripieri & Ross 2004) and these differences have been related to differences in adult social behavior. In addition, sexual dimorphism in both social and foraging behavior of juvenile primates has been observed in a variety of species (Pereira 1988; Strier 1993; van Noordwijk et al. 1993; Agostini and Visalberghi 2005). These differences have been related to the divergent social and foraging skills of adult males and females and have been interpreted as reflecting juvenile primates' preparation for adulthood. However, it is unknown whether infant gender influences the patterning of social behavior even among very young infants who are dependent on their mothers as their primary caregiver and social partner.

In this study, we found evidence of emerging sex differences in the mother-infant relationship in the first eight weeks of infancy, differences that hint at the future social lives of offspring as adults. Male infants initiated more changes in mother-infant contact than female infants, a finding that suggests that mothers of male infants were more permissive and encouraging of infant independence than mothers of female infants. In addition, mothers were more restrictive and less permissive of female infants spending time off the nipple, and presumably out of body contact, the lower they ranked in the group's dominance hierarchy. Furthermore, maternal rank-related differences in prenatal estrogens and postnatal progesterone were associated with variation in suckling patterns in dyads with female infants, but not in dyads with male infants. These sex differences in the effects of rank on the mother- infant relationship suggest that the mother's social world has a greater influence on the lives of female than on the lives of male infants.

Male baboons typically disperse from their group of birth as they near adult size and many continue to migrate between social groups their entire lives (Alberts and Altmann 1995). In contrast, female baboons remain in their natal group their entire lives, inheriting their mother's rank in the group's dominance hierarchy as juveniles (Walters 1980). Our results suggest that, from a very early age, male infants are encouraged to explore the wide physical and social world beyond their mother's body, behavior which may help prepare them for their adult lives as migrants. In contrast, the options and experiences of female infants were more strongly influenced by their mother's dominance rank. Dominance rank is a good predictor of lifetime reproductive success for both males and females in many animal populations, including the baboons at Amboseli (Altmann et al. 1996; Altmann and Alberts 2003). But while male rank in adulthood in baboons depends largely on male fighting ability (Alberts et al. 2003), female rank in adulthood depends on their mother's rank (Walters 1980) and thus the social experiences of females as immatures are expected to be closely tied to those of their mothers. Taken together, the results of our study highlight the emergence of developing sex differences in the behavior of newborn infants that may become magnified during ontogeny.

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