



Sex differences in the mother–neonate relationship in wild baboons: social, experiential and hormonal correlates

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In mammals, maternal care is essential for offspring survival, yet individual differences in this care can dramatically affect offspring growth and development. Few studies have, however, investigated the sources, magnitude and consequences of naturally occurring interindividual variation in maternal care during the neonatal period. In this study, we examine several hormonal and nonhormonal predictors of naturally occurring variation in the mother–neonate relationship during the first 8 weeks of infancy in 34 wild baboon (*Papio cynocephalus*) mother–infant dyads in Amboseli, Kenya. We use data on physical contact and suckling patterns to assess the quality of the mother–neonate relationship and to evaluate the extent to which variation in this relationship is predictable from perinatal ovarian steroids (i.e. faecal oestrogen and progesterone metabolites), previous infant care experience, maternal dominance rank and offspring sex. We found that newborn infants of more experienced mothers initiated higher rates of changes in mother–infant contact than newborns of less experienced mothers. However, at each level of maternal experience, newborn males initiated higher rates of changes in mother–infant contact than newborn females. Moreover, we found evidence suggesting that variation in suckling activity among daughters (but not sons) was predictable from maternal dominance rank and faecal oestrogen (fE) concentrations before birth. To our knowledge, our study provides the first evidence of (1) the influence of cumulative maternal experience on the mother–infant relationship and (2) the emergence of sex differences in the mother–infant relationship during the neonatal period in wild primates. Our results suggest that the well-documented sex differences in life history, behaviour and ecology in primates (and other social mammals) may originate very early in life.

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For vertebrates, mammalian newborns are unusually dependent on their mothers for nourishment, transport, protection and support (Clutton-Brock 1991). Although offspring eventually transition from complete reliance on their mothers to nutritional, locomotor and social independence, the timing of these events can vary widely across individuals of the same species (Clutton-Brock 1991). Despite the critical importance of the neonatal period in the life of each individual, few studies have investigated the sources, magnitude and consequences of interindividual variation in the mother–offspring relationship during the neonatal period in wild mammals (Altmann 1980; Bales et al. 2002). In this study, we provide, to our knowledge, the first evidence of sex differences in the mother–neonate relationship in a wild nonhuman primate, and

evaluate the social, experiential and hormonal predictors of this finding.

Individual differences in the mother–infant relationship and in the timing of infant independence have been observed in a variety of mammals, from rodents (reviewed in McGuire & Bemis 2007) to nonhuman primates (reviewed in: Fairbanks 1996; Maestripietri 2009). These differences have been reported to affect offspring survivorship and social and physical development (Abbott 1987; Fairbanks 1996; Weaver et al. 2004; McGuire & Bemis 2007), yet information on the factors that underlie differences in offspring care is scarce. Among mammals, variation in the mother–infant relationship is frequently associated with differences among mother–infant pairs in several maternal and infant characteristics, including the mother's previous infant care experience (prairie voles, *Microtus ochrogaster*: Wang & Novak 1992), physical condition (horses, *Equus caballus*: Cameron & Linklater 2000), social status (red deer, *Cervus elephus*: Clutton-Brock et al. 1986), and the

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offspring's sex (red deer, *Cervus elephus*: Clutton-Brock et al. 1981; African elephant, *Loxodonta africana*: Lee & Moss 1986).

Studies of the sources of variation in maternal care in our closest relatives, the nonhuman primates, have traditionally focused on three variables thought to be particularly salient to the social lives of immature primates: (1) mother's prior infant care experience, (2) mother's social status and (3) offspring sex. Most studies have reported a dichotomy between first-time (or primiparous) and experienced (or multiparous) mothers, with inexperienced mothers typically more protective of infants than experienced mothers (Hiraiwa 1981; Hooley & Simpson 1981; Berman 1984; Fairbanks 1988; Gomendio 1989; Schino et al. 1995; Fairbanks 1996; but see Paul et al. 1993). Experience with previous infants is believed to provide opportunities for mothers to enhance their parenting skills, and increased exposure to infants may make mothers more competent or efficient at infant care (Fairbanks 1996). Consequently, experienced mothers may adopt a more relaxed attitude towards infant care and be more tolerant or even more encouraging of infant independence than inexperienced mothers (Fairbanks 1996).

Most primate mothers do not rear their offspring in isolation, but in social groups characterized by (sometimes strict) dominance hierarchies. Evidence of dominance rank-related differences in the patterning of mother–infant interactions has now been reported in several primate societies. Low-ranking mothers in three primate species have been found to be more protective of their infants than higher-ranking mothers (yellow baboons, *Papio cynocephalus*: Altmann 1980; common marmosets, *Callithrix jacchus*: Digby 1995; rhesus macaques, *Macaca mulatta*: White & Hinde 1975). In addition, higher rates of social aggression (the social risk factor most often associated with low dominance rank) is associated with greater maternal protectiveness of infants in two other primate species (chimpanzees, *Pan troglodytes*: Hemelrijk & Dekogel 1989; rhesus macaques: Simpson & Howe 1986). Taken together, these studies suggest that mothers may be more protective and less encouraging of infant independence when they themselves (and by extension their infants) are at greater risk from social aggression (Fairbanks 1996).

Although sexual differences in behaviour is well documented in adults, whether (and how much) offspring sex influences the manner in which maternal care is delivered is poorly understood. Research conducted over the last two decades on wild and captive primates has revealed striking sex differences in the social and foraging behaviour of juveniles across a range of ages (from several months to several years old) and species (e.g. capuchin monkeys, *Cebus nigritus*: Agostini & Visalberghi 2005; blue monkeys, *Cercopithecus mitis*: Cords et al. 2009; western lowland gorillas, *Gorilla gorilla*: Maestriperi & Ross 2004; yellow baboons: Pereira 1988; muriqi monkeys, *Brachyteles arachnoides*: Strier 1993; long-tailed macaques, *Macaca fascicularis*: van Noordwijk et al. 1993), differences that mirror sex differences in adults of these species. Juveniles (unlike infants) are likely to survive the death of their mothers (and the loss of maternal care) but have not yet matured sexually (Pereira 1993). In echoing the divergent social and foraging skills of adult males and females, juvenile sex differences in behaviour and ecology are believed to reflect juvenile primates' preparation for adulthood (Pereira 2002). However, our understanding of the processes of behavioural and physical development and maturation of immature primates is hampered by limited comparative information about the social lives of newborn infants. Furthermore, information about how the mother–infant relationship varies as a function of infant sex remains largely unavailable for any primate species.

In addition to social, experiential and behavioural influences on the mother–infant relationship, maternal care in mammals generally, and primates in particular, is also expected to be sensitive

to hormonal regulation, given the supreme importance of maternal care to offspring survival. Indeed, nearly all mammals exhibit elevations in the ovarian steroids oestrogens (and declines in progesterone) around the time of birth, and these hormones have now been found to be critical for the onset and maintenance of maternal behaviour in several laboratory mammals (rodents: Bridges 1990; Rosenblatt 1990; sheep: Poindron & Levy 1990; Dwyer et al. 2004; rabbits: Gonzalez-Mariscal & Rosenblatt 1996). In rats (the best studied of all mammalian mothers), oestrogens probably prime the brains of females to respond to pups in a nurturing manner by facilitating neuroendocrine changes that regulate this behaviour, and through steroid-dependent up-regulation of peptide hormones and receptors important for inducing the expression of maternal behaviours (Insel 1990; Bridges 1996).

While hormones appear to be critical for priming mothers to behave maternally around the time of birth, their role (if any) in regulating well-documented intraspecific variability in the mother–infant relationship remains largely unknown. Only recently have investigators begun to turn their attention to this topic. Although it is too soon to draw general conclusions about the influence of any one class of hormones on any one component of maternal behaviour, natural variation in oestrogens and oestrogen receptor expression (in the brain) have (to date) been associated with individual differences in the performance of maternal behaviour in two laboratory mammals, rats (Champagne et al. 2001) and sheep (Dwyer et al. 2004).

Our knowledge of the influence of hormones on the expression of offspring care behaviour in primates (including humans) lags far behind that for other mammals, because of both the long-held assumption that parenting in primates is relatively free of hormonal regulation and the ethical barriers to invasively measuring (and manipulating) hormones in primate mothers and other caretakers (Maestriperi 1999). Recent findings suggest the potential for ovarian steroids, particularly oestrogens, to influence the growth of maternal attachment feelings to infants during pregnancy in humans (Fleming et al. 1997) and the expression of postnatal maternal behaviour in nonhuman primates (Pryce 1993; Maestriperi & Zehr 1998). However, neuroendocrine sources of interindividual variability in maternal care remain poorly understood for any primate. Research on this topic has produced equivocal results, with some studies finding a positive relationship (Pryce et al. 1988), and others a negative relationship (Fite & French 2000; French et al. 2004) or no relationship at all between maternal oestrogens and infant survivorship or the patterning of mother–infant interactions (Bales et al. 2002; Bardi et al. 2004). Most prior research on this topic has, however, been confined to small sample sizes of individuals (i.e. <10) in captive or laboratory populations.

While research on captive or laboratory animals is valuable for identifying potential causal links between hormones and behaviours of interest, captivity and provisioning can modify neural processes and brain structures (Barnea & Nottebohm 1994; Healy et al. 1996; Rosenzweig & Bennett 1996), influence the pattern of secretion of hormones (Wingfield et al. 1990; Gardiner & Hall 1997; Baker et al. 1998), and affect the expression of social behaviours (Groothuis & Vanmulekom 1991; McPhee 2004). For example, studies of the influence of maternal hormones on offspring care in captive primates frequently use neonatal mortality due to maternal rejection to assess maternal investment patterns (e.g. Pryce 1988; Fite & French 2000), even though maternal rejection of newborns and neonatal death resulting from it are rarely observed in wild animals, except under conditions of extreme deprivation or nutritional stress (e.g. Langenau & Lerg 1976). Research on wild animal populations is, therefore, invaluable because the robustness of hormone–behaviour relationships established in captivity can be

assessed in nature, where animals are exposed to a diversity of ecological and social stimuli often absent from captive settings (Costa & Sinervo 2004; Fusani et al. 2005).

Recently, we showed that prenatal maternal glucocorticoid hormones predicted maternal responsiveness to infant distress cries (which are widely believed to be honest indicators of infant need or condition; Kilner & Johnstone 1997) after birth in wild yellow baboons at Amboseli, Kenya (Nguyen et al. 2008). These results suggest that glucocorticoid hormones secreted during late pregnancy may help to prepare expectant baboon mothers for the predictable challenges associated with offspring care (Nguyen et al. 2008). In this study, we focus instead on pre- and postnatal maternal sex steroid hormones (oestrogen and progesterone), as well as postnatal mother–infant interactions in order to obtain a more complete understanding of the factors influencing the development of the mother–neonate bond and offspring independence. Specifically, we investigate the effects of maternal sex steroids and mother and infant characteristics on the patterning of mother–infant contact and suckling interactions in 34 wild yellow baboon mother–infant dyads at Amboseli.

Few studies have evaluated the influence of both physiological and nonphysiological variables on the development of the mother–infant relationship, and only one prior study has done so in a wild nonhuman primate population (Bales et al. 2002). Bales and colleagues focused their study on golden lion tamarins, *Leontopithecus rosalia*, cooperatively breeding New World monkeys in which most forms of offspring care can be (and are) provided by group members other than the mother. Our study focuses on a primate species in which mothers (like most mammalian mothers) provide almost all offspring care. We use aspects of contact and nursing behaviour as measures of the mother–offspring relationship, and examine the extent to which maternal oestrogens and progesterone (excreted in faeces), previous maternal care experience, maternal dominance rank and infant sex contribute to variation in the mother–neonate relationship during the earliest period of infant growth and development. We hypothesized that variation in this relationship is contingent on infant sex and maternal experience. In addition, given the metabolic costs associated with many hormone-dependent reproductive activities (Nelson 2011), we hypothesized that maternal dominance rank would influence both the patterning of perinatal hormone secretion and the mother–neonate relationship, possibly through its effects on the mother's access to resources and potentially her body condition as well.

METHODS

Subjects, Study Site and Behavioural Data

The subjects for this study were part of a larger population of wild-feeding, free-ranging baboons inhabiting the Amboseli basin, a semi-arid, short-grass savannah ecosystem situated at the base of Mt. Kilimanjaro in East Africa. Baboons are nonseasonal polygynandrous breeders and are among the largest, most sexually dimorphic, omnivorous and terrestrial of the monkeys (Estes 1992; Kingdon 2003). Males typically disperse from their natal groups as they near adult size and many continue to migrate between groups throughout their lives (Pusey & Packer 1987). Females, in contrast, remain in their natal group their entire life (Pusey & Packer 1987).

The baboon population at Amboseli has been under continuous observation since 1971, and data on life history are known since birth from near-daily records of demographic events and reproductive cycles for several hundred animals (Altmann 1980; Alberts & Altmann 2003; Altmann & 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; Altmann 1998).

Thirty-four mother–infant pairs, members of five distinct social groups, were studied from July 2002–November 2003 by N. N. (Nguyen 2006) (Supplementary Material, Table S1). For each mother–infant dyad, we determined (1) the sex of the infant, (2) maternal parity and (3) maternal dominance rank. We used parity (defined as a female's total number of pregnancies, irrespective of outcome, and including the current infant; Altmann et al. 1988) as a measure of each mother's prior infant care experience. For the subjects of this study, parity, which ranged from one to nine (mean \pm SD = 4.2 ± 2.5), was correlated with maternal age ($r^2 = 0.91$, $N = 34$, $P < 0.0005$), which ranged from 5.3 to 17.8 years (mean \pm SD = 10.2 ± 3.4 years). Subjects included five first-time mothers with no prior experience caring for offspring, and 29 multiparous mothers with experience rearing one to eight prior infants. For the six mothers with only a single previous pregnancy, each had prior experience rearing offspring to at least 4.5 months of age. A female's maternal dominance rank for a given infant was defined as her ordinal rank number among the adult females in her group in the month her infant was conceived (Altmann 1980). Data on the outcomes of agonistic interactions (collected as part of regular monitoring of the study groups) were used to assign ordinal ranks (with 1 being the highest) 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 they gave only aggressive, or neutral (nonsubmissive), gestures while their opponent gave submissive gestures and no aggressive gestures (Hausfater 1975; Alberts et al. 2003). Stability of dominance ranks throughout adulthood and even across generations has been well documented for baboon and macaque females (Melnick & Pearl 1987; Pereira 1995).

Each mother–infant pair was observed throughout the first 8 weeks of the infant's life, and particular effort was made to ensure that observations of each pair were evenly distributed between morning and afternoon samples, and between the earlier and later of these weeks of infancy. Between 17 and 64 focal animal samples (Altmann 1974) of 20 min duration were collected for each mother–infant dyad, giving an average \pm SD of 11.6 ± 4.5 actual insight hours of observation per pair. Although the total number of focal animal samples varied across mother–infant pairs, we found no relationship between observation time and any of the behavioural measures included in this study.

Data were collected on a handheld computer, the Psion Workabout™, using a custom program. During each sample, continuous data were collected on (1) all changes (or 'transitions') in mother–infant contact (categorized as in or out of physical contact) including the identity of the individual who effected (or performed) each change in mother–infant contact and (2) all occurrences of affiliative and agonistic interactions involving the mother or infant. Within the focal samples, embedded point samples (Altmann 1974) were made every 5 min on the activity (i.e. feeding (or suckling in the case of the infant), resting, walking, grooming, or other social) of the female and her infant.

Mother–Neonate Interactions

In contrast to some reports from captive primates (e.g. Hoage 1978; Pryce et al. 1988; Maestripieri et al. 1997, 1999), the 34 mothers in our study were never observed biting, hitting, sitting on, or engaging in any other type of overtly abusive behaviours towards their newborn infants. Furthermore, at Amboseli, maternal rejection (of infants' attempts to establish contact) and restraint of newborns (by preventing them from breaking mother–infant

contact), behaviours sometimes directed at captive newborns by their mothers (e.g. Bardi et al. 2003), very rarely occurred, thus preventing us from making meaningful comparisons across mother–neonate pairs in the occurrences of these behaviours. Maternal rejection and restraint are, however, directed at older offspring on a more frequent basis at Amboseli (Altmann 1980; N. Nguyen, personal observation). At Amboseli, a mother could easily re-establish contact with an infant that was out of physical contact, or move closer to the infant to encourage it to re-establish contact with her.

In this study, we used measures of mother–infant bodily contact and nursing (i.e. nipple contact) to characterize the mother–neonate bond and describe the developmental dynamics of neonatal independence. For each mother–neonate pair, we determined (1) the proportion of changes in mother–infant contact or transitions made by the infant, (2) the hourly rate of transitions initiated by the infant and (3) the percentage of time infants spent off the nipple.

Contact between mother and infant is essential for normal offspring growth and development, providing offspring transportation, protection, thermoregulation and nourishment (Altmann 1980). Although mothers and infants spent the vast majority of their time in physical contact during the earliest stages (i.e. 1–2 months) of infancy, considerable variation existed among dyads in the frequency with which changes (both ‘makes’ and ‘breaks’) in mother–infant contact occurred. Because most changes in contact were initiated by infants (rather than mothers), we determined the proportion and rate of changes in mother–infant contact performed by each infant as a measure of its relative degree of physical activity and maturation.

Lactation affects the length of the interval between successive births (McNeilly et al. 1994) and is thus a major determinant of female fertility among mammals (e.g. Williams 1990; McNeilly 2001). Although it is not possible to distinguish nutritive from non-nutritive suckling in the field, we assessed the amount of time each infant spent off the nipple (measured as the proportion of point samples in which the infant was not observed on the nipple) to obtain an estimate of its relative degree of suckling activity. Like all mammalian infants, baboon infants are initially dependent on mother’s milk for all their nutritional needs (Altmann 1980). As they grow in size and energy requirements, however, infants transition from complete reliance on mother’s milk to nutritional self-sufficiency (a process known as ‘weaning’; Altmann 1980). Unlike mother–infant contact, we were not able to determine (with accuracy) the identity of the individual responsible for the onset and termination of most suckling bouts. Therefore, in our analyses, we used time spent off the nipple as our indirect measure of each infant’s relative degree of suckling activity.

Faecal Hormone Sampling and Measurement

Faecal samples were opportunistically collected from each mother throughout the last 8 weeks of pregnancy and the first 8 weeks of motherhood. A total of 694 faecal samples were collected from the 34 mothers, giving an average of 1.3 faecal samples per female per week for each of the 16 weeks. Faecal samples were collected from an average \pm SE of 5.9 ± 0.2 weeks per female (range 3–8 weeks) during the prenatal period, and 4.6 ± 0.2 weeks per female (range 2–7 weeks) during the postnatal period. Faecal sample collection, storage, extraction and assay techniques for pregnant and lactating females in this population have been described in detail elsewhere (Altmann et al. 2004; Beehner et al. 2006). In brief, samples were thoroughly mixed, placed in 95% ethanol and stored in a charcoal refrigerator (~ 20 – 25 °C) at Amboseli until shipment to the University of Nairobi (once every 2 weeks), where the ethanol was evaporated

and samples were lyophilized. Lyophilized samples were stored at -20 °C until shipment to Princeton University, where each sample was sifted to remove vegetative matter and 0.2 g of faecal powder was extracted into 2 ml of 90% methanol and then run through a prepped Oasis cartridge for solid phase extraction. Extracts were stored at -20 °C prior to assay.

All 694 faecal samples were assayed for oestrogen (E) and progesterone (P) metabolites using commercially available radio-immunoassay kits that had been modified and validated for use in this population (see protocols in: Khan et al. 2002; Lynch et al. 2003; Altmann et al. 2004). The primary antibody in the Total Estrogens Kit (ICN Diagnostics, Costa Mesa, CA, U.S.A.) cross-reacts 100% with oestradiol- 17β and oestrone, 9.0% with oestriol, 7.0% with oestradiol- 17α and 2.5% with equilin (ICN Diagnostics). The primary antibody in the I125 Direct Progesterone Kit (Pantex, Santa Monica, CA, U.S.A.) cross-reacts 100% with progesterone, 0.5% with 17 α -hydroxyprogesterone and 0.1% with androstenedione (Pantex). All samples were assayed in duplicate and mean concentrations were expressed as nanograms of hormone per gram of dry faecal matter, to control for dietary differences between individuals and seasons (Wasser et al. 1993). All data collection procedures adhered to the Institutional Animal Care and Use Committee guidelines of Princeton University.

Hormone data were divided into days and weeks from parturition, with the day before parturition (day -1) considered the last day of week -1 , the day of parturition (day 0) considered the first day of week 1, and the day after parturition (day 1) considered the second day of week 1. We excluded samples from day 0 to day 3 from analyses of the postnatal period because there is a 1–3-day lag time between steroid hormone secretion and excretion in faeces (Wasser et al. 1994), so values from this period probably reflect prenatal levels.

Data Analysis

Assessing individual consistency in behavioural and hormonal measurement

Females varied in the number of faecal samples they contributed to the data set. These same females and their infants also differed in the days (relative to parturition) on which they were behaviourally sampled. Uneven sampling across subjects can potentially bias analyses of between-subject differences in behaviour and hormones, especially during a period of rapid changes in both. To avoid any bias of an uneven sample distribution and control for time from parturition, we generated residual behavioural and hormonal values using a locally weighted regression procedure (LOWESS) in SigmaPlot 8.0 (2002, SPSS Inc., Chicago, IL, U.S.A.) (for similar analyses see Altmann & Alberts 2005; Beehner et al. 2006; Nguyen et al. 2008). This allowed us to generate a single residual for each female (for the hormonal values) and each mother–infant pair (for the behavioural measures) in each week of observation (from week -8 , indicating 8 weeks before parturition, to week $+8$, indicating 8 weeks after parturition). These residuals are hereafter called the ‘weekly residuals’. We chose LOWESS (with a sampling proportion of 0.5) because it is more ‘locally sensitive’ to time-specific deviations from the average pattern (Moses et al. 1992; Altmann & Alberts 2005; Nguyen et al. 2008). All subsequent analyses, therefore, use deviations or residuals from the LOWESS-determined class average at each point in time relative to parturition.

For each behaviour, we plotted the value for each mother–infant pair as a function of the week from parturition, using the LOWESS residuals for each female in each week. The weekly residuals were calculated as the difference between the observed values (e.g. a mother–infant pair’s rate of infant-initiated transitions for a given

week from parturition) and the predicted values as determined by the LOWESS regression (e.g. the mean rate of infant-initiated transitions among all mother–infant pairs that week). Pairs with positive residuals for a given week have values above the class average, while those with negative residuals have values below the class average for that week. For the two contact measures, we omitted data from the first postnatal week because few changes in mother–infant contact occurred during this week.

We also generated residual hormone values using a LOWESS on the full set of raw hormone values. We plotted the hormone concentration of each sample as a function of the day from parturition on which it was collected. The residuals were calculated for each sample as the ratio of the observed to the predicted values as determined by the LOWESS regression (e.g. class average for that day from parturition). Pairs with residuals above 1.0 have values above the class average while those with residuals below 1.0 have values below the class average for that point in time. We then calculated mean residual values for each female each week from parturition.

We then evaluated the stability of individual differences in behaviour and hormones by applying linear regression analysis to each animal's residual scores across weeks from parturition. We did this to determine whether any departure from stability was systematic and might, therefore, affect subsequent tests for sources of individual differences during a time of rapid changes in both behaviour and hormones (for similar analyses, see: Bloch & Moses 1988; Altmann & Alberts 2005; Beehner et al. 2006; Nguyen et al. 2008; for further details on this approach, see Moses et al. 1992).

In addition, we assessed whether mother–infant pair identity, or week, or both, explained a significant proportion of the variance in each of the three weekly residual behavioural measures using general linear model (GLM) procedures. If pair identity emerged as a significant (or sole) predictor of variance in these measures, we could (more confidently) infer that stable pair differences in these behavioural measures existed in this population. For the hormonal values, we also compared the within-individual variance in weekly mean residuals to that among individuals using ANOVA. If within-individual variance in faecal oestrogen (fE) or progesterone (fP) concentration for the entire 16-week peripartum period is less than that between individuals, we could (more confidently) infer that variation in residual fE and fP values due largely to individual identity was more important than that due largely to chance or measurement error. The results of these analyses (see below) justified our next step, which included determining individual averages from the weekly behavioural and hormonal residuals, and applying regression and general linear model procedures to these data to evaluate predictors of variability in mother–infant interactions.

Finally, we calculated, for each mother–infant pair, one value, representing the mean of the pair's weekly residual values for the 8-week postnatal period (i.e. weeks 1–8), for each of the three mother–infant interaction measures. In addition, for each female, we calculated two values for each of the two hormones (fE and fP), a 'prenatal' mean, representing the average of the female's prenatal residuals (comprising weeks –8 to –1), and a 'postnatal' mean, representing the average of the female's postnatal residuals (comprising weeks 1–8). We then log transformed these mean hormone values to achieve a normal distribution before entering them into our analyses.

One previous study (Nguyen et al. 2008) focused on the same sample of mothers and infants studied here. However, that study focused on a different dimension of the mother–infant bond (i.e. maternal responsiveness to infant stimuli) and its relationship to different perinatal hormones (i.e. glucocorticoids, which are frequently associated with arousal and attentiveness) than the ones explored in this study. The mother–infant relationship is a complex,

multifaceted one, encompassing a suite of behavioural and physiological phenomena that collectively function to enhance offspring growth and survival (Krasnegor & Bridges 1990). Even in laboratory rats, maternal care includes a variety of behaviours (from nest building to pup retrieval) that are themselves regulated (or influenced) by a range of neuroendocrine factors and processes (Bridges 1990, 1996; Nelson 2011).

Predictors of individual differences in faecal hormones and mother–infant interactions

We applied general linear model (GLM) and multiple regression procedures to evaluate (1) the sources of variability in pre- and postnatal sex steroid hormones, before proceeding to evaluate (2) the sources of variability in the mother–infant relationship. To evaluate the sources of variability in pre- and postnatal hormones, we used GLM procedures to examine the effects of the mother's parity, maternal rank at conception and infant sex on mean pre- and postnatal maternal fE and fP values. To evaluate the sources of variability in mother–infant interactions across all dyads, we used GLM procedures to examine the effects of parity, maternal rank, infant sex, and pre- and postnatal fE and fP values on each of the three mother–infant interaction measures.

In cases where the results of our GLM indicated that infant sex had a significant effect on a mother–infant interaction measure, we subsequently conducted separate analyses for male and female infants. If, instead, the results of our GLM indicated that two or more dependent variables had significant effects on a mother–infant interaction measure, we used hierarchical multiple regression to sequentially enter the variables into the equation (from largest to smallest effect size) to assess the relative contribution of each variable to the prediction of the mother–infant interaction measure.

All statistical analyses were conducted using SPSS 19.0 (2011, SPSS Inc.). Relationships between explanatory variables were explored using Pearson's correlation coefficients. Values reported are means \pm SE unless otherwise noted. All analyses were two tailed with $P < 0.05$.

RESULTS

Overall Changes in Behaviour and Hormones during the Perinatal Period

Infants became increasingly responsible for changes in mother–infant contact across the perinatal period. The rate of change in contact initiated by infants rose 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 across weeks (Fig. 1b). Similarly, infants spent increasing amounts of time off the nipple as they aged (Fig. 1c).

Both fE and fP 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 fE and fP concentrations had returned to levels characteristic of nonpregnant females (see Beehner et al. 2006) and remained at these levels to the end of the sampling period.

Individual Differences in Hormones and Behaviour during the Perinatal Period

We found that mother–infant dyads varied widely in the patterning of mother–infant interactions and these between-dyad differences were moderately stable across weeks, with most dyads showing a degree of within-dyad consistency in values for all three

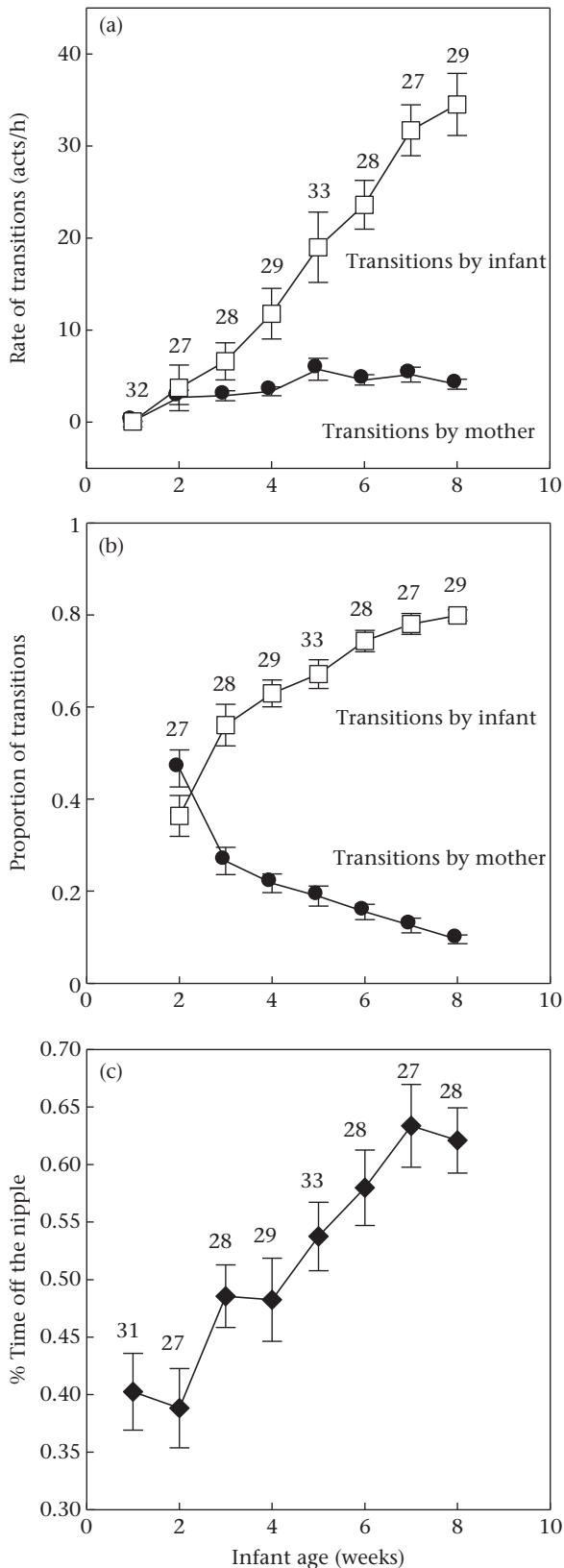


Figure 1. Change in mother–infant contact in yellow baboons by week from birth. (a) Proportion of changes in mother–infant contact initiated by the infant or by the mother by week from parturition, (b) Rate of changes in mother–infant contact initiated by the infant or by the mother by week from parturition, (c) Proportion of

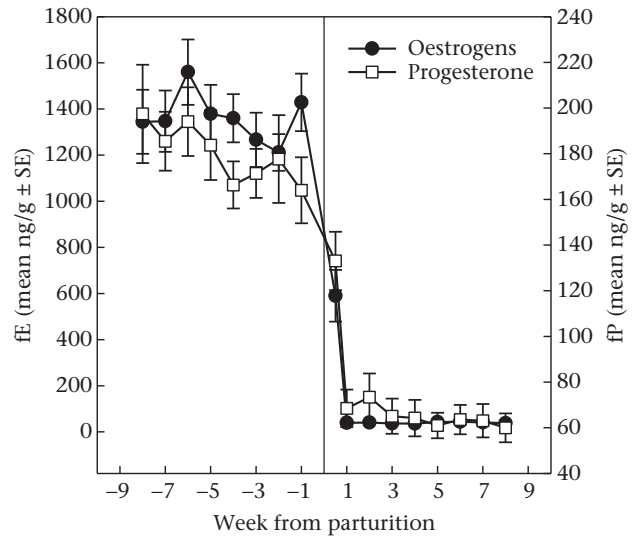


Figure 2. Mean concentrations of total oestrogens and progesterone (ng/g of faeces \pm SE) in female yellow baboons by week from parturition. Because of the 1–3-day lag time between steroid hormone secretion and excretion in faeces (Wasser et al. 1993), values from the first postnatal week are divided into two periods, one encompassing days 0–3, presumed to reflect prenatal values, and one encompassing days 4–6.

mother–infant interaction measures. Over 82% of the 34 dyads showed no significant time trend up or down in the weekly residual values for transitions initiated by the infant across weeks. In addition, over 88% of dyads showed no significant trend up or down in the weekly residuals for proportion of infant-initiated changes in contact across weeks (mean \pm SD = 5.9 \pm 1.0 weekly values/dyad for each measure). Finally, over 88% of dyads showed no significant trend up or down in the weekly residuals for proportion of time off the nipple (mean \pm SD = 6.8 \pm 1.2 weekly values/dyad). In addition, while week of sampling alone had no effect on any of the behavioural measures, mother–infant pair identity was a significant predictor of weekly residual values for all three behavioural measures (general linear model: $F_{33,129} = 1.68$, $P = 0.02$; $F_{33,113} = 2.65$, $P < 0.0005$; $F_{30,151} = 1.78$, $P = 0.01$, respectively). We infer from these findings that stable differences in the patterning of mother–infant interactions existed across dyads, with some dyads showing consistently lower levels and others showing consistently higher levels of each behaviour.

We also found that females varied widely in fE and fP values and that these between-individual differences were moderately stable across weeks, with most females showing a degree of within-individual consistency in values for both hormones. For example, over 71% of the 28 females with samples from at least 5 of the 8 prenatal weeks showed no significant trend across weeks in the weekly residuals for fE scores, and over 85% of the 21 females with samples from at least 5 of the 8 postnatal weeks showed no significant trend in their weekly residual fE scores across time. We could discern no characteristic shared by those individuals that did change in either period. Moreover, we found that variance in the weekly values for both fE and fP within individual females was less than that between individuals (general linear model: $F_{33,332} = 2.80$,

time spent off 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.

$P < 0.0005$; $F_{33,331} = 4.70$, $P < 0.0005$, respectively). We infer from these findings that stable differences in pre- and postnatal fE and fP concentrations existed across individuals, with some females characterized by consistently lower weekly residual values and others characterized by consistently higher weekly residual values for each steroid.

We next proceeded to apply regression and GLM procedures to each dyad's mean mother–infant interaction measures (for each of the three interactions) and each female's mean pre- and postnatal scores (for fE and fP) to evaluate the sources of variability in the mother–infant relationship and in perinatal hormones.

Predictors of Variability in Perinatal fE and fP

Individual variability in both pre- and postnatal fP and in postnatal fE was not predictable from infant sex, maternal rank or parity (Supplementary Material, Table S2). However, variability in prenatal fE was predictable from maternal rank (Supplementary Material, Table S2), with higher-ranking females characterized by higher prenatal fE values than lower-ranking females (Fig. 3). Although infant sex had no direct effects on prenatal fE, the relationship between high rank and high prenatal fE was stronger among mothers of female infants (simple linear regression: $r^2 = 0.35$, $N = 15$, $P = 0.02$) than among mothers of male infants ($r^2 = 0.10$, $N = 19$, $P = 0.19$; Fig. 3).

Predictors of Variability in the Mother–Infant Relationship

Transitions in and out of mother–infant contact

Infants that initiated higher rates of transitions in mother–infant contact also made a greater proportion of transitions ($r^2 = 0.30$, $N = 34$, $P = 0.002$), indicating that these two measures of infant physical activity and maturation were coordinated in more active infants. For simplicity, we use the rate of transitions initiated by infants as the measure of mother–infant contact interactions in subsequent analyses.

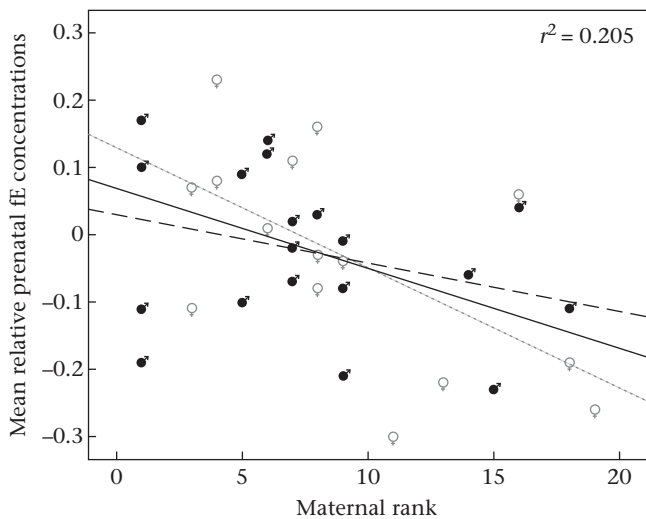


Figure 3. Relationship between mean prenatal faecal oestrogen (fE) concentrations and maternal rank for yellow baboon mothers with male (♂) and female (♀) infants. Each point represents a mother's rank at conception and the mean of the mother's weekly fE residual concentrations during the last 2 months of pregnancy. The solid line represents the regression line for all 34 mother–infant dyads combined ($r^2 = 0.205$, $N = 34$, $P = 0.007$). The dotted line represents the line for dyads with female infants ($r^2 = 0.35$, $N = 15$, $P = 0.02$) and the dashed line represents the regression line for dyads with male infants ($r^2 = 0.10$, $N = 19$, $P = 0.19$).

Neither pre- or postnatal hormones nor maternal rank predicted the rate of infant-initiated transitions in contact (Table 1). However, the rate of transitions initiated by infants was predictable from both maternal parity and infant sex (Table 1, Fig. 4). The higher the mother's parity, 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). The results of a hierarchical multiple regression indicated that maternal parity alone explained 34% of the variance in the rate of infant-initiated transitions in contact while infant sex explained an additional 24% of the variance (Table 2). These results suggest that more experienced mothers and mothers of male infants are more encouraging or tolerant of infant independence than less experienced mothers and mothers of female infants.

Infant's time off the nipple

The rate at which infants initiated changes in mother–infant contact was correlated with the percentage of time infants spent off the nipple, although this relationship was not significant (Pearson's correlation: $r_{32} = 0.11$, $P = 0.061$). This result suggests that more active infants tended to spend more time off the nipple than less active infants.

Although male infants were significantly more active (i.e. showed higher rates of infant-initiated transitions) than female infants (independent samples t test: $t_{32} = 2.4$, $P = 0.02$), the two sexes did not differ in the amount of time spent off the nipple ($t_{32} = 0.74$, $P = 0.47$). Indeed, when all 34 infants were considered, the amount of time infants spent off the nipple was not predictable from infant sex, maternal parity, or pre- or postnatal hormones. However, maternal rank had a 'moderate' (but nonsignificant) effect (partial eta-squared = 0.118; see Cohen 1988) on the amount of time infants spent off the nipple, with newborns of high-ranking mothers spending more time off the nipple (or less time on the nipple) than newborns of lower-ranking mothers (Table 3).

Because maternal rank was more strongly associated with prenatal fE in mothers of female infants than in mothers of male infants (Fig. 3), we investigated whether the 'moderate' effect of rank on time off the nipple differed by infant sex by evaluating the influence of rank and prenatal fE on infants' time off the nipple separately for each sex using multiple regression analysis. The results indicated marked sex differences in the influence of maternal rank and prenatal fE on infants' time off the nipple. In dyads with female infants, maternal rank and prenatal fE together explained a large (45.4%) and significant percentage (hierarchical

Table 1
Effects of infant sex, maternal parity, dominance rank and perinatal hormones (pre- and postnatal faecal oestrogen, fE, and faecal progesterone, fP) on variation in infant-initiated transitions in contact in yellow baboons

Overall model	Rate of infant-initiated transitions		
	$r^2_{adj,5} = 0.538$, $N = 34$		
	Mean square	F	P
Model	194.538	6.487	<0.0005
Error	29.989		
Predictor variables			
Infant sex*	517.413	17.254	<0.0005
Parity	710.125	23.680	<0.0005
Maternal rank	50.176	1.673	0.207
Prenatal fE	50.054	1.669	0.208
Postnatal fE	11.188	0.373	0.547
Prenatal fP	42.742	1.425	0.243
Postnatal fP	65.116	2.171	0.153

Results of the GLM indicate that observed differences between dyads in rate of infant-initiated transitions in contact were significantly predicted by infant sex and maternal parity (in bold).

* A dichotomous variable: 0 = female infant; 1 = male infant.

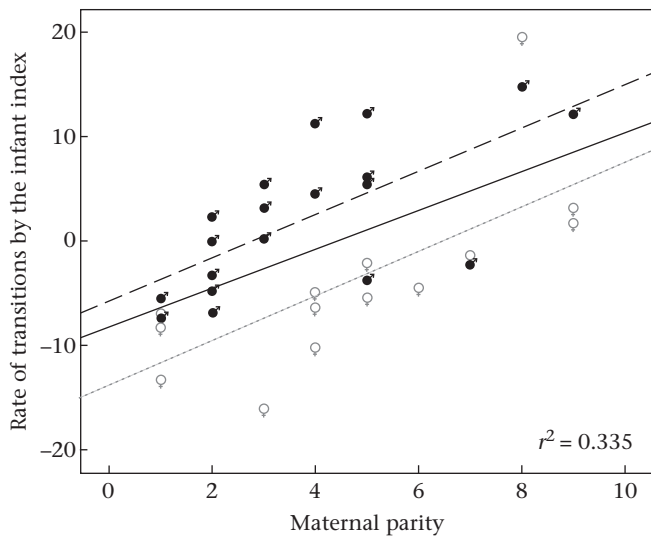


Figure 4. Rate of infant-initiated transitions in yellow baboons as a function of maternal parity for dyads with male (♂) and female (♀) infants. Each point represents a given mother–infant dyad's maternal parity and the mean for the dyad's weekly residuals for the rate of infant-initiated transitions (see text). The solid line represents the regression line for all 34 mother–infant dyads combined ($r^2 = 0.335$, $P < 0.0005$). The dotted line represents the line for dyads with female infants ($r^2 = 0.51$, $N = 15$, $P = 0.003$) and the dashed line represents the regression line for dyads with male infants ($r^2 = 0.47$, $N = 19$, $P = 0.001$).

multiple regression: $P = 0.011$) of the variance in infants' time off the nipple (i.e. female infants of high-ranking mothers with high prenatal fE spent the most time off the nipple), although neither rank nor prenatal fE alone made a statistically significant unique contribution to the equation (Table 4). In contrast, in dyads with male infants, maternal rank and prenatal fE did not explain a significant percentage (3.4%, $P = 0.296$) of the variance in infants' time off the nipple (Table 4).

DISCUSSION

In the wild baboon population at Amboseli, we found that newborn infants of more experienced mothers initiated more changes in mother–infant contact than infants of less experienced mothers. These results suggest that baboon mothers at Amboseli become incrementally less restrictive with each subsequent offspring. In addition, we found evidence of striking sex differences in the mother–infant relationship during the neonatal period. At each level of maternal experience, newborn sons initiated higher rates of changes in mother–infant contact than did newborn daughters. Moreover, maternal rank and prenatal fE combined

influenced suckling activity among newborn daughters, but had no detectable effects on the suckling behaviour of newborn sons. These results suggest that a baboon mother's social world has a greater influence on the life of her newborn daughter than on the life of her newborn son. To our knowledge, this study is the first in a wild primate to provide evidence of sex differences in the perinatal mother–infant relationship and to evaluate the social, experiential and hormonal correlates of these differences.

Effects of Maternal Experience on the Development of Infant Independence

Considering all mother–infant dyads irrespective of infant sex, mothers with more prior infant care experience had infants that were more active in initiating changes in physical contact. Because age is related to prior infant care experience in this population, these results suggest that as females grow older (and gain experience), they become increasingly less restrictive, or more tolerant or encouraging of infant independence.

Although a number of previous studies have reported marked differences between first-time (i.e. primiparous) and experienced (i.e. all other) mothers in maternal behaviour towards offspring (Hiraiwa 1981; Hooley & Simpson 1981; Berman 1984; Fairbanks 1988, 1996; Gomendio 1989; Schino et al. 1995), to date, no study has evaluated the influence of continuous changes in maternal experience on the mother–infant relationship. Here, to our knowledge, we provide the first evidence for a wild social mammal that the number of successfully reared previous offspring impacts the relationship between a mother and her current infant. In wild baboons, infant physical activity and maturation, measured as the rate of infant-initiated transitions in mother–infant physical contact, increased continuously with maternal experience (and age). Our results suggest that the common practise of combining all multiparous females into a single category when measuring mother–infant interactions and examining hormone–behaviour interactions during the peripartum period may not be sufficient for capturing all the variability in these relationships.

Our results are consistent with the hypothesis that more experienced mothers are more permissive or tolerant of infant independence because they are more competent or efficient at providing infant care than less experienced mothers (Green 1993; Fairbanks 1996; Cameron et al. 2000). Experienced mothers may target their infant care efforts more effectively (i.e. to those periods in which they are most critical for infant survival, growth or development) without investing more, and possibly investing less, in each offspring (Cameron et al. 2000). Data consistent with this 'targeted investment' hypothesis have also been reported in wild horses (Cameron et al. 2000) and bison (Green 1993), and in several populations of captive or provisioned cercopithecine primates

Table 2
Effects of maternal parity (Model 1) and (additionally) infant sex (Model 2) on variation in infant-initiated transitions in contact in yellow baboons

		Unstandardized coefficients		Standardized coefficients	P	Change in r^2
		B*	SE	β^*		
Model 1	(Constant)	−8.243	2.250		0.001	0.335
	Parity	1.861	0.464	0.579	<0.0005	
Model 2	(Constant)	−5.791	1.933		0.005	0.235
	Parity	2.102	0.384	0.653	<0.0005	
	Infant sex	−7.836	1.906	−0.490	<0.0005	

Results of the hierarchical multiple regression indicate that observed differences between dyads in rate of infant-initiated transitions in contact were significantly predicted by maternal parity and infant sex. Parity alone explained 34% of the variance in rate of infant-initiated transitions in contact, and infant sex explained an additional 24% of the variance.

* Positive regression coefficients (B, unstandardized; β , standardized) indicate a positive relationship between parity and infant-initiated transitions (i.e. infants of more experienced mothers initiated relatively more transitions than did infants of less experienced mothers), while the negative regression coefficients for infant sex (a dichotomous variable: 0 = female; 1 = male) indicate that male infants initiated relatively more transitions than did female infants.

Table 3

Effects of infant sex, maternal parity, dominance rank and perinatal hormones (faecal oestrogen, fE, faecal progesterone, fP) on variation in the percentage of time infants spent off the nipple in yellow baboons

Overall model	% Time off the nipple		
	Mean square	F	P
Model	0.014	2.362	0.052
Error	0.006		
Predictor variables			
Infant sex*	0.001	0.206	0.654
Parity	0.005	0.850	0.365
Maternal rank	0.021	3.477	0.074
Prenatal fE	0.006	1.038	0.318
Postnatal fE	0.007	1.195	0.284
Prenatal fP	0.000	0.057	0.813
Postnatal fP	0.008	1.327	0.260

Infants of higher-ranking females tended to spend more time off the nipple, but the difference was not statistically significant.

* A dichotomous variable: 0 = female infant; 1 = male infant.

(vervet monkeys: Hooley & Simpson 1981; Fairbanks 1988; Gomendio 1989; Japanese and rhesus macaques: Hiraiwa 1981; Berman 1984; Schino et al. 1995).

Targeted investment in offspring by mothers may lead to more rapid infant independence. Infants of more experienced mothers may be permitted or encouraged to seek locomotor, nutritional or social independence at an earlier age, and this precociousness can have important life-history consequences for both mothers and offspring (Fairbanks 1996). For example, bolder offspring may suffer greater risk of predation, while cautious offspring may miss out on social opportunities that might be valuable later in life (Altmann 1980; Fairbanks 1996). Data from studies of captive primates suggest that some attributes of infant temperament can persist (at least) into the second year of life (Weinstein & Capitanio 2008). Although the costs and benefits of being precocious or enterprising are not well known, the fitness value of any temperament or personality type will invariably depend on the ecological and social conditions under which individuals mature and reproduce (Roulin et al. 2010).

If targeted investment by more experienced mothers results in more rapid infant independence or maturation, experienced mothers might benefit from reduced reproductive costs or enhanced future fecundity (Fairbanks 1996). Following individuals of known age and reproductive history throughout their lifetime would provide the only definitive test of these ideas. At Amboseli, birth rates are relatively stable throughout adulthood for female baboons, declining after about 18 years of age (Altmann et al. 2010). All of the mothers in our study were less than 18 years old, and nearly 90% of females (30/34) were less than 15 years of age;

consequently, the females in our study represented age groups with relatively homogeneous fertility rates. Nevertheless, our results suggest that as mothers gain experience, they also grow (continuously) in 'wisdom', and by targeting their reproductive investment, can lower the cost of reproduction with each subsequent offspring.

Effects of Infant Sex on the Mother–Infant Relationship

Sex differences in infant-initiated changes in contact

Sex differences in adult social behaviour and ecology in mammals originate in the perinatal period with fetal exposure to sexually differentiating hormonal events (Goy & McEwen 1980; Arnold 2002). Prior to birth, exposure of the developing fetal brain to testosterone and other androgens causes masculinization and defeminization of the parts of the nervous system governing the expression of sexually dimorphic behaviours (Nelson 2011). Events after birth can also have a profound influence on the development of sexually dimorphic behaviours. In many species, the expression of male- and female-typical patterns of reproductive, affiliative and agonistic behaviours appears dependent on early social contact with conspecifics (reviewed in Meaney et al. 1985). Furthermore, in laboratory rats, *Rattus norvegicus*, mothers treat newborn male and female offspring differently, and this differential treatment modifies the neural tissues that underlie sexual differences in adult behaviour (Moore et al. 1992). It is unclear whether mothers also treat male and female offspring differently in other mammalian species, and if so, to what extent differential maternal treatment of infants by sex contributes to the development of adult behavioural sex differences.

Although the literature on the social lives of immature primates is rife with examples of sex differences in affiliative and agonistic behaviours (e.g. social play and mounting behaviours) in juveniles that mirror species-typical sex differences in adulthood (reviewed in: Pereira & Fairbanks 2002; Cords et al. 2009; Hassett et al. 2010), few studies have examined the social lives of newborn primates (e.g. Schino et al. 1999). To our knowledge, our study provides the first evidence of sex differences in the mother–neonate relationship in a wild primate population. At Amboseli, newborn male baboons initiated more changes in mother–infant contact than did newborn females. These sex differences are consistent with sex-specific patterns of behaviour characteristic of the adults of this species (Walters 1980; Alberts & Altmann 1995).

Like males in many species of Old World monkeys, 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 & Altmann 1995). In contrast, female baboons (like females in several Old World monkeys, including macaques and

Table 4

Effects of infant sex, maternal dominance rank and prenatal faecal oestrogen (fE) on variation in the percentage of time that infants spent off the nipple in yellow baboons

		% Time off the nipple					
		Model significance	r^2_{adj}	Independent variables	Standardized coefficients (β)*	P	Change in r^2
Female	Model summary	0.011	0.454				
				Prenatal fE	0.473	0.078	0.145
				Maternal rank	−0.342	0.189	0.075
Male	Model summary	0.296	0.034				
				Prenatal fE	0.193	0.440	0.033
				Maternal rank	−0.268	0.289	−0.065

Results of hierarchical multiple regressions indicate that prenatal fE together with maternal rank explained a significant proportion of the variance in the percentage of time that infants spent off the nipple for female (but not male) infants.

* Positive regression coefficients indicate a positive relationship between maternal prenatal fE and time off the nipple (i.e. infants whose mothers had higher prenatal fE spent more time off the nipple than infants whose mothers had lower prenatal fE), while the negative regression coefficients indicate a negative relationship between maternal rank (with 1 being the highest) and time off the nipple (i.e. infants of lower-ranking females spent less time off the nipple, or more time on the nipple, than infants of higher-ranking females).

vervets) 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, very early in life, male baboons are permitted or encouraged to explore the wider physical and social world beyond the safety of their mother's body, and this greater tolerance of male infants' emerging independence may help prepare male offspring for their adult lives as migrants.

Other studies have reported similar sex differences in the social lives of immature primates. In several laboratory and captive populations of macaques, male infants show greater activity or enjoy greater freedom of movement than female infants (Jensen et al. 1968; Mitchell & Brandt 1970; Mitchell 1979; Eaton et al. 1985; Nakamichi et al. 1990). Moreover, among juvenile primates, males of several species become independent of their mothers at an earlier age than females (chimpanzees: Nicolson 1977; pigtail macaques: Jensen et al. 1967; Erwin et al. 1975; Japanese macaques: Itani 1959; bonnet macaques: Simonds 1974; rhesus macaques: Hinde 1971). In contrast, longitudinal data from several primate species indicate that female primates frequently maintain close affiliative ties to their mothers long after sexual maturation (Gouzoules & Gouzoules 1987; Borries et al. 1994; Williams et al. 2002; Kapsalis 2004; Silk 2006).

Our results suggest that adult sex differences in behaviour and ecology characteristic of many Old World primates (including humans) are foreshadowed by the early social interactions between an infant and its mother (its earliest social partner). Very early in life, newborn male baboons initiate more changes in mother–infant contact than their female peers. Are these sexually dimorphic patterns of behaviour during neonatal life a consequence of differential maternal treatment of male and female offspring? Or are they the result of sex differences in the behaviour of newborns? Given that the mother–infant relationship is a dynamic product of both the behaviour of mothers and infants, we cannot know (for certain) whether male infants initiate higher rates of transitions because they are more active or energetic than their female peers, or because their mothers are more permissive (or less restrictive) of infant independence than mothers of female infants. Differential maternal treatment of offspring has been found to contribute to the development of individual differences in offspring temperament and social relationships (reviewed in Champagne 2010). Regardless of the party responsible for these sex differences, sexually dimorphic patterns of behaviour between mothers and newborns may help place offspring on the appropriate path towards sex-specific adult social life, responsibilities and expectations.

Maternal rank and prenatal fE predict daughters' time off the nipple

In Old World primates (including baboons and humans), oestrogens and progesterone are elevated throughout pregnancy, then decline precipitously around parturition (Coe 1990; Warren & Shortle 1990). In addition to supporting pregnancy, oestrogens play a number of other important roles throughout the body, including promoting water retention, bone deposition and memory formation (Nelson 2011). Because of the metabolic costs of many oestrogen-dependent activities, one might reasonably assume that an individual in better physical condition would show above-average levels of oestrogens while an individual in poorer physical condition would show below-average levels. Indeed, we found that, during the last trimester of pregnancy, higher-ranking females showed higher fE levels than did lower-ranked females, regardless of infant sex. This result is consistent with the finding from several long-term studies of group-living primates that higher-ranking females generally have greater access to food resources than lower-ranking females (Post et al. 1980; Whitten 1983; Barton & Whiten 1993; Saito 1996; Sterck et al. 1997).

Our preliminary findings that (1) the positive relationship between maternal dominance rank and prenatal fE was stronger in

mothers of daughters (than in mothers of sons) and (2) among mother–daughter pairs, high maternal rank and high prenatal fEs predicted less suckling time for infants suggest that, at Amboseli, baboon mothers in better physical condition (i.e. females with high rank and high prenatal fE levels) suckle their newborn daughters less often than mothers in poorer physical condition (females with low rank and low prenatal fE levels). Variation in infant suckling activity, possibly to overcome variation among mothers in milk quality or quantity (Loudon et al. 1983; Lunn 1985; Brown et al. 1986; Hinde 2009), could affect a mother's ability to invest in future offspring (Bercovitch 2002). Greater suckling activity has been shown to lengthen the interval between births among some low-ranking primate mothers (e.g. Gomendio 1990; Garcia et al. 2009), possibly by increasing the inhibitory effects of nipple stimulation on the hormones of the hypothalamic–pituitary–ovarian (HPO) axis (Delvoye et al. 1978; McNeilly et al. 1994), which are of primary importance in the regulation of postpartum fertility (Short 1993; McNeilly 2001).

It is worth noting that although time spent on the nipple varied among mother–infant dyads in our study, total milk energy intake by infants may not. Variation in the suckling ability of infants and in milk composition across mothers may confound efforts to relate the amount of time spent suckling with milk energy intake (Cameron 1998). Indeed, in a recent study of captive macaques, Hinde (2009) reported that although first-time mothers showed some sex bias in milk production (producing richer milk for sons and more milk for daughters), the total energy available in milk did not differ between sons and daughters, and mothers' subsequent reproduction was not influenced by the sex of the previous offspring. Unfortunately, techniques to measure milk or energy transfer more accurately using radioactively labelled milk are currently 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. Once noninvasive techniques for measuring milk or energy transfer become available, further research on wild populations (where food supplies are more limiting and variation in maternal condition is expected to be greater than in captivity) will provide critical advances in our understanding of the impact of maternal condition on milk production and the patterning of mother–infant interactions.

One intriguing question remains. Why would maternal social status or condition influence suckling activity for daughters, but not for sons? One possible explanation is that while maternal traits can have long-lasting effects on fitness components for adults of both sexes (Altmann & Alberts 2003b, 2005; Onyango et al. 2008), as newborns, the social life of baboon daughters may be more immediately 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 & Pearl 1987; Walters 1987). Because juvenile daughters usually 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 (White & Hinde 1975; Simpson & Howe 1986; Hemelrijk & Dekogel 1989; Digby 1995), 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, the daughters of lower-ranking baboons spent less time off the nipple than did the daughters of higher-ranking baboons. Since maternal control over lactation and other forms of investment in offspring is widely reported in the literature (e.g. Wade & Schneider 1992; Therrien et al. 2008), a likely source of

this difference in time spent off the nipple was maternal behaviour. If lower-ranking mothers were more restrictive and less permissive of female infants spending time off the nipple than higher-ranking mothers, this greater protectiveness may discourage the daughters of low-ranking females from venturing far from their mother's protection, where they are at greater risk of social aggression. Indeed, 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 & Smale 1991).

It is possible that the sex difference we detected in the influence of maternal dominance rank on neonate suckling patterns (i.e. present in daughters, but absent in sons) may be due to stochastic variation arising from our limited sample size (e.g. Silk et al. 2005). However, most prior research on neuroendocrine sources of individual differences in primate parenting has been confined to an even smaller number of individual mothers (e.g. Bales et al. 2002), often in captive or laboratory settings (e.g. Pryce et al. 1988; Fite & French 2000). Our study builds on previous work by including a larger sample of mothers and neonates and by evaluating hormone–behaviour relationships within the selective environments in which these interactions most likely evolved. Furthermore, our results indicate that the behavioural and hormonal measures we used showed a degree of within-individual stability during a period of rapid changes in both behaviour and hormones. Our findings suggest that these measures, and the relationships we identified among them, are most likely representative of the animals we studied (rather than reflecting a snapshot from a brief moment in time). Additional research into the impacts of offspring sex and maternal rank on maternal investment strategies using a larger population of individuals over a longer time span would help shed more light on this topic.

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

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Supplementary Material

Supplementary material for this article is available, in the online version, at [doi:10.1016/j.anbehav.2012.01.003](https://doi.org/10.1016/j.anbehav.2012.01.003).

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