



Hedging their bets? Male and female chacma baboons form friendships based on likelihood of paternity

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In chacma baboons (*Papio hamadryas ursinus*), adult males and lactating females form preferential associations, or 'friendships', that provide protection against potentially infanticidal attacks. Little is known about the mechanisms by which males and females form friendships, or the function of friendships for males. We examined the relationship between mating activity, paternity and friendships over a 3-year period. A male's proportion of consort activity with a female within and outside of her period of most likely conception, along with his dominance rank, each contributed importantly in models of paternity outcomes and formation of friendships. In 87% of births, the male that monopolized the greatest proportion of a female's consort days during her last conceptive cycle was the father of her offspring. In 82% of the births where the female's primary consort partner was present at parturition, he became her friend. When the primary consort partner was absent at parturition, females formed friendships with males that had monopolized the second or third greatest proportion of their previous consort days. Similarly, 78% of males became friends with females with whom they had obtained their greatest consort success. Such a flexible strategy based on probabilistic assessment of paternity may be adaptive for females, given unpredictable fluctuations in male presence within the group. In a mating system with high dominance-based reproductive skew, males may benefit by investing preferentially in those infants that they are most likely to have fathered.

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Although adult males and females associate only during the females' fertile period in the majority of mammalian species (Clutton Brock 1989), long-term male–female associations occur in over two-thirds of primate genera (Wrangham 1987). The greater prevalence of such associations may reflect increased selection pressure for male investment in offspring due to the long period of offspring dependence and high risks of infanticide (Hamilton 1984; van Schaik & Kappeler 1997; Palombit 2000). Most research on long-term male–female associations and paternal care has focused on monogamous mating systems (e.g. Kleiman & Malcolm 1981; Snowdon 1996). However, preferential associations between males and lactating females, often termed friendships, have also been described for species that live in large multimale, multifemale

groups and exhibit promiscuous mating systems, including macaques (*Macaca fuscata*: Takahata 1982; *M. mulatta*: Manson 1994; *M. sylvanus*: Paul et al. 1996) and baboons.

Friendships between males and lactating females occur in some form in all baboon subspecies (chacma baboons, *Papio hamadryas ursinus*: Seyfarth 1978b; Palombit et al. 1997; Weingrill 2000; olive baboons, *P. h. anubis*: Smuts 1985; yellow baboons, *P. h. cynocephalus*: Altmann 1980; Nguyen et al. 2009). Friendships are distinguished by high rates of spatial proximity and grooming and low rates of submission and aggression between lactating females and their male friends compared with other males (Smuts 1985; Palombit et al. 1997; Lemasson et al. 2008). Friendships also result in high rates of association and affiliative contact between a male and the infant of his female friend (Palombit et al. 1997; Lemasson et al. 2008; Moscovice et al. 2009).

The primary function of friendships may differ across baboon subspecies (Smuts 1985; Palombit et al. 1997, 2000; Lemasson et al. 2008; Nguyen et al. 2009). In both olive and yellow baboons, where

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rates of infanticide are relatively low, friendships appear to function primarily to protect lactating females and their infants from nonlethal harassment by other females (Lemasson et al. 2008; Nguyen et al. 2009). In chacma baboons, where rates of infanticide are higher than in other subspecies (Palombit et al. 2000), observational and experimental evidence indicate that friendships may function as a counterstrategy against infanticidal attacks by recent immigrant males (Busse & Hamilton 1981; Palombit et al. 1997; Henzi & Barrett 2003; Palombit 2003). Chacma females are primarily responsible for the initiation and maintenance of friendships (Palombit et al. 2001), and each female forms friendships exclusively with males that were present in the group when she conceived and that were either likely or confirmed consort partners (Palombit et al. 1997; Weingrill 2000). Males show strong responses to actual or simulated infanticidal attacks against their female friends (Busse & Hamilton 1981; Palombit et al. 1997, 2000; Weingrill 2000). Furthermore, the duration of friendships is closely linked to the duration of the infant's vulnerable period, ending after either the resumption of sexual cycling (Moscovice et al. 2009) or the infant's death (Palombit et al. 1997).

Despite the critical protection that male friends provide to vulnerable infants, relatively little is known about the mechanisms by which males and females choose friends, or the function of friendships for males. There is little evidence that male–female friendships in baboons function to enhance a male's future mating opportunities (e.g. Weingrill 2000; Nguyen et al. 2009). Instead, most studies have suggested that friendships represent paternal care, based on evidence that males form friendships only with females whose infants they may have fathered (Palombit et al. 1997; Weingrill 2000). This hypothesis has received mixed support. In one study of yellow baboons (*P. h. cynocephalus*), only 50% of friendships reflected true paternity (Nguyen et al. 2009). However, males in this population preferentially supported their juvenile offspring in conflicts, suggesting direct discrimination of kin (Buchan et al. 2003). In another study of chacma baboons (*P. h. ursinus*), only half of male caretakers of juveniles were biological fathers, but in almost all cases caretakers had previously been a friend of the juvenile's mother (Moscovice et al. 2009). It is possible that male baboons are able to recognize their own offspring, but that friendships and patterns of long-term investment in juveniles reflect a range of different male strategies, including but not exclusive to paternal care (e.g. Nguyen et al. 2009). Alternatively, if males lack a mechanism for phenotype matching, they may form friendships that reflect investment in probable offspring based on relatively reliable behavioural cues about paternity, such as previous mating activity.

The majority of mating activity in baboons occurs during consortships, when a male maintains close proximity to a female, mates frequently and guards her against mating with other males (Seyfarth 1978a). Male baboons show high reproductive skew (Bulger 1993; Alberts et al. 2003, 2006); dominant males monopolize the majority of consort opportunities and subordinate males' mating success is largely determined by the number of simultaneously consorting females. All males appear to use external signals from females' sexual swellings to focus their mate-guarding efforts in ways that increase their chances of paternity, and most consortships occur during the follicular phase of a female's sexual cycle (Gesquiere et al. 2007). Alpha males show even greater levels of selectivity and tend to focus their consortships within a brief periovulatory period of most likely conception, when the female's sexual skin is maximally swollen (Gesquiere et al. 2007).

High selectivity, in combination with rank-based priority of access to females, creates circumstances in which a male's consort activity during a female's period of most likely conception may act as a reliable indicator of paternity. But even if males have access to

relatively reliable behavioural cues of paternity to determine investment in friendships, fathers may not always be available to form friendships, because of death or emigration (Cheney et al. 2004). Additionally, competition among females for access to friends may prevent subordinate females from forming friendships with preferred males (Palombit et al. 2001). Considering such constraints, a number of authors have suggested that females may benefit by distributing mating opportunities across multiple potential caretakers, in essence confusing paternity, reducing the threat of infanticide, and providing incentives for multiple males to invest in infant care (e.g. Hrdy 1979; Ebensperger 1998; Nunn 1999; van Schaik et al. 2000; Boyko & Marshall 2009; Clarke et al. 2009). Dominant males may secure a high degree of paternity certainty by monopolizing consorts during the period of most likely conception. Females may have greater control over their mating partners outside of this period, when male mating competition is reduced and low-ranking males have more opportunities to mate (Nunn 1999; Gesquiere et al. 2007; Boyko & Marshall 2009). Consort activity outside of the periovulatory period, although associated with a reduced likelihood of paternity, may represent a low-ranking male's greatest opportunity to increase his reproductive success and a female's best strategy to secure future investment in her offspring from several males. Evidence for inter- and intra-female variation in the timing of ovulation relative to detumescence (van Schaik & Paul 1996; Gesquiere et al. 2007) suggests some, albeit low, possibility of paternity through mating outside of the brief period of maximal swelling. If males and females use memory of previous mating activity during the period of most likely conception when forming friendships, then friendships should mainly be formed with males of high rank and should reflect a high degree of paternity certainty. Alternatively, if males and females form friendships based on memory of more general mating activity within and/or outside of the period of most likely conception, then friendships may be formed with males of any rank and may reflect lower degrees of paternity certainty.

Here we use behavioural and genetic data to examine the factors that influence friendship formation in chacma baboon males and females. We evaluate the extent to which dominance rank and mating activity within and outside the period of most likely conception predict paternity and the formation of friendships. We also discuss how the mating strategies of females and males may interact to influence paternity certainty and subsequent male investment.

METHODS

Study Site and Population

The study includes data collected over 39 months from July 2004 through September 2007 on a troop of wild chacma baboons in the Moremi Wildlife Reserve in the Okavango Delta of Botswana. All research was conducted using noninvasive methods approved by the Animal Care and Use Committee of the University of Pennsylvania (Protocol no. 19001). The group had been observed since 1978 and all animals were fully habituated to human observers on foot. Daily demographic data collected during the study period included information on births, deaths, immigration and emigration, dominance relationships (based on approach–retreat interactions) and consortship activity (Cheney et al. 2004; Crockford et al. 2007). Matrilineal relatedness of all individuals was known. As in other species of Old World monkeys, female baboons remain in their natal group throughout their lives, usually attaining a rank adjacent to their mothers by sexual maturity, at 5–6 years. Males typically emigrate from their natal group at between 8 and 11 years (Cheney et al. 2004). Throughout the study, group size remained

close to 70 individuals, including 20–26 adult females and 5–10 adult males.

Female subjects for this study were 20 individuals that carried at least one pregnancy to term and whose offspring survived for at least 2 months postparturition. These females represented a total of 30 conceptive cycles with sufficient data to determine one or more of the following: complete consort activity during the conceptive cycle, association patterns with males for 2 months postparturition, and/or genetic analyses of paternity. Not all of these data were available for all 30 conceptive cycles because of gaps in data collection and incomplete genetic sampling. Each analysis is based on the subset of conceptive cycles with complete data available for the variables of interest (Table 1). Male subjects included 11 immigrant and two natal males that were ranked within the adult male dominance hierarchy for at least 2 months during the study period (Table 2); no more than nine adult males were present at any given time. Male subjects were present for 5–30 conceptive cycles (median = 12 cycles), and all subjects, including natal males, formed consortships with females. Six males disappeared from the group during the study period, as a result of either confirmed emigration ($N = 2$) or suspected death ($N = 4$). Males' dominance ranks for any given time period were calculated as the proportion of males dominated, to control for variation in the number of males present.

Behavioural Data

Consort behaviour

Throughout the study period, data on consort activity were noted ad libitum during daily observations 5–6 days per week, with the exception of two periods during July–August 2005 and December 2005–January 2006, when daily consort activity was not recorded. Consort activity was noted by research teams consisting of at least one of the authors, working with trained assistants. Consort behaviour consisted of conspicuous male mate guarding accompanied by frequent mating with a female whose sex swelling was typically at maximum tumescence (Seyfarth 1978a), although we also observed consort behaviour preceding and following the period of maximum tumescence. In addition to being highly conspicuous, most consortships lasted at least one and often up to several days, making ad libitum observations sufficient to record a majority of consort activity. The consortship records should be considered representative, but not comprehensive, because of some gaps in daily recording and the lack of monitoring of late afternoon and evening consort activity.

To examine the relationship between mating activity and paternity, we analysed data from all female conceptive cycles where paternity was confirmed via genetic analyses. Each conceptive cycle included five 'fertile' days when the female's sexual swelling was at maximum size and conception was most

likely to have occurred, plus a variable number of 'other' days outside of the five 'fertile' days, when the female also formed consortships. We determined 'fertile' days by counting back 5 days prior to the onset of detumescence, which was visually distinctive. The vast majority of 'other' consort days involved consorts preceding the 'fertile' days, but during five conceptive cycles consorts were also formed 1–2 days following the onset of detumescence. Each male present in the group was assigned a 'fertile' consort score and an 'other' consort score that was calculated by dividing the total number of observation days in which the male consorted with the female by the total number of observation days in which the female consorted with any male during the same period of her cycle. For example, during one of female VD's conceptive cycles she formed consortships with a total of two males. Male SP consorted with her on four of her 'fertile' days, whereas male RY consorted with her on four of her 'other' days. Male SP therefore had a 'fertile' consort score of $4/4 = 1.0$, and male RY had an 'other' consort score of $4/4 = 1.0$. When a female consorted with multiple males on the same day, each male received an equal fraction of the consort score for that day. The resulting data set contained 101 records of males' consort scores during females' conceptive cycles, involving 15 different females and 12 different males.

For statistical analysis we used a general linear mixed model (GLMM) in which fertile consort score, other consort score and dominance rank (all z -transformed) were entered as predictor variables and paternity was entered as a categorical dependent variable. Because different males and females appeared with different frequencies in the overall data set, we entered male identity and female identity as random factors. We tested for collinearity among predictors using a program written by R. Mundry (personal communication) and the 'collin.fnc' program (Baayen 2008, page 181), both written for R statistical software (version 2.9.1). To begin analysis, we used a likelihood ratio test to compare a full model that included all predictors against a null model that included only the random effects (Crawley 2008, page 109). When this revealed that the predictors collectively had a significant effect, we used the 'lmer' command in R to compare all possible models that could be built out of the three predictor variables, and the 'anova' command in R to select the best model using Akaike Information Criterion (AIC) values (Crawley 2008, page 208).

Friendship behaviour

We identified friendships by association patterns recorded during daily 10 min focal observations of adult females (e.g. Palombit et al. 1997). All female group members were observed three to four times weekly throughout the study period, with the exception of the two breaks in observation mentioned previously, plus an additional period during January–February 2006, when observations did not occur as often. We tallied all tolerated approaches by lactating females to every male for the 2-month period following parturition. A tolerated approach occurred when a lactating female moved to within 2 m of an adult male without subsequently being displaced to more than 2 m away or receiving other agonistic behaviour from him. A male was considered a friend when a female's proportion of tolerated approaches to him was at least twice as large as her proportion of tolerated approaches to her next closest male associate. For 12 births (40%), females could not be monitored continuously for the 2 months immediately following parturition, because of breaks in behavioural observation ($N = 11$) or the death of an infant ($N = 1$). In six of these cases (including the infant death), data on association patterns were available for at least 1 month postparturition, and friendships were determined based on these data. For the remaining six cases, association patterns were calculated during the first continuous 2-month

Table 1

Sample sizes for each analysis, indicating the total number of conceptive cycles with complete data available for the variables of interest, and the number of females and males involved

Data set	No. of conceptive cycles	No. of females	No. of males
Complete consort activity	26	19	13
Paternity assignments	19	16	6
Postpartum associations	26	20	12
Consort activity and paternity	15	13	5
Paternity and postpartum associations	18	15	6
Consort activity and postpartum associations	22	19	11

Table 2
Attributes of adult males that were present for at least 2 months during the study period, ordered by descending dominance rank

Male	Status*	Dates present (month/year)	Cause of departure	Mean proportion of males dominated	No. of conceptive cycles present	No. of confirmed offspring	No. of lactational periods present	No. of friendships	Mean proportion of females' consort days monopolized	Mean proportion of females' tolerated approaches received
SP	I	6/2004–6/2005	Suspected death	1	12	7	3	1	0.51	0.03
BY	I	3/2006		0.99	11	4	21	4	0.27	0.26
HA	I	8/2005–4/2007	Suspected death	0.86	18	3	20	7	0.15	0.21
EF	I	3/2006		0.71	11	0	21	1	0.02	0.07
CS	I	9/2004–1/2005	Suspected death	0.67	7	0	0	0	0.09	N/A
NA	N	11/1995–10/2006	Immigration	0.62	24	0	19	4	0.12	0.25
FT	I	5/2004		0.54	24	1	29	2	0.04	0.05
DY	I	1/2006–8/2006	Suspected death	0.53	5	0	4	0	0.04	0.02
RY	I	3/1998		0.38	29	0	30	1	0.05	0.09
RL	I	7/2006		0.30	6	0	9	0	0	0
NK	N	11/1994–12/2004	Immigration	0.29	6	0	0	0	0.06	N/A
LO	I	4/2003		0.16	30	1	30	0	0.03	0.04
EL	I	5/2003		0.15	30	2	30	6	0.17	0.27

* Status refers to immigrant (I) versus natal (N).

period following parturition when behavioural observations occurred. This period began a median of 72.5 (range 32–170) days after parturition. Within a lactational period, female chacma baboons tend to maintain friendships with the same male (Palombit et al. 1997), although females may form new friendships in response to female competition (Palombit et al. 2001) or to the death of a former friend. In only two of the 18 births where complete data on association patterns were available for the first 6 months of lactation did females change their friendships, and in both cases this was due to the death or disappearance of their original friend.

To examine whether preferential associations observed between friends soon after birth were correlated with male investment in females and their dependent young, we measured patterns of male intervention on behalf of lactating females when they were recipients of aggressive acts from any other group members. An aggressive act occurred when one individual directed one or more of the following behaviours at an unambiguous target: threat-grunts, head bob and ground slaps, lunges, chases and/or bites. Interventions occurred when a third individual aided the recipient of an aggressive act by threatening the original antagonist. Between June 2006 and August 2007, we evaluated all interventions on behalf of 18 lactating females with infants, representing 60% of the conceptive cycles included in the study. We calculated the total number of interventions that each lactating female received from all adult males and measured the proportion of aid that she received from each male, considering only the time period when the male and female were both present.

To examine the relationship between previous mating activity and formation of friendships after an infant was born, we analysed data for all conceptive cycles where the infant survived to at least 2 months of age and the mother formed a friendship. We included in statistical analysis only males that were present in the group both at the time of conception and after the infant's birth. Several males present at the time of conception (some of them fathers) had died or disappeared by the time the infant was born; other males joined the group after conception but were present when the infant was born. These cases are discussed separately below. The resulting data set contained 114 records of females' proportion of tolerated approaches to males, for 18 different lactating females and 9 different males whose dominance rank, fertile consort score, other consort score, and friendship status were available.

For statistical analysis we followed the same procedure as that described for paternity but using friendship (1/0) as the dependent variable.

Genetic Data

Between July 2004 and July 2007, we obtained samples for genetic analyses from 19 of the 30 infants that were born during the study period and survived to at least 2 months of age. Six infants died before sufficient genetic samples could be collected, and five infants were born after the period of genetic sampling had ended. We also obtained corresponding samples for all 19 mothers and 25 potential fathers, including all adult and subadult males more than 7 years old that were present when the infant was conceived. In most cases, between three and four fresh faecal samples were collected for each individual. For two individuals, tissue samples were recovered after death. Samples were extracted at the Molecular Anthropology Laboratory, New York University, using the QIAamp DNA Stool Mini Kit (QIAGEN, Valencia, CA, U.S.A.) and the DNeasy Tissue Kit (QIAGEN), with slight modifications of the protocols (for further information refer to Moscovice et al. 2009).

Samples were genotyped using PCR at 9–10 human-derived MapPairs microsatellite marker loci found in initial screenings to amplify reliably and to be variable in this baboon population. PCR amplifications were performed using QIAGEN Multiplex PCR kits with between one and five loci run in a single PCR reaction. One primer of each pair contained a 5' fluorescent label to facilitate visualization. PCR products were separated via capillary electrophoresis on an ABI 3730 automated DNA analyser. GeneMapper 3.5 software was used to assign fragment size and to make preliminary allele calls, which were verified by A.D.

Maximum likelihood-based paternity was assigned using the software Cervus 3.0 (Marshall et al. 1998). Known mothers for all immature baboons were assigned maternity with greater than 95% confidence in likelihood-based analyses, and in no case did offspring mismatch from their putative mothers at any locus. For the final paternity assignment, Cervus paternity simulations were run assuming a pool of 20 candidate fathers for each offspring (which we presumed to represent 95% of total possible candidate fathers), 95.7% of all loci typed, and a conservative genotyping error rate of 0.05 (the estimated genotyping error rate was less

than 0.002). The confidence levels associated with paternity assignments were obtained by simulating parentage for 100 000 offspring based on allele frequencies derived from the study population.

Paternity was assigned with 95% confidence for all 19 infants from whom we obtained samples. For 18 individuals, paternity was unambiguous, since the male identified as the maximum-likelihood father also could not be excluded from paternity at any locus, while all other sampled males could be excluded at one locus or more. For one remaining infant (SB), the two most likely candidate fathers were both excluded at a single locus and all other males were excluded at multiple loci. The maximum-likelihood father, JL, was a subadult male when the infant was conceived, while the second most likely candidate father, HA, was the alpha when the infant was conceived and also formed a friendship with the infant's mother. We compared SB and both putative fathers at four additional loci, but were unable to resolve his paternity. As a result, we did not assign a father to SB and did not include him in any analyses requiring paternity data.

RESULTS

Predictors of Paternity

During each female's conceptive cycle, there was a mean \pm SE of 7.2 ± 1.5 adult males present, of which 2.3 ± 1.0 (or $34 \pm 13\%$) obtained some consort days with the female at any point during her cycle. In addition to the conceptive female, there were 1.5 ± 1.1 other females also forming consorts during the same time period. Across cycles, the number of males obtaining some consortships increased as the number of simultaneously consorting females increased (Spearman rank correlation: $r_s = 0.419$, $N = 25$, $P = 0.037$).

The alpha male monopolized the greatest proportion of total consort days in 56% of conceptive cycles. In the remaining cycles, a lower-ranking male (mean rank = 3.2 ± 1.2) either tied with or exceeded the alpha male in monopolization of consort days. Over the course of the study, 10 of the 13 male subjects obtained the highest proportion of a female's total consort days during at least one of the conceptive cycles for which they were present. Most fathers (67%) had consorted with the female both within and outside of her fertile period. Four fathers (27%) consorted only during the fertile period, and one father consorted only outside of the fertile period. In 87% of the cycles with known paternity, the male that monopolized (or tied for) the greatest proportion of a female's total consort days was also the father of her offspring, whether he was the alpha male ($N = 10$) or a lower-ranking male ($N = 3$). In the remaining two cases, the father was an alpha male that monopolized the greatest proportion of the female's fertile consort days, despite receiving a lower proportion of overall consort days compared with other males.

The three predictor variables in the paternity analysis (male dominance rank, fertile consort score, and other consort score) were highly correlated with each other. The strongest correlation (Spearman rank correlation: $r_s = 0.531$, $N = 101$, $P < 0.01$) was between dominance rank and fertile consort score, indicating that high-ranking males were disproportionately responsible for consorts during females' fertile periods. High-ranking males were also disproportionately responsible for consorts outside fertile periods ($r_s = 0.268$, $P < 0.01$), with the result that consort scores during the fertile and other periods were also correlated ($r_s = 0.498$, $P < 0.01$). However, the effect of dominance rank was less pronounced outside fertile periods than during fertile periods. Outside fertile periods, lower-ranking males gained relatively greater access to females. Two tests for collinearity, one using

a program written by R. Mundry (variance inflation factors all < 2.5) and another using the program 'collin.fnc' in R (Baayen 2008, page 181, condition numbers all < 4), revealed no important collinearity and suggested that each predictor variable accounted for its own unique portion of the variance.

The GLMM in which fertile consort score, other consort score and dominance rank were entered as predictors of paternity was significantly more effective than the null model that included only random effects ($\chi^2_3 = 37.37$, $P < 0.001$). When all possible models that could be built with the three predictors were compared against each other, the best model (that is, the model with the lowest AIC), was one in which all three predictors were entered separately and there were no interaction terms (Table 3).

Characterizing Friendships

During the 2 months following parturition, each female had the opportunity to interact with 5.7 ± 1.2 males that were present during her last conceptive cycle. These males represented $82 \pm 12\%$ of the total males present when the female conceived. The remaining males had either died or emigrated before the female gave birth. In addition, 77% of new mothers ($N = 20$) also co-resided with 1.8 ± 1.7 recently immigrated males that had not been present at conception.

Friendships were identified for 96% ($N = 25$) of births. One female had a similarly high proportion of tolerated approaches to two males, both of whom were identified as friends. Only one female did not show preferential associations with any male. Every male friend had been present during the female's last conceptive cycle and was thus a potential father.

Approaches to male friends accounted for $78 \pm 19\%$ of a female's total tolerated approaches to any male during the first 2 months of lactation. In contrast, females' tolerated approaches to the next closest male affiliate that had also been present at the time of conception accounted for only $12 \pm 8\%$ of their total approaches to males (Wilcoxon signed-ranks test: $T_+ = 325$, 0 ties, $N = 25$, $P < 0.001$; Fig. 1). Females that co-resided with recent immigrants approached these males less often than they did nonfriend males that had been present at conception ($12 \pm 8\%$ versus $1 \pm 1\%$; Wilcoxon signed-ranks test: $T_+ = 165$, 2 ties, $N = 20$, $P < 0.001$; Fig. 1).

Males accounted for 73% of the 139 observed interventions on behalf of lactating females, and 82% of males' interventions were made on behalf of their female friends. Males provided a significantly greater proportion of support to their lactating female friends than to other lactating females ($72 \pm 37\%$ versus $3 \pm 3\%$; $T_+ = 27$, 0 ties, $N = 7$, $P = 0.028$; Fig. 2).

Predictors of Friendships

For five (26%) of the 18 births where paternity was confirmed, the father was an alpha male that disappeared from the group before his offspring were born and was presumed to have died. For nine (69%) of the remaining 13 births where fathers were present

Table 3

Comparison of general linear mixed models describing the relationships among measures of consort activity and paternity

Best model	AIC	χ^2	df	$P(\chi^2)$
Dom + fertile consort score + other consort score	35.53	4.619	1	0.032*
Fixed effects	Estimate	SE	z	$P(z)$
Dominance	2.337	1.402	1.667	0.095
Fertile consort score	1.455	0.776	1.876	0.061
Other consort score	1.437	0.773	1.859	0.063

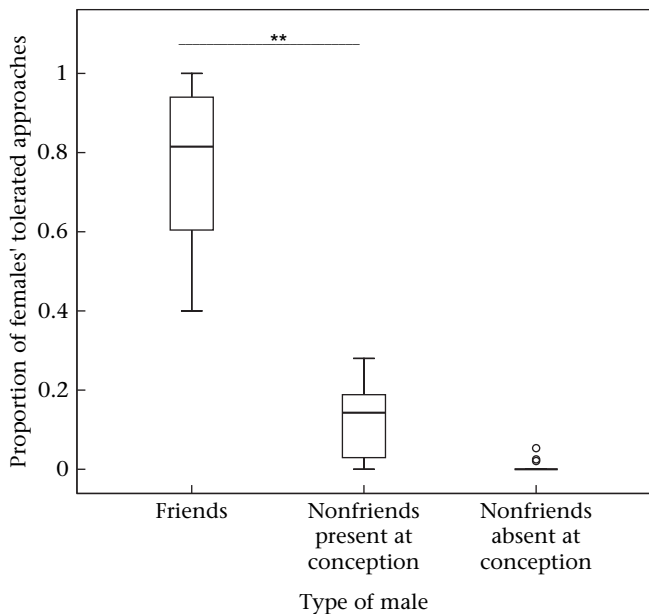


Figure 1. Proportion of a lactating female's tolerated approaches to male friends, and to male nonfriends that were present or absent when the female conceived (for $N = 20$ females that co-resided with recently immigrated males). Box plots indicate median values and second and third quartiles. Error bars represent minimum and maximum values. Circles above or below the box plots represent outliers. * $P \leq 0.05$; ** $P \leq 0.01$.

postpartum, females formed friendships with the father of their offspring. For three births (23%), females formed a friendship with a different male, and for one birth (6%), the female did not form an association with any male.

For five (23%) of the 22 births where data on consort activity and subsequent friendships were available, the father was absent. For ten births (45%), the father was present, although for only seven of these births did he form a friendship with the mother of his offspring. For an additional seven births (32%) paternity was unknown. Of the 21 observed friendships, 14 (67%) were formed

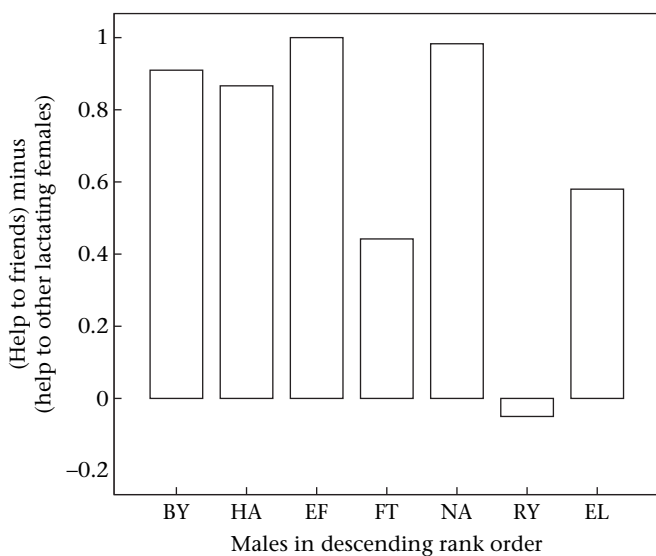


Figure 2. Difference between each male's proportion of interventions on behalf of lactating female friends and on behalf of lactating nonfriends (Wilcoxon signed-ranks test; $P < 0.05$). Bars above zero indicate males that helped their female friends more often than they helped other lactating females.

with the male that had monopolized (or tied for) the greatest proportion of the female's consort days. In an additional four friendships (19%), the male obtained the second greatest proportion of the female's consort days. In two of these cases the male that had monopolized the female's consort activity was still present, while in the other two cases he was absent. Only three females formed a friendship with a male that had obtained few or no consorts during her conceptive cycle (although it remains possible that these males had mated with their female friends during observer absence). In two of these cases, the male that had monopolized the female's consort activity was no longer present in the group.

Importantly, when a male that had monopolized (or tied for) the greatest proportion of a female's overall consort days (a primary consort partner) was present at parturition ($N = 17$), he almost always became her friend ($N = 14$; 82%; Fig. 3). When the primary consort partner had disappeared from the group before parturition ($N = 4$), in one case none of the remaining males had consorted with the female during her conceptive cycle. In the other three cases, females formed a friendship with the male that had obtained either the second ($N = 2$) or the third ($N = 1$) highest proportion of her total consort days (Fig. 3). When only the consort scores of those males that were still present in the group at parturition were included in the analysis, 16 (73%) friendships were formed with the female's primary consort partner (binomial test: $q = r = 0.5$, $N = 22$, $P = 0.052$).

Eleven of the 13 males in this study were present during both the conceptive cycles and lactational periods of some females. Two of these males (RL and DY) were recent immigrants that obtained few consorts, were rarely approached by females and did not form any friendships. Of the remaining nine males, seven (78%) became friends with the female with whom they had monopolized their highest proportion of consort days across all of the conceptive cycles for which they were present. This included one birth where

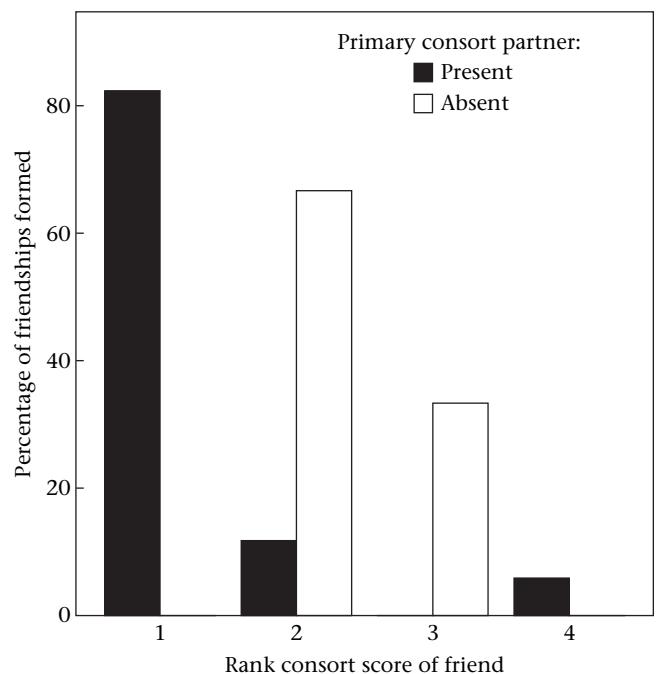


Figure 3. Proportion of friendships formed with males in relation to their previous consort activity. When a female's primary consort partner (the male that monopolized, or tied for, the greatest proportion of a female's consort days) was present at parturition ($N = 17$), in most cases ($N = 14$) he became her friend. When a female's primary consort partner was absent at parturition ($N = 3$), she became friends with the male that received the second ($N = 2$) or third ($N = 1$) highest proportion of her consort days.

another male had monopolized a higher proportion of total consorts and was the true father.

There was a correlation between a male's average proportion of consort days and the average proportion of tolerated approaches that he received from lactating females (Spearman rank correlation: $r_s = 0.630$, $N = 11$, $P = 0.038$, including only situations where the male was present during both periods). There were 10 males present during conceptive cycles and lactational periods between June 2006 and August 2007, when data on postpartum interventions were also available. The average proportion of interventions by these males on behalf of lactating females was strongly correlated with their average proportion of consort days (Spearman rank correlation: $r_s = 0.880$, $N = 10$, $P = 0.001$; Fig. 4) and their average proportion of tolerated approaches received ($r_s = 0.942$, $N = 10$, $P < 0.001$). Thus, males' investment in lactating females and their infants reflected their previous consort activity with those females.

As in the analysis of paternity, the analysis of the factors predicting friendship revealed that the three predictor variables (dominance rank during the postparturition period, fertile consort score and other consort score) were correlated with each other. High-ranking males accounted for a significant proportion of consorts during a female's fertile period ($r_s = 0.341$, $N = 114$, $P < 0.01$). Outside the fertile period, the correlation between dominance rank and mating score was not significant ($r_s = 0.143$), indicating that lower-ranking males had gained relatively greater access to females during this time. Mating scores during the fertile and other periods, however, remained highly correlated ($r_s = 0.527$, $P < 0.01$). Two tests (see above) revealed no important collinearity (Mundry program, variance inflation factors all < 2 , collin.fnc condition numbers all < 3), suggesting that each predictor variable accounted for its own unique portion of the variance.

The GLMM in which fertile consort score, other consort score and dominance rank were entered as predictors of friendship was significantly more effective than the null model that included only random effects ($\chi^2_3 = 43.31$, $P < 0.001$). When all possible models that could be built with the three predictors were compared against each other, the best model was one in which all three predictors

were entered separately, together with an interaction between dominance rank and fertile consort score (Table 4).

DISCUSSION

Infanticide is the leading cause of infant mortality in chacma baboons at this study site (Cheney et al. 2004), and protection from male friends probably increases infant survival (Palombit et al. 1997, 2000). During our study, all but one lactating female formed a close association with either one or two adult males shortly after parturition. These males assisted their lactating female friends (and their infants) when they were the recipients of agonistic attacks significantly more often than they assisted other lactating females. Moreover, males continued to invest in the juvenile offspring of their former friends long after the friendship had ended (Moscovice et al. 2009).

Male–female friendships in chacma baboons are formed within the context of a dynamic and often fluctuating social environment punctuated by the immigration and disappearances of males. Such changes in male demography can have broad implications for cohorts of lactating females and their offspring. For example, as a result of the disappearance of one alpha male, five of the offspring in this study (representing 28% of the offspring of known paternity) were born without their father present. Such fluctuations in male demography are characteristic of all chacma baboon study sites. As a result of stochastic events at a study site in South Africa, for example, 28% of infants did not have their putative fathers present at birth, and by 7 months postpartum, 47% of infants did not have their putative fathers present (Clarke et al. 2009).

Several previous studies have suggested that friendships in chacma baboons may reflect paternal care, although paternity has seldom been confirmed with genetic analyses (Busse & Hamilton 1981; Palombit et al. 1997, 2000; Weingrill 2000; but see Nguyen et al. 2009). Our study combines paternity analyses with detailed observations of consort activity across conceptive cycles to further suggest that friendships are flexible and may be based on a probabilistic assessment of paternity.

Females were most likely to form friendships with the male that had monopolized the greatest proportion of their total consort days. Importantly, this preference by females and acceptance by males appeared to be relative rather than absolute. If one of the female's top-ranked consort partners had disappeared from the group, the female usually formed a friendship with her next highest-ranking consort partner, even when that male was not her infant's father. Similarly, the majority of males formed friendships with females with whom they had achieved their greatest consort success, even in one case when another male had monopolized a higher proportion of the females' total consort days. Males appeared to base their decisions about friendships on memory of their own mating success, rather than on the absolute mating success of others. There was a remarkable concordance between

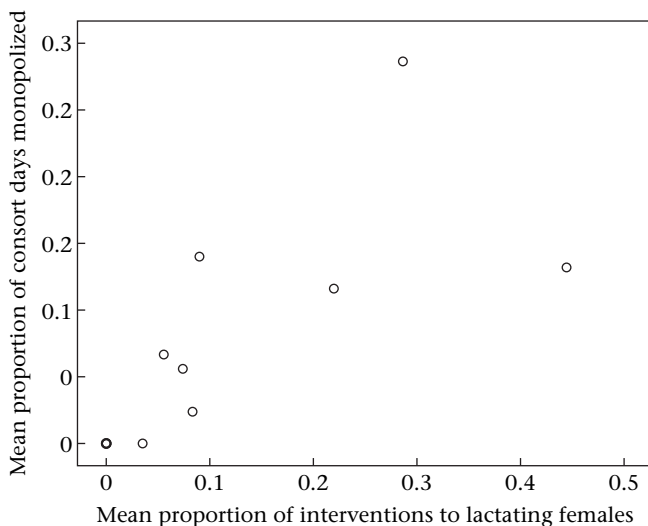


Figure 4. Relationship between a male's average consort score and his average proportion of interventions on behalf of lactating females, considering only the births where the male was present during a female's conceptive cycle and for at least 2 months postparturition. The bold circle indicates $N = 2$ males with identical values for consorts and interventions.

Table 4
Comparison of general linear mixed models describing the relationships among measures of consort activity and friendship

Best model	AIC	χ^2	df	$P(\chi^2)$
Dom + fertile consort score + other consort score + dom × fertile consort score	67.22	5.161	1	0.023*
Fixed effects	Estimate	SE	z	$P(z)$
Dominance	0.566	0.560	1.010	0.312
Fertile consort score	3.076	0.894	3.440	0.0005**
Other consort score	0.926	0.348	2.662	0.008**
Dom × fertile consort score	−1.358	0.636	−2.133	0.033*

the factors that best predicted paternity (dominance rank, consorts during the fertile and other periods; see Table 3) and the factors that best predicted the formation of a friendship (Table 4). This is just what one would expect if natural selection had favoured males and females that form friendships based on their memory of those behaviours most closely correlated with paternity.

In almost all cases where paternity was confirmed, the male that monopolized the greatest proportion of a female's total consort days during her last conceptive cycle was also the father of her offspring. The two exceptions both involved alpha males that monopolized the females' fertile period but not her total consort days. These exceptions are consistent with broader evidence that alpha males' decisions about consortships are less constrained by male–male competition and may be more influenced by assessments of fertility (Gesquiere et al. 2007).

Our results indicate that males of all ranks formed consortships with females, mainly prior to but also after the period of peak swelling. Dominant males monopolized consort activity within the fertile period, but rank was a weaker determinant of consort success outside of the fertile period. In comparison with other subspecies, chacma baboons show relatively high levels of mating competition and rank-based priority of access to females (Bulger 1993; Weingrill et al. 2000, 2003). Despite this, in 64% of the conceptive cycles where complete consort activity was available, more than one male obtained consorts with a female during her time of most likely conception (or 'fertile' consort days).

Although the majority of male friends had obtained at least some consorts during the female's time of most likely conception, only 50% of friendships reflected actual paternity. This figure is similar to that obtained in a recent study of yellow baboons (*P. h. cynocephalus*; Nguyen et al. 2009), although in that study none of the nonfathers had consorted with their female friend during that female's 5-day period of most likely conception. Because the authors only evaluated females' consort activity during this brief period of most likely conception, it remains possible that some of these nonfather friends had obtained consorts outside of this period, and that they used memory of this mating activity as a guide in forming friendships. Indeed, in our study 19% of friendships involved males that had monopolized 'other' consorts outside of the fertile period, despite obtaining few or no consorts within the fertile period.

These friendships offer some interesting insights into ways that females' mating strategies may influence both perceived and actual paternity. If males make decisions about postconception investment that reflect their overall consort activity across a female's conceptive cycle, they may be willing to invest in offspring even in cases when they consorted very little or not at all during the female's brief period of most likely conception. While these males may have a low absolute probability of paternity, their probability of paternity relative to other males, or to previous conceptive cycles, may still be high, and because of variation in the timing of ovulation relative to detumescence (van Schaik & Paul 1996; Gesquiere et al. 2007), this strategy may sometimes result in low-ranking males investing in friendships that reflect true paternity. Indeed, in our study, one friendship involved a fourth-ranked male (EL) who was only observed to consort with his friend outside of her fertile period, but was nevertheless the father of his friend's offspring.

A recent study of chacma baboons in South Africa has suggested that females may actively attempt to distribute their mating behaviour among multiple males to increase the number of males willing to protect an infant from infanticidal attack (Clarke et al. 2009). However, the combined impact of rank-based priority of access to females and mate guarding may effectively limit a female's potential partners to only a subset of the males present.

Consistent with this idea, in our study most females consorted with two to three males during each conceptive cycle, representing only 34% of all adult males present. By distributing consort activity across a subset of the males present, this may help to ensure that at least one other male is willing to form a friendship with a female if her primary consort partner disappears, without increasing overall levels of paternity confusion to the point that no male is willing to invest in infant care.

In chacma baboons, biological fathers may not be present throughout their offsprings' vulnerable period because of stochastic events (Clarke et al. 2009; Moscovice et al. 2009). Furthermore, since the average tenure length for alpha males is shorter than typical lactational periods (Palombit et al. 2000), even fathers that are still present may have limited ability to defend their offspring if they have fallen in rank to a recent immigrant. For these reasons, successful male reproductive strategies may involve a trade-off between increasing paternity certainty and conceding some probability of paternity to other males, to reduce the risk of infanticide (Boyko & Marshall 2009) and to increase chances that other nongenetic, likely fathers may be willing to assist the true father in defending his infant from potentially infanticidal attacks (Clarke et al. 2009). There is evidence for such coordinated defence of infants from potentially infanticidal attacks at this study site (Palombit 2000).

Our results can help to explain why adult male chacma baboons form friendships and show forms of infant caretaking despite their promiscuous mating system and lack of evidence for a deterministic mechanism, such as phenotype matching, to identify offspring. Both males and females appear to use behavioural cues about previous consort activity to form friendships that reflect a relatively high likelihood of paternity. From the female's perspective, this may mean forming a friendship with the male that monopolized a greater proportion of her previous consort days than the other males also present when her infant is born. From the male's perspective, this may mean becoming friends with females when they had achieved their personal greatest consort success. Males' and females' sensitivity to their relative amount of consort activity with other individuals should usually result in friendships involving biological fathers if biological fathers are still present in the group when infants are born. When fathers are absent, it should result in friendships involving males that have a greater than average probability of being the biological father and that are therefore willing to invest in infants. This behavioural flexibility may be highly adaptive both for females faced with unpredictable fluctuations in male presence and for males faced with high levels of mating competition (Bulger 1993). Within the context of friendships, male chacma baboons appear willing to invest in probable, although not always actual, offspring.

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