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Male–female relationships in olive baboons (*Papio anubis*): Parenting or mating effort?

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ABSTRACT

Long-term male–female bonds and bi-parental investment in offspring are hallmarks of human society. A key question is how these traits evolved from the polygynandrously mating multimale multifemale society that likely characterized the *Pan-Homo* ancestor. In all three species of savanna baboons, lactating females form strong ties (sometimes called “friendships”) with one or more adult males. For yellow baboons (*Papio cynocephalus*) and chacma baboons (*Papio ursinus*), several lines of evidence suggest that these relationships are a form of male parenting effort. In olive baboons (*Papio anubis*), females are thought to preferentially mate with their “friends”, and male-female bonds may thus function as a form of mating effort. Here, we draw on behavioral and genetic data to evaluate the factors that shape male-female relationships in a well-studied population of olive baboons. We find support for the parenting effort hypothesis in that sires have stronger bonds with their infants' mothers than do other males. These bonds sometimes persist past weaning age and, in many cases, the sire of the previous infant is still a close partner of the female when she nurses her subsequent offspring. We find that males who have the strongest bonds with females that have resumed cycling, but are not currently sexually receptive, are more likely to sire the female's next offspring but the estimate is associated with large statistical uncertainty. We also find that in over one third of the cases, a female's successive infants were sired by the same male. Thus, in olive baboons, the development of stable breeding bonds and paternal investment seem to be grounded in the formation of close ties between males and anestrous females. However, other factors such as male dominance rank also influence paternity success and may preclude stability of these bonds to the extent found in human societies.

1. Introduction

Modern humans form long-term pair bonds and both males and females invest heavily in the welfare of their offspring. In most other mammals, enduring pair bonds and male investment in offspring are limited to species that are pair-living or live in small family groups (Lukas and Clutton-Brock, 2013). In these species, selection is thought to favor greater male investment in parenting effort because males have limited alternative mating opportunities and relatively high paternity certainty. Many primates live in multimale multifemale groups in which alternative mating opportunities are more abundant and paternity certainty is likely lower (Shultz et al., 2011). In these species, males typically mate with multiple females and sexually receptive females may mate with more than one male. There is often considerable male reproductive skew and limited paternal investment (Kutsukake and Nunn, 2006). Thus, a key

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question is how stable pair bonds and paternal investment might have evolved in descendants of the *Pan-Homo* ancestor which likely lived in multimale multifemale groups like chimpanzees (*Pan troglodytes* ssp.) and had a polygynandrous mating system (Lovejoy, 2009; Chapais, 2013).

There is growing evidence that stable breeding bonds can evolve in species that form multimale multifemale groups and have polygynandrous mating systems. For the multilevel societies of geladas (*Theropithecus gelada*), Guinea (*Papio papio*) and hamadryas baboons (*Papio hamadryas*), in which stable breeding bonds are embedded in multimale multifemale groups, parsimony suggests the evolution from an ancestral polygynandrously mating multimale multi-female social system (Grueter et al., 2012; Fischer et al., 2017). In the large Ngogo chimpanzee community, females selectively associate with particular males over extended periods, and association patterns and dominance rank both predict paternity (Langergraber et al., 2013). In the Amboseli yellow baboon (*Papio cynocephalus*) population, there are a number of cases in which the same male sired multiple offspring of the same female; some females produced up to four infants with the same sire. As a result, 21% of the infants of known paternity have at least one full sibling in the group (Alberts et al., 2006).

In several macaque and baboon species, males form strong ties with certain lactating females (e.g. olive baboons [*Papio anubis*: Ransom and Ransom, 1971; Strum, 1984]; chacma baboons [*Papio ursinus*: Seyfarth, 1978]; yellow baboons [Altmann, 1980]; Japanese macaques [*Macaca fuscata*: Takahata, 1982]; rhesus macaques [*Macaca mulatta*: Hill, 1990]; Assamese macaques [*Macaca assamensis*: Ostner et al., 2013]). These relationships, which are sometimes called “friendships” (Smuts, 1985) or “special relationships” (Ransom and Ransom, 1971; Strum, 1975), are characterized by high levels of proximity, grooming, and support, and low rates of aggression (Takahata, 1982; Smuts, 1985; Manson, 1994; Lemasson et al., 2008; Haunhorst et al., 2016, 2017). Two main hypotheses have been suggested to explain the existence of these relationships. First, male–female bonds may represent a form of male parenting effort enhancing the survival of offspring. Evidence for the parenting effort hypothesis has been found in a number of species. Males selectively associate and interact with their own offspring in chimpanzees, Assamese and rhesus macaques, but not in Barbary macaques (*Macaca sylvanus*) and crested macaques (*Macaca nigra*) (Ménard et al., 2001; Alberts et al., 2006; Lehmann et al., 2006; Langos et al., 2013; Ostner et al., 2013; Kerhoas et al., 2016; Murray et al., 2016). In yellow and chacma baboons, the parenting effort hypothesis is supported by evidence that a large proportion of male partners are the sires of the females' infants (chacma baboons: Palombit et al., 1997; Huchard et al., 2010; Moscovice et al., 2010; Baniel et al., 2016; yellow baboons: Nguyen et al., 2009). Yellow baboon males are significantly more likely to support their own offspring than other males' offspring (Buchan et al., 2003). Infant chacma baboons spend more time in proximity to their own fathers than to other males, and juveniles are more likely to gain access to high quality food resources when their fathers are present in food patches (Huchard et al., 2013). In chacma baboons, a species in which infanticide is an important source of infant mortality (Palombit, 2003), playback studies show that males are alert to the distress of their female partners, but their responsiveness drops if the infant dies or disappears from the group (Palombit et al., 1997). In species in which infanticide is rare, males may protect both mothers and infants from predation or nonlethal harassment by conspecifics (Ransom and Ransom, 1971; Altmann, 1980; Nguyen et al., 2009; Haunhorst et al., 2017). The hypothesis relies on the assumption that males can reliably discriminate between their own offspring and those of other males, and selectively direct care toward their own offspring.

The second hypothesis proposes that close ties between males and females represent a form of male mating effort. According to this hypothesis, males form a relationship with the lactating female that persists into the fertile phase and increases the males' chance of siring the female's next offspring (Seyfarth, 1978; Smuts, 1985). The hypothesis is sometimes also referred to as ‘care-then-mate’ (Ménard et al., 2001) and assumes that females prefer to mate with males that behave benevolently towards them and their current offspring. It also assumes that females can exercise effective mate choice. Support for the mating effort hypothesis comes from a study of Barbary macaques in which male caretakers of infants had higher mating frequencies with the infants' mothers than did other males (Ménard et al., 2001). In contrast, male–female relationships outside the mating season or male caretaking of infants did not predict the probability of siring the female's next infant in four other studies of macaques (Takahata, 1982; Manson, 1994; Paul et al., 1996; Ostner et al., 2013). Similarly, two studies in baboons found that ties to lactating females did not predict male consort success during the female's next cycling period (yellow baboons: Nguyen et al., 2009; chacma baboons: Baniel et al., 2016).

There are several reasons to suspect that the function of male–female bonds in olive baboons may be somewhat different than in chacma and yellow baboons. Male dominance hierarchies are not as well defined in olive baboons and studies of male mating activity suggest that the extent of male reproductive skew may be lower as well (Strum, 1982; Bercovitch, 1986). Olive baboon males also have substantially larger testes in relation to body size than yellow baboons (Jolly and Phillips-Conroy, 2006), which suggests that reproductive skew is less dependent on male dominance rank. If this is the case, female mate preferences may have a greater impact on male mating success in olive baboons. This may in turn favor males who behave benevolently toward females and their offspring as originally suggested (Strum, 1982; Smuts, 1985).

Here, we examine predictions derived from the parenting effort hypothesis and the mating effort hypothesis in a population of wild olive baboons in central Kenya. We draw on behavioral data to characterize the strength of male–female relationships and genetic data to assess paternity and the stability of breeding bonds. If bonds between males and females are a form of parenting effort, we predict the relationship between sires and mothers to be stronger than between mothers and other males. If parenting mainly serves to protect infants from infanticide and harassment, we also predict that these relationships will become weaker as infants become older, because older infants are expected to be less vulnerable to these threats. We therefore also investigate the strength of the relationship between females and the sires of their infants after lactation ends, when the females have resumed cycling, but exhibit no sexual swelling.

If males indeed selectively associate with their offspring's mother, how do they recognize their offspring? Paternal kin recognition may be based on phenotype matching (Holmes and Sherman, 1983) or behavioral proxies that are reliably associated with paternity (Buchan et al., 2003) such as the relationship with the female during the time of conception. If males use phenotype matching to recognize their offspring, their bond with the mother should arise only once the infant is born. We therefore investigate the strength of the mother-male relationship during pregnancy when phenotype matching is unlikely. Alternatively, males or females may use their mating history or more generally the strength of their relationship around the time of conception to gauge their probability of paternity (Moscovice et al., 2010). If this is the case, the strength of the male–female ties during the conceptive cycle, when the female exhibits a full sexual swelling, will be a reliable predictor of paternity. If bonds are a form of mating effort, we predict that a strong relationship with a lactating female increases a male's probability of becoming the sire of her next offspring. The two hypotheses are not mutually exclusive and if both apply, they might lead to the emergence of long-term bonds. Taken together, these analyses provide insight into the selective factors favoring extended male–female ties in baboons, and by extension provide insight about the evolutionary forces that may have facilitated the initial development of stable pair bonds in ancestral hominins.

2. Methods

2.1. *Ethical statement*

The study conformed to U.S. and Kenyan laws and was approved by the National Commission for Science and Technology of Kenya and the Kenya Wildlife Service. The project was approved by the Arizona State University Institutional Care and Use Committee. All animal protocols followed the guidelines for the treatment of animals for teaching and research recommended by ASAB/ABS (2014).

2.2. *Study population*

We studied wild olive baboons (*Papio anubis*) ranging on the Laikipia Plateau of central Kenya in the Mukogodo region of Laikipia North. Five groups (ENK, NGE, NMU, PHG and YNT) are habituated to human presence and have been monitored by the Uaso Ngiro Baboon Project (UNBP), directed by S.C. Strum, since 1972. We determined paternity for the infants in this study genetically as part of a larger assessment of paternity in this population, and the genetic analysis of paternity is therefore based on samples from all five groups monitored by the UNBP. We analyzed behavioral data collected on members of only two of the five groups, PHG and ENK. Therefore, all subsequent analyses, with the exception of the assessment of the “Stability of breeding relationships”, are based on only these two groups. ENK fissioned from PHG in 2010. During the period of behavioral data collection (November 2013–September 2016), ENK consisted of 26–54 individuals among which 13–22 were adults and subadults and PHG consisted of 45–59 individuals among which 21–28 were adults and subadults. For more details about the study site and the study population, see Strum (2005, 2012) and Silk et al. (2017).

2.3. *Genotyping*

We collected faecal samples in RNAlater® (Ambion). We extracted DNA using the GeneMATRIX Stool DNA Purification Kit (Roboklon) according to manufacturer's instructions. We then genotyped DNA extracts at 14 microsatellite loci. All microsatellite loci had been used previously for genotyping of the closely related hamadryas baboon (*Papio hamadryas*) (Städele et al., 2015). We genotyped all available extracts for each individual at four test-loci (Supplementary Online Material [SOM], Table S1) to control for possible misidentifications of individuals or misassignment of faecal samples in the field. We controlled for allelic drop-out and used CERVUS 3.0.3. (Kalinowski et al., 2007) and Micro-Checker 2.2.3. (Van Oosterhout et al., 2004), to test for deviance from Hardy–Weinberg equilibrium, occurrence of null alleles, large allele drop-out and scoring error due to stutter. Additional details on genotyping and genotype quality control can be found in the SOM.

2.4. *Genetic analysis of paternity*

We wanted to assess paternity for 137 individuals born between January 2011 and May 2016 in all five groups monitored by UNBP. We determined paternity genetically by conducting parentage analysis in CERVUS 3.0.3 (Kalinowski et al., 2007). Birth dates were precisely known or could be closely estimated. For the simulations determining the likelihood odds-ratio threshold, we divided the analysis into two periods, January 2011–December 2013 (78 offspring) and January 2014–May 2016 (59 offspring). The program CERVUS assigns parentage from a pool of candidate parents based on microsatellite genotypes. Males were included as candidate sires if they were at least 5 years old and present during the conceptive cycle. This age threshold was based on the earliest age males were observed consorting with females. Males with unknown birthdates were included as potential sires if they were larger than adult females and showed first signs of the development of secondary sexual characteristics. Analyses were performed jointly for all groups as males may change troop membership or visit other troops for short periods. We ran simulations to determine the critical LOD-thresholds for 90% and 95% confidence in assignments, respectively. As parameters for the simulation we used the known number of candidate parents, the observed proportion of candidate parents sampled, the observed proportion of loci typed and assumed a genotyping error of 0.01. In period 1, genotypes were available for 28 (41%) candidate sires and 61 (78%) mothers. In period 2, genotypes were available for 49 (56%) candidate sires and 59 (100%) candidate mothers.

2.5. *Behavioral data collection*

We conducted 15-min focal observations on all adult females in PHG and ENK between November 2013 and September 2016. During focal sampling, observers continuously recorded all of the focal female's social interactions. Observers recorded the type of social behavior, the identity of the partner, and whether the interaction was initiated by the focal female, the partner, or jointly. On average, every female was the focal of an observation once every four days. All data were collected on hand-held computers in the field and transferred onto computers for error-checking and storage. Aggressive interactions and supplants were also recorded ad libitum by observers.

Analyses are based on behavioral data collected on 23 adult females (eight in ENK, ten in PHG and five who moved from PHG to ENK) who produced a total of 56 offspring (32 in PHG, 24 in ENK). For two additional adult females in PHG, the sire of their offspring was unknown. We analyzed the rate of interactions between females and 11 subadult males (two in ENK, nine in PHG), six adult males (two in ENK, three in PHG and one who changed group membership) and five males who became adults during the study period (one in ENK and four who changed group membership). Males are categorized as subadults when they have grown larger than adult females and have begun to show the first signs of development of secondary sexual characteristics (≈5–6 years of age). Males are considered to be adults when growth has stopped and secondary sexual characteristics are fully developed (≈10 years of age). It is important to note that males can consort with females, sire infants, and reach alpha male status before they are considered adults morphologically (this study, data not shown).

2.6. *Characterizing female–male relationships*

To characterize the strength of the male–female relationships, we tabulated the rates of approaches (to within 1 m), grooming, grunts of males towards females, and the proportion of time spent within 1 m for each male-female dyad. The rates of these behavioral measures were positively correlated, so we calculated the dyadic sociality index (DSI; Silk et al., 2013). The DSI is a normalized composite of multiple correlated variables. To avoid biases towards the most common behaviors, the values for each behavior and dyad are divided by the mean value of the behavior in the group. The resulting values are then summed and divided by the number of behaviors. We provide averages for the rates of each behavior in each reproductive state in the SOM (Table S2). The index can assume values from zero to infinity, with an average value of 1. We calculated the DSI for each female-male dyad separately for four female reproductive states: 1) during pregnancy, 2) during lactation, 3) after the resumption of cycling when the female had no sexual swelling (referred to as cycling/flat, hereafter) and 4) during the conceptive cycle when the female exhibited a full sexual swelling. The date of conception was estimated by subtracting mean gestation time (178 days; Gesquiere et al., 2018) from the birthdate. The date of conception was used to estimate the beginning of pregnancy and to identify the estrous period in which females conceived. We defined lactation as the period from birth until the resumption of cycling or until the death of the infant if the infant died before the female resumed cycling. During the study period, females resumed cycling after 6.3 ± 1.7 months on average and were cycling for 3.8 ± 2.3 months until their next conception. Analyses are based on a total of 1014 h of observation (12.3 ± 3.7 h per female during pregnancy; 12.9 ± 4.6 h per female during lactation; 3.6 ± 4.7 h per female while the female was cycling and exhibited no sexual swelling; 1.3 ± 0.5 h per female during the conceptive cycle when the female exhibited a full sexual swelling). Because several males and five females moved from one group to the other during the study period, we restricted the analysis to male-female dyads that were in the same group for the whole time the female was in a particular reproductive state.

2.7. Determining male dominance rank

We assessed male dominance rank in PHG and ENK from the outcome of supplants and aggressive interactions (threats, chases, attacks, submission) using the likelihood-based Elo-rating method developed by Foerster et al. (2016). This modeling approach implements maximum likelihood fitting of individuals' initial Elo-scores when entering the hierarchy. It also implements maximum likelihood fitting of the constant k which, multiplied by the winning probability of the loser prior to the interaction, determines the increase in Elo-score for the winner and the corresponding decrease in Elo-score for the loser following the interaction. Nearly 30% of all aggressive interactions involved males who resided in different troops at the time of the interaction. Interactions between males of different groups often occurred when a male ‘visited’ the other group for a period of hours or days, or when the two groups ranged close together. In addition, some of these intergroup interactions involved males who were in the process of moving from one group to another. Because of this fluid movement of males between groups, which is a likely consequence of the common history of the two groups, group residence was assessed monthly, and males were assigned to the group in which they spent more than 15 days. We excluded five males with fewer than ten interactions from the analyses. The final dataset consisted of 2343 interactions among 23 males with 204 ± 143 interactions per male (range: 17–419). The value of k was 21 and prediction accuracy was 74%. Elo scores are only updated on days on which individuals interacted. We inferred Elo-scores on days with no interactions by linear interpolation between days with known Elo-scores. For each day, we then standardized rank within groups to be between 1 (highest rank) and 0 (lowest rank), so the alpha male in each group has rank 1. This retains the cardinal information about rank differences among males provided by the Elo-scores.

2.8. Statistical analyses

We modeled the effects of paternity and male rank on the DSI of male–female dyads when the female was pregnant, lactating or cycling/flat. We constructed zero-augmented gamma (ZAG) generalized linear mixed-effects models (GLMMs). These are mixture models of a Bernoulli distribution which estimates the probability of the DSI being 0, and a gamma distribution estimating the magnitude of the DSI conditional upon DSI > 0. Distributional assumptions that match the scale on which the outcome variable is measured are imposed by ZAGs. The outcome variable (DSI) is then estimated by mixing the Bernoulli and gamma components of the model. Zero-augmented gamma models are appropriate for modeling DSIs, which are heavily skewed towards (and may include) zero.

In ZAG models, negative coefficients from the Bernoulli component suggest a decreased probability of observing a DSI of zero. Positive values for the gamma component indicate higher, on average, DSI values. We estimated correlations between random effects in the Bernoulli and gamma components of the model in a variance covariance matrix. These correlations can be informative. For example, individuals who are less likely to interact overall might have very high dyadic association with the partners that they do interact with. Similarly, it is possible for the Bernoulli and the gamma components of fixed effects to show “opposite” effects. For example, dyads that include high-ranking males could be less likely to interact overall, but when they do interact they may have higher DSIs than dyads including low-ranking males. The joint likelihood is calculated by multiplying the likelihoods of the Bernoulli and gamma outcomes. While the magnitude and direction of the regression coefficients are informative about effects, it may be challenging to understand their joint effect on posterior predictions. We suggest that readers focus on graphs of model predictions over raw data for all variables of interest to aid in interpretation. These figures provide information regarding the relative magnitude and certainty of effects on the scale of the outcome variable.

We accounted for repeated measures of individuals and dyads by including varying effects. It is not possible to correctly specify varying effects structures for individuals in non-directional dyadic data with commercially available statistics software or commonly used open-source tools such as “glmer” in the “lme4” package. In a dataset, each row contains an observation of a single dyad of two individuals. However, many model fitting tools only permit the estimation of individual-level varying effects for a single individual for each dyadic observation. This inhibits accurate pooling of information across dyads and can negatively impact model prediction. We aim to estimate parameters for both individuals simultaneously to inform model estimates and make more accurate predictions. In analytical approaches in which all details of the model are explicitly specified, this can be accomplished by programming the model to estimate varying effects for both individuals in a dyad (often through looping over a vector of individuals called forth by indexing notation associated with each observation). Alternatively, one may estimate varying effects at the individual level for dyadic data by using indexing notation stored in two different columns of the dataset—a simpler shortcut. This requires that each individual occurs at least once in both columns where the indexing notation is stored. As a consequence of this shortcut, 3–5 observations had to be removed in each dataset because an individual appeared only once. Additional information and mathematical detail about model specification and varying effects structure can be found in the supplementary material of Silk et al. (2017). Model code for the dataset can be found here: https://github.com/coryphella/Parenting-or-mating-effort.

Paternity status was scored as a categorical variable indicating whether a male was: 1) the sire of the female's current infant, 2) the sire of the female's next infant or, 3) any other male. During pregnancy, “current infant” refers to the infant the female is pregnant with. We set “other male” as the intercepts only reference category and included the other categories as predictors. Because we included dyads for which the identity of the sire of the mother's subsequent offspring was unknown, some males in the “other” category may actually be sires of the female's next offspring. To estimate variation among individuals with repeated measures and varying male rank or paternity status (sire of current infant, sire of next infant, other), we included individual-level varying slopes of male rank and paternity status. We averaged male rank over the period of a given female reproductive state. We fit two models for each reproductive state: PE1, including male dominance rank and paternity status, and PE2, adding an interaction between rank and paternity status to estimate if the relationship of male–female DSI and male rank varied in relation to male paternity status. We included male rank as a variable because higher-ranking males might have better access to females or be more attractive to females.

We ran a binomial GLMM to assess whether males could use the strength of their relationship with the female around the time of conception to determine their probability of paternity (C1). We assessed the influence of male–female DSIs during the conceptive cycle on all days the female exhibited a full sexual swelling, and male dominance rank on the day of conception, on the probability of the male siring the female's infant. DSIs are based on behavioral data collected in and outside of consortships. We included male and female identity as a varying intercepts.

To evaluate the mating effort hypothesis, we ran binomial GLMMs to assess the relationship of male–female DSI during lactation and cycling/flat on the probability of the male siring the female's next infant. We restricted the datasets to cases in which we knew who sired the mother's subsequent offspring (18 infants for lactation/15 infants for cycling/flat). We fit three models for each of the two reproductive states: ME1, including male–female DSI and male rank on the estimated day of conception, as well as male and female identity as a varying intercepts; ME2, in addition to the variables in ME1 also including a variable indicating whether the male was the sire of the female's current offspring; ME3, also including an interaction effect of DSI and whether the male was the sire of the female's current offspring. We included whether the male was the sire of the current offspring as a variable because we expected that, if the parenting effort hypothesis applied, sires of the current infant might have high DSI values with the infant's mother even if they did not sire the next infant.

We fit all our models using the map2stan function in the ‘rethinking’ package (v. 1.59) (McElreath, 2016). This function is a convenient front-end which uses an efficient Hamiltonian MCMC, r-STAN v.2.17.2 (Stan Development Team, 2018) to fit models in R v.3.4.3. (R Core Team, 2017). All continuous predictors were transformed to a mean of 0 and a standard deviation of 1 to allow for meaningful interpretation and prediction for interaction effects. Dyads including males who were sires of both the current infant and the next infant received a dummy variable of 1 in both columns. In all models, we also controlled for group membership by including group as a categorical variable with group ENK as the intercept-only reference category. We removed mother-son dyads to eliminate the effects of kinship on rates of association (6–8 dyads excluded). For ZAG models, we applied non-centered parameterization using a Cholesky decomposition to the varying effects priors to improve model efficiency (McElreath, 2016). We used conservative, regularizing priors on all of our predictor parameters to ensure that our models were skeptical of large effects. For each analysis, we also ran intercept-only models (PE0, ME0, C0) and compared all models using WAIC (Widely Applicable Information Criterion) values. We then model-averaged predictions based on WAIC weights. This means that, for each model, we draw a number of posterior predictions proportional to its assigned weight and calculate posterior densities, medians and credible intervals for this composite set of predictions. For categorical predictors, we plot full posterior distributions of 1000 predictions. For continuous predictors, we plot the posterior median alongside 100 randomly drawn posterior predictions and 89% credible intervals over the raw data to visually check model predictions and visualize uncertainty.

To assess whether sires of the current/sires of the next infant were among the two males with the highest DSIs for each female and infant more often than expected by chance, we randomly assigned a sire to each infant 1000 times. For each permutation, we then divided the observed value by how often randomly assigned sires were among the top two male partners (the two partners with the highest DSI). We report the mean and standard deviation of this calculation. We considered the top-two male partners for this analysis and for the assessment of the stability of close bonds because many females had more than one close partner.

3. Results and preliminary discussion

3.1. Genotyping and analysis of paternity

All loci were in Hardy–Weinberg equilibrium. There was no evidence for scoring error. D6s1056 showed evidence for null alleles (frequency = 0.062) and was excluded from further analyses. The remaining 13 loci had an average of 8.2 ± 2.6 (range: 3–12) alleles (SOM, Table S1). The combined non-exclusion probabilities were $2.8 \cdot 10^{-3}$, $4.6 \cdot 10^{-5}$ and $4.5 \cdot 10^{-8}$ for the first parent, the second parent and parent pair, respectively. We obtained 277 unique genotypes. Genotypes were typed at 12.6 ± 0.7 (range: 9–13) loci on average and were thus 97% complete. Genotypes can be found in SOM Table S4.

Across all five study troops, 90 infants had sires assigned to them with >95% confidence. The mothers of 81 of these 90 offspring were also genotyped. Two offspring with genotyped mothers had sires assigned to them with >90% confidence. The youngest sire was 6.3 years old. For offspring born in ENK and PHG, we could assign sires to 44 (79%) of the 56 offspring that females in these two groups produced during the study period. The remaining 12 infants (21%) born in these groups were not sampled or we could not obtain a genotype. For 21 (38%) of these offspring, we also knew the sire of the females' subsequent offspring.

3.2. Distribution of social bonds

Male–female bonds were well-differentiated in all three reproductive states (Fig. 1). The DSI of the dyad with the highest DSI was around three times higher than the average DSI of one (median of the highest DSI for all females; Pregnancy: 3.1, Lactation: 3.2, Cycling/flat: 2.9). Many females also had a second close male partner. Median DSIs were close to the average DSI (median 2nd highest DSI; Pregnancy: 0.9, Lactation: 1.2, Cycling/flat: 0.9) but many dyads also had DSIs well above the average (Fig. 1). Most females did not have a third close male partner as indicated by median DSIs well below the average DSI (median 3rd highest DSI; Pregnancy: 0.4, Lactation: 0.4, Cycling/flat: 0.2) and distributions of DSI were heavily skewed towards zero (Fig. 1).

3.3. Parenting effort

If close bonds between males and females represent a form of male parenting effort, we would expect sires to remain in the mother's group during lactation. This information was available for 43 infants with known sires in PHG and ENK. In 38 cases (88%), the father remained in the group until the mother resumed cycling. In

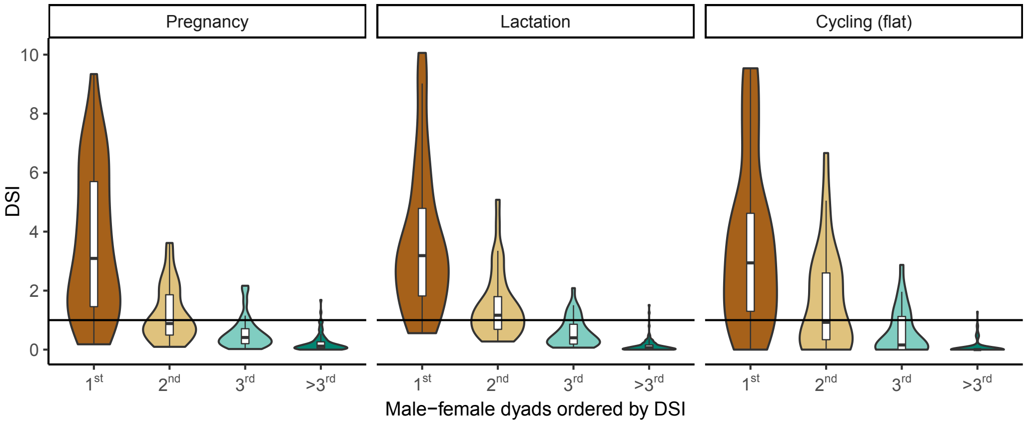

Figure 1. Distribution of dyadic sociality indices. Violin and boxplots of the distribution of the dyadic sociality indices (DSIs) between females and males in three female reproductive states. Female–male dyads were ranked by DSI for each infant with the first dyad having the highest DSI. Tops and bottoms of the violins indicate the full range of values. The horizontal line marks the average DSI.

one of the remaining cases, the sire left the group four months after his infant was born. The other four cases involved the same natal male in PHG who transferred to ENK, and was eventually followed to ENK by the mothers of his infants. For comparison, about one-fourth (mean ± standard deviation [SD]: 23% ± 17%) of the males who were present at the beginning of a lactational period and had no known nursing offspring in the group had changed group membership when the female resumed cycling (mean ± SD: 1.1 ± 0.9 transferring males; 4.5 ± 2.1 total males).

Paternity influenced the strength of male-female ties during lactation. Sires were among lactating mothers' two closest male partners 29 times (83%, $n = 35$), i.e. 2.4 ± 0.6 times more often than expected by chance. There was a strong effect of paternity status on female-male DSI (Table 1; Fig. 2). The posterior median DSI (PMD) of lactating females and the sires of their infants was much higher than the PMD of these females with all other males during lactation (PMD, 89% confidence interval [CI]: sires of current infant (1.7, 0.9–2.7); sires of next infant (0.8, 0.3–1.3); other males (0.7, 0.5–0.9); Fig. 2b).

After females resumed cycling, the strength of their ties to the sire of their last infant was equivalent to the strength of their ties to the sire of their next infant (PMD, 89% CI: 1.3, 0.0–2.7), and for both the PMD was higher than the PMD of other males (0.5, 0.1–0.9; Fig. 2c). The models including the interaction of male-rank and paternity status were assigned the highest WAIC weights (Table 1). However, as we had no specific prior hypothesis about this interaction, we refrain from drawing strong conclusions about the effects but still consider it valuable to present the results. During lactation, there was a positive effect of male rank on male–female DSI for sires of the current infant (Fig. 3a) but a near-zero effect for sires of the next infant and other males (Fig. 3b–c). After females resumed cycling, there was a positive effect of male rank on DSI for all three categories of males (Fig. 3a–c). This effect was more pronounced for sires of the current infant and sires of the next

Table 1
Coefficients for Model PE1 (no interaction) and Model PE2 (including an interaction of paternity status and male rank) evaluating the effect of paternity on female–male dyadic sociality indices in three female reproductive states.[a]

	Pregnancy				Lactation				Cycling/flat			
	Model PE1		Model PE2		Model PE1		Model PE2		Model PE1		Model PE2	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
α_z Intercept	−3.91	0.94	−4.09	0.99	−3.61	0.83	−3.70	0.83	0.30	0.87	0.34	0.88
α_g Intercept	−0.41	0.16	−0.43	0.16	−0.27	0.19	−0.29	0.19	0.41	0.30	0.34	0.33
ß$_z$ Sire current infant*Male rank			−1.65	1.48			−2.54	1.43			−0.06	1.55
ß$_g$ Sire current infant*Male rank			−0.22	0.41			0.36	0.34			0.05	0.45
ß$_z$ Sire next infant*Male rank			−0.26	1.89			−1.00	1.70			−0.40	1.78
ß$_g$ Sire next infant*Male rank			−0.21	0.89			0.13	0.62			0.33	0.69
ß$_z$ Sire current infant	−2.99	1.33	−2.56	1.56	−2.52	1.15	−1.55	1.36	−1.28	1.31	−1.12	1.52
ß$_g$ Sire current infant	1.11	0.32	1.28	0.39	1.02	0.23	0.75	0.32	0.51	0.34	0.51	0.44
ß$_z$ Sire next infant	−0.91	1.75	−0.95	1.84	−2.45	1.45	−2.28	1.57	−2.61	1.73	−2.18	1.87
ß$_g$ Sire next infant	0.40	0.49	0.33	0.68	0.08	0.33	−0.01	0.43	0.11	0.44	0.19	0.54
ß$_z$ Male rank	1.09	0.52	1.20	0.57	1.06	0.45	1.16	0.48	−0.69	0.64	−0.71	0.69
ß$_g$ Male rank	−0.12	0.08	−0.10	0.09	0.00	0.09	−0.02	0.10	0.10	0.20	0.07	0.24
ß$_z$ Group (PHG)	1.09	0.87	1.13	0.90	1.76	0.82	1.85	0.84	0.49	1.05	0.46	1.08
ß$_g$ Group (PHG)	0.10	0.18	0.13	0.18	0.08	0.19	0.05	0.20	−0.01	0.35	0.01	0.39
Scale	1.02	0.16	0.99	0.15	1.42	0.24	1.35	0.24	1.20	0.43	0.93	0.39
WAIC	429		427.6		524.7		521.6		467		450.2	
wWAIC	0.33		0.67		0.18		0.82		0		1	
N (m/f/i/d/o)	16/22/33/158/195				20/22/37/168/229				18/20/30/142/179			

[a] All parameters with a subscript of z correspond with the Bernoulli component of the model, while those with a subscript of g correspond with the gamma component. Negative coefficients from the Bernoulli component (parameters with subscript z) indicate a lower probability of observing a DSI of zero, while positive values for the gamma component (parameters with subscript g) indicate higher DSI values. Posterior means and standard deviations (SD) are shown. Intercept-only models were fitted and had <0.001 wWAIC values and are not presented. The last row indicates the number of males (m), females (f), infants (i), dyads (d) and observations (o) included in each model.

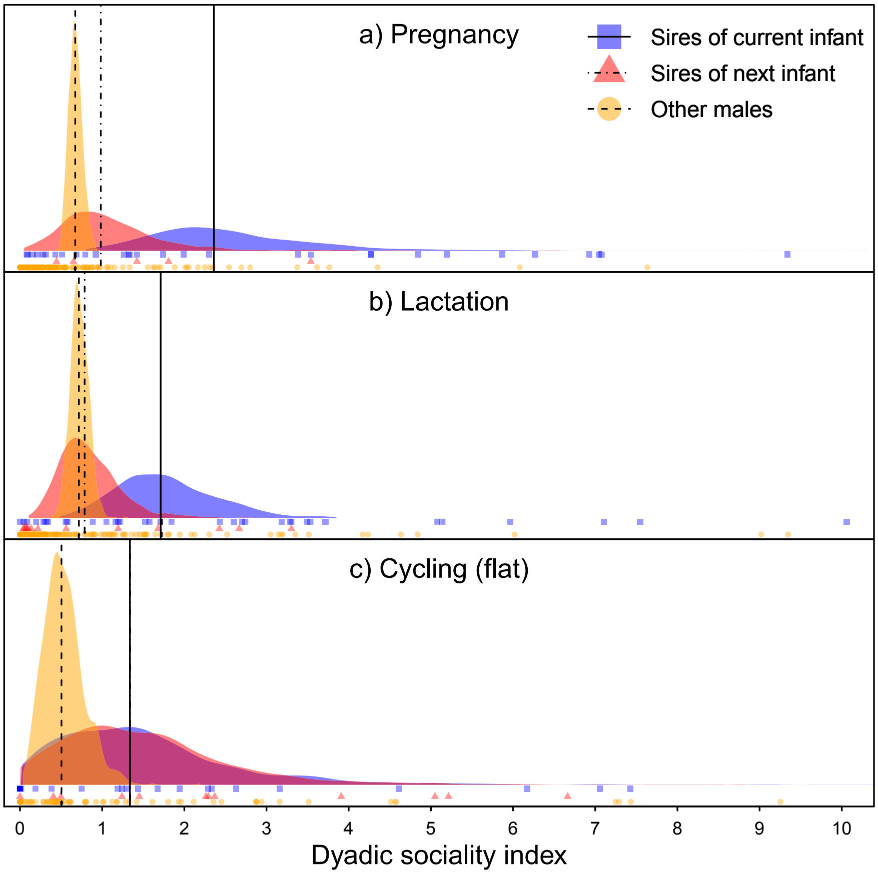

Figure 2. Parenting effort – Dyadic sociality index. Model-averaged posterior predictions for dyadic sociality indices (DSIs) of females and males of each category during (a) pregnancy, (b) lactation and (c) when the female was cycling but had no sexual swelling. During pregnancy, 'current infant' refers to the infant the female is pregnant with. Vertical lines are posterior median predictions. Two lines in panel c) overlap and appear as one line. Points are the raw data. The shape of posterior predictions and widths of the credible intervals of parameter estimates provide information about the certainty of the posterior estimates. The height of peaks in the posterior distribution indicates the probability of that DSI being observed.

infant than for other males; however, the uncertainty around these median estimates was large.

3.4. Paternal kin recognition

3.4.1. Mother-male bonds during pregnancy For the 30 infants whose sires were present for their mothers' entire pregnancy, sires were among the mother's top two partners 20 times (67%), i.e. 1.9 ± 0.5 times more often than expected by chance. There was a strong effect of paternity status on female–male DSI during pregnancy (Table 1; Fig. 2). The posterior median DSI (PMD) of pregnant females and the sires of their infants was much higher than the PMD of these females with all other males during pregnancy (PMD, 89% CI: sires of current infant (2.4, 1.1–3.9); sires of next infant (1.0, 0.1–1.8); other males (0.7, 0.5–0.8); Fig. 2a). Dyads that included low-ranking males had higher DSIs than dyads that included high-ranking males (Fig. 3a–c). This was particularly pronounced for sires of the current infant (Fig. 3a).

3.4.2. Mother-male bonds during the likely time of conception We found a clear positive relationship between the value of the male–female DSI when the female exhibited a full sexual swelling during the conceptive cycle and the probability of the male siring the female's offspring ($ß_{DSI} = 0.82$, Table 2; Fig. 4).

3.5. Mating effort

The mating effort hypothesis relies on the assumption that females can exercise effective mate choice and that not all conceptions are monopolized by the top-ranking male. Male rank was positively associated with the probability of siring infants ($ß_{rank} = 1.33$, Table 2; Fig. 4), but the top-ranking male obtained only 25% of all conceptions ($n = 44$).

We found no evidence that male–female DSI during lactation predicted the probability of siring the female's next offspring. This was true for sires of the current infant as well as sires of the next infant (SOM, Fig. S1 and Table S3). In contrast, we found a strong positive effect of male–female DSI when the female was cycling/flat on the probability of siring the female's next offspring for males who were not the sire of the current infant (Fig. 5a). There was no effect of male–female DSI on the probability of siring the female's next offspring for males who were the sire of the current infant (Fig. 5b). However, the dataset contained only two instances in which a male was both the sire of the current and the next infant (there were more instances in which we knew that the sire of a female's successive infants was the same, see "Stability of breeding relationships", but focal observation data were not available for all females in all reproductive states and all of their infants and the genetic data span a longer time frame than the behavioral data). This information limitation is one of the reasons that the model including the interaction (ME3, Table 3) received the highest WAIC

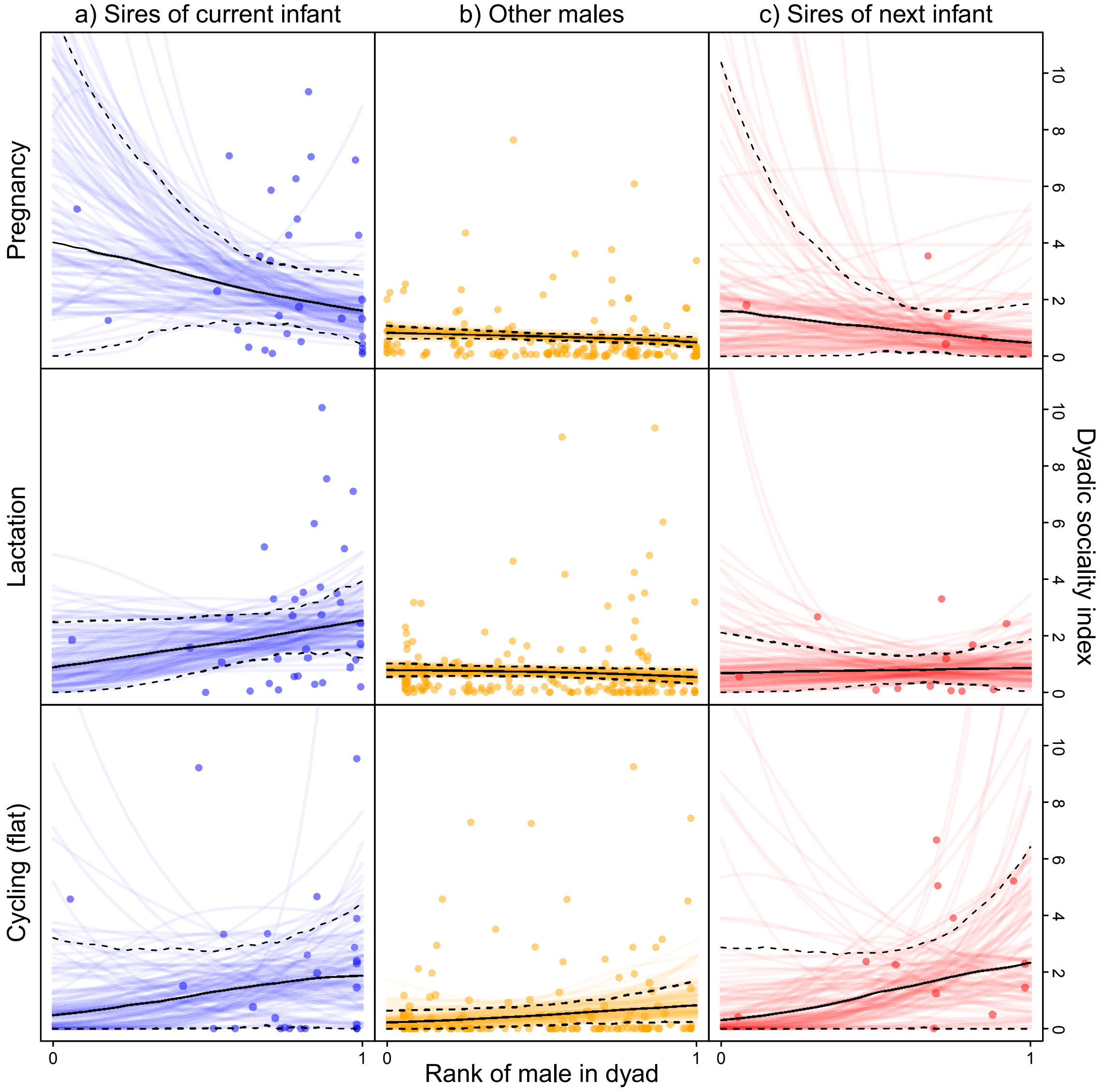

Figure 3. Parenting effort — Rank. Model-averaged posterior predictions for the influence of male rank on male—female dyadic sociality indices (DSIs) for each male category during pregnancy (top panel), lactation (mid panel) and when the female was cycling but showed no sexual swelling (bottom panel). During pregnancy, 'current infant' refers to the infant the female is pregnant with. Rank was standardized to be between 1 (highest rank) and 0 (lowest rank). Points are the raw data. Solid black lines represent the median estimates; dashed lines indicate 89% credible intervals. Colored lines are 100 randomly drawn posterior predictions.

Table 2
Coefficients for the model investigating the influence of female—male bonds during the likely time of conception on the males' probability of siring the offspring (C1).[a]

	Mean	SD
α Intercept	−1.86	0.52
β DSI	0.82	0.25
β Male rank	1.33	0.45
β Group (PHG)	−1.15	0.58
WAIC	81.7	
N (m/f/i/d/o)	17/17/20/138/145	

[a] Shown are posterior means and standard deviations (SD). An intercept-only model was fitted and had <0.001 wWAIC values and is not presented. The last row indicates the number of males (m), females (f), infants (i), dyads (d) and observations (o) included in each model.

weight. For all mating effort models (ME1-ME3), the included parameters do not strongly improve the fit of the models in comparison to their corresponding intercepts-only models as indicated by a comparison of their WAIC values, and averaged posterior predictions include predictions from the intercepts-only model (ME0, Table 3; Fig. 5). Information about estimated relationships can be inferred from Table 3, but we remain hesitant about making strong claims about these patterns.

Although limitations of the available data prevent us from making any claims with much certainty, the estimated patterns were consistent with sires of the next infant having higher posterior median DSIs with females than other males during cycling/flat but not during lactation (Fig. 2). We were able to calculate mother-male DSI during lactation for 13 infants (30%) for which we also knew the identity of the sire of the mother's subsequent offspring. The sire of the next infant was among the female's top two male partners six times (46%) during lactation, 1.2 ± 0.4 times more often than expected by chance, indicating that strength of male-female DSI during lactation did not strongly increase the males' probability of siring the next offspring. We were able to calculate mother-male DSI during cycling/flat for 12 infants (27%) for which we knew the identity of the sire of the mother's subsequent offspring.

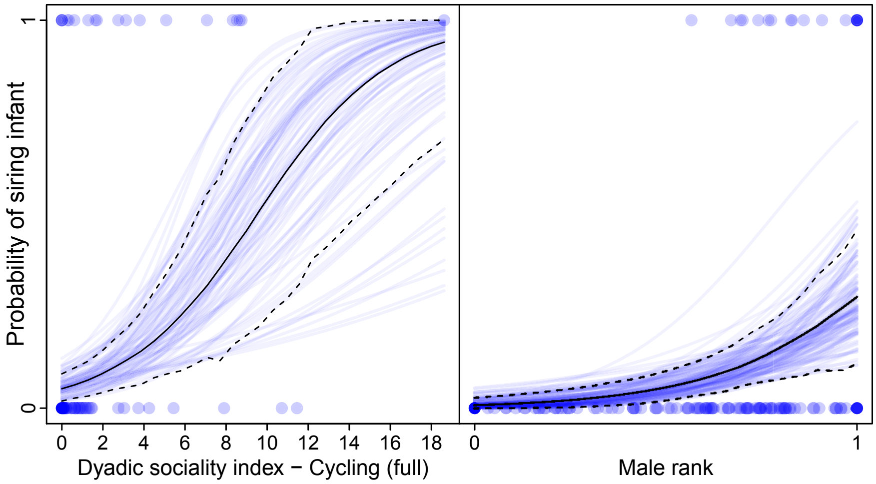

Figure 4. Female–male bonds during the likely time of conception. The effect of female–male dyadic sociality indices during the conceptive cycle when the female exhibits a full sexual swelling and male dominance rank on the estimated day of conception on the probability of the male siring the female's offspring. Rank was standardized to be between 1 (highest rank) and 0 (lowest rank). Solid black lines represent posterior median estimates; dashed lines indicate 89% credible intervals. Blue lines are 100 randomly drawn posterior predictions.

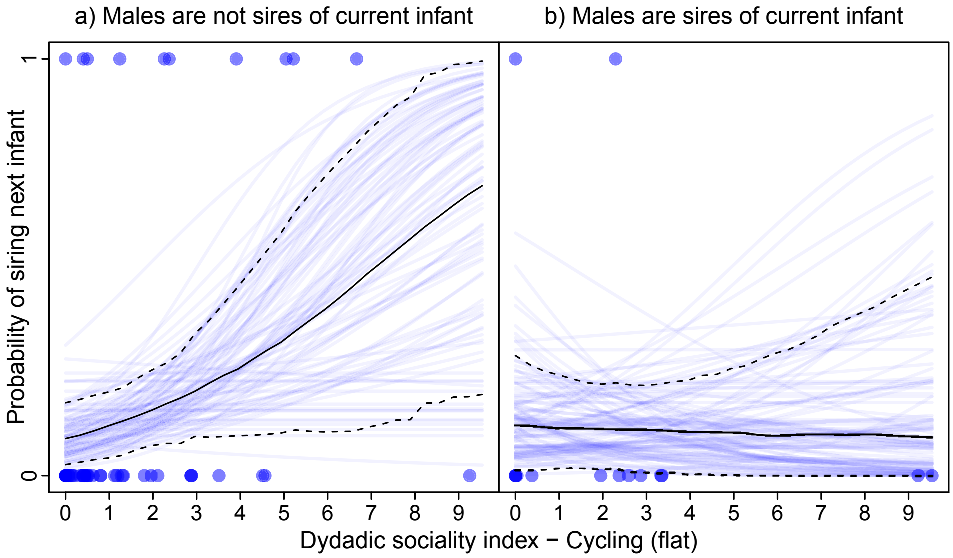

Figure 5. Mating effort – Cycling/flat. Model-averaged posterior predictions of the influence of the dyadic sociality index (DSI) between males and females after females resumed cycling but had no sexual swellings (flat), on the male's probability of siring the female's next offspring. Solid black lines represent posterior median estimates; dashed lines indicate 89% credible intervals. Blue lines are 100 randomly drawn posterior predictions.

The sire of the subsequent infant was among the female's top two male partners eight times (67%) while she was cycling/flat, 2.2 ± 1.1 times more often than expected by chance, indicating that strength of male-female DSI during cycling/flat increased the males' probability of siring the next offspring.

3.6. *Stability of close bonds*

We were able to assess the stability of close male–female bonds across successive lactational periods for 12 females (Table 4). Nine of these females each produced two infants, and three females each produced three infants ($n = 27$ infants, 15 consecutive lactation periods). For 21 of these 27 infants (78%), the mother's two closest partners during lactation included the sire of her current infant. In five cases, the two males that were the females' top partners in the first lactation period, were also the two top male partners in the next. In seven cases, only one of the top two males in the first lactation period was also one of the top two males in the next lactation period. This means that at least one of the top-two male partners was the same in 12 out of 15 (80%) consecutive lactation periods. In three cases, neither of the top two males in the first lactation period were the top two males in the next lactation period. For one female, who was observed during three successive lactation periods, one male was among the top two males in all three lactation periods. Sires were among females' top two partners substantially more often in successive lactation periods than non-sires. In 10 of 13 cases (77%) in which the sire was one of the females' top two partners in the first lactation period, the sire was also one of the top two partners in the next lactation period (Table 4). In contrast, in 7 of the 17 cases (41%) in which non-sires were among the top two partners during one lactation period, they were also among the top two partners in the next lactation period.

Table 3
Coefficients for the mating effort models – Cycling/flat.[a]

	Model ME1		Model ME2		Model ME3		Model ME0	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
α Intercept	−1.48	0.49	−1.38	0.53	−1.38	0.51	−1.70	0.41
β DSI*male sired current infant					−1.13	0.63		
β Male sired current infant			−0.55	0.71	−0.28	0.72		
β DSI	0.47	0.31	0.53	0.32	0.85	0.39		
β Male rank	0.24	0.41	0.26	0.43	0.26	0.44		
β Group (PHG)	−0.88	0.63	−0.92	0.64	−0.97	0.65		
σ male id	0.90	0.58	0.87	0.61	0.94	0.58	0.83	0.55
σ female id	0.50	0.41	0.52	0.50	0.52	0.48	0.45	0.4
WAIC	71.9		72.3		67.6		71.6	
wWAIC	0.09		0.07		0.74		0.10	
N (m/f/i/d/o)	16/14/15/78/81							

[a] The effect of female–male dyadic sociality indices when the female is cycling but exhibits no sexual swelling (flat) on the probability of the male siring the female's next offspring. Shown are posterior means and standard deviations (SD), wWAIC, and WAIC weight. The last row indicates the number of males (m), females (f), infants (i), dyads (d) and observations (o) included in each model.

Table 4
Top two male partners during consecutive lactation periods.[a]

Female	1st offspring		2nd offspring		3rd offspring		Group
	1.	2.	1.	2.	1.	2.	
BY	SN	**TP**	S1	**JJ**	**S1**	JJ	ENK
UA	**TP**	JJ	**YR**	S1	S1	**YR**	ENK
UT	S1	**TP**	S1	TP			ENK
UV	**TP**	S1	TP	YY			ENK
QN	**TP**	JJ	TP	S1			ENK
QP	**TP**	S1	JJ	**TP**			ENK
BF	PZ	FH	PZ	**OZ**			PHG
FD	PZ	BT	**OZ**	PZ			PHG
FX	**BT**	FH	**JY**	BT	**BT**	JY	PHG
OY	**BT**	PH	**JY**	BT			PHG
UN	**OE**	PZ	PZ	OE			PHG
UR	**OE**	PH	PZ	**OZ**			PHG

[a] For each female and offspring, the identities of the two males with the highest and 2nd highest dyadic sociality indices during lactation are shown. Sires are shown in bold.

3.7. *Stability of breeding relationships*

The full paternity dataset for all five troops (n = 92) included 36 cases in which we identified the sires of successive infants born to the same female. The same male sired both infants in 13 cases (36%; ENK: 5/14 = 36%, NGE: 2/4 = 50%, NMU: 1/2 = 50%, PHG: 5/16 = 31%, YNT: identity of sires of successive infants unknown). Two females had three consecutive offspring with the same sire.

4. Discussion

Our data provide support for the parenting effort hypothesis. Based on our behavioral data, pregnant and lactating females formed stronger ties with the sires of their infants than with sires of the next infant and other males. The patterns we observed for pregnant females are consistent with findings previously reported for chacma baboons (Baniel et al., 2016). Associations between sires and pregnant females may seem surprising because females have not yet produced infants who require protection. However, a recent study of yellow baboons shows that pregnancy losses are associated with the arrival of immigrant males, and the authors suggest that new residents may target pregnant females and induce abortions (Zipple et al., 2017). Associations between sires and pregnant females may provide some protection against feticide. Our findings for lactating females are consistent with results of studies on yellow and chacma baboons, which show that females' close partners during lactation are often the sires of their current infants. During lactation, high-ranking sires had stronger bonds with females than low-ranking sires and other males, suggesting that high rank may convey an advantage in gaining access to females or that high-ranking fathers are more attractive companions. Our data also show that females' ties to the sires of their current infants often persist after they resume cycling. In over three-quarters of the cases in which the sire of the current infant was among the two closest male partners, he was also one of the two closest male partners during the next lactation period. This suggests that males may maintain lasting connections to the mothers of their infants and may continue to provide benefits to their infants after they are weaned. However, future research should investigate the nature of male-infant relationships to identify the benefits infants gain from the presence of their fathers.

The parenting effort hypothesis assumes that males can identify their own offspring with some degree of accuracy. Our data suggest that this is the case. Preferential associations with sires emerge during pregnancy; this suggests that phenotyping matching is not necessary for paternal kin recognition. It seems likely that baboons rely on behavioral proxies, such as recent mating history to estimate their likelihood of paternity. Our data suggest that the strength of the male-female relationship while females were fully swollen during the conceptive cycle was a reliable predictor of paternity. Similar findings have previously been reported for yellow and chacma baboons (Buchan et al., 2003; Moscovice et al., 2010). As in previous studies, we found that lactating females' close male partners were not always the sires of their infants. Ties between lactating females and non-sires may represent a form of bet-hedging in which males rely on mating history as a proxy for paternity and “males may benefit by investing preferentially in those infants that they are most likely to have fathered” (Moscovice et al., 2010: 1007).

Our data provide limited support for the mating effort hypothesis. As in two studies of yellow and chacma baboons, the strength of lactating females' ties to males was not a reliable predictor of paternity (Nguyen et al., 2009; Baniel et al., 2016). However, we did find some evidence that the strength of males' ties to cycling females (when they did not have sexual swellings) was associated with the probability of siring the female's next infant. Similarly, in Assamese and rhesus macaques, high rates of affiliation with females during the mating season are associated with increased male mating success and/or paternity (Kulik et al., 2012; Massen et al., 2012; Ostner et al., 2013). However, in contrast to our study, these analyses included female fertile periods.

Our data also suggest that ties with cycling females are not the only factor that may influence paternity. Male dominance rank also has an important effect on the probability of siring infants. Although our analyses, which included young subadult males, may overestimate the magnitude of the effects of dominance rank on paternity success, the alpha male obtained 25% of all conceptions. Interestingly, this value is lower than figures reported for yellow baboons (34%, Alberts et al., 2006) or chacma baboons (48%, Moscovice et al., 2010). In yellow and olive baboons, coalitionary consort takeovers occur in which two males oust the consorting male and one of the coalitionary partners takes over the consortship, thus weakening the correlation between male rank and reproductive success (Bulger, 1993; Alberts et al., 2003; Danish and Palombit, 2014). In olive baboons, more so than in yellow baboons where no evidence for the mating effort model has been found, a female's preference for a particular male could influence the outcome of these takeovers and the frequency of copulations, and contribute to the reduced level of reproductive skew observed in this study (Smuts, 1985; Walz, 2016).

Alternatively, relationships may provide benefits to mothers and their male companions that are not directly related to either male parenting effort or mating effort. Males may benefit from being groomed by their female partners or having access to their female partners' infants for use as “agonistic buffers”, while females may benefit from male support in conflicts (Ransom and Ransom, 1971; Altmann, 1980; Strum, 1984).

A likely scenario for the evolution of the human social system is an ancestral system of polygynadrously mating multimale multifemale groups in which stable, initially polygynous, breeding bonds arose (Chapais, 2013). It is unclear whether these pair bonds initially arose as a form of mating effort, parenting effort or due to other selective pressures altogether (Dunbar and van Schaik, 1990; Chapais, 2008; Quinlan, 2008; Dunbar, 2010; Gavrilets, 2012; van Schaik and Kappeler, 2013; Coxworth et al., 2015). Phylogenetic analyses suggest that true paternal care is a consequence and not a cause of pair bonding (Lukas and Clutton-Brock, 2013; Opie et al., 2013); however these studies investigated evolutionary transitions to pair-living (or living in family groups) and not the emergence of pair bonds within multimale multifemale social groups. The baboon data suggest that male parenting effort could be the foundation for the evolution of more stable breeding bonds in multimale multifemale groups. In contrast, a study on Eastern chimpanzees concluded that mating effort, rather than parenting effort, could be the foundation of stable bonds. Males formed extended social and breeding bonds with certain females with whom they selectively ranged in specific areas of the communal territory and a male's association with a female predicted his probability of paternity (Langergraber et al., 2013). These chimpanzees differ from baboons in that they do not in live in cohesive groups but in fission-fusion societies in which females occupy distinct core areas. This makes it likely that the male–female bonds observed in the two species have different evolutionary causes and the question remains which social organization characterized the *Pan-Homo* ancestor.

However, in this study we also found evidence that the strength of ties with cycling females who are not sexually receptive increases a male's probability of siring the next offspring. Thus, sires of the current offspring could have an increased probability of also siring the female's next offspring. In our study groups, mothers' ties to the sires of their infants sometimes persisted after the mothers resumed cycling and gave birth to their next infant and mating and parenting effort in concert could lead to the emergence of long-term breeding bonds. A number of females in our study groups produced successive infants that were sired by the same male, and similar patterns have been reported for yellow baboons (Alberts et al., 2006).

There seems to be a tension between the strength of male-female bonds and male dominance rank. High male dominance rank enhanced the strength of ties to females while they were cycling (without a sexual swelling), and during their conception cycles when they had sexual swellings. Thus, a reduction in interbirth intervals, which increases the number of infants females produce while certain males are high in the dominance hierarchy, could lead to extended breeding bonds. However, selective forces that reduced the effects of dominance rank on males' access to females might allow for the development of more stable breeding bonds after their initial establishment. During human evolution, this could have been facilitated by male philopatry, increased costs of male competition for mates, or a need for high levels of cooperation among males (Gavrilets, 2012; Chapais, 2013). Alternatively, factors that increased the value of paternal care, such as a heightened need for protection of young from predation after the transition to a terrestrial lifestyle in savanna or savanna mosaic habitats with their large complement of predators, or a necessity for male provisioning, could have led to a shift to more stable breeding and social bonds (Quinlan, 2008; Gavrilets, 2012; Chapais, 2013).

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Supplementary Online Material

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