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More than friends? Behavioural and genetic aspects of heterosexual associations in wild chacma baboons

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Abstract In mammals, fathers are facultative caretakers, and male care is expected to evolve only if it is directed towards related young. Yet, in several promiscuous primate societies, males seem to care for infants despite a presumably low paternity confidence. In cercopithecines, cohesive associations ('friendships') between a lactating female and an adult male are frequent and provide the female and her infant with protection against various sources of aggression, including infanticide. However, the benefits gained by males through such relationships remain unclear, in part, because the relatedness between males and their protected infants has rarely been examined. Moreover, little is known about the nature of the cues underlying kin discrimination by males in societies where females mate polyandrously. In this study, we combine behavioural and genetic data from wild chacma baboons (*Papio ursinus*) in Namibia to investigate (1) whether males are related to their friend's infant and (2) whether similarity between the major histocompatibility complex (MHC) genotype of males and infants (potentially perceived through odour phenotype) favours the establishment of friendships. We first show that males share close genetic ties with their friend's infants, most often by having sired the infant. Secondly, we find that male–infant MHC (Class II–*DRB*) similarity, in contrast to paternity, does not predict male–infant associations. Overall, our results clarify the nature of the evolutionary benefits gained by males in these heterosexual associations, which can be considered as true paternal care. However, the proximate mechanisms underlying paternity recognition remain to be identified.

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Introduction

Paternal care is traditionally defined as any behaviour that improves the survival chances of a given offspring at the cost of the father's ability to reproduce in the future (Trivers 1972). It is, therefore, expected to evolve only if the improvement in offspring survival outweighs the potential

losses of future mating opportunities and if correctly directed towards those offspring that the male has fathered. The latter condition requires paternity confidence to be high (Perrone and Zaret 1979; Birkhead and Møller 1996). Consequently, paternal care is typically associated with social monogamy in insects, birds and rodents (reviewed by Palombit 2000) and remains rare in mammals (e.g., 10% of species: Kleiman and Malcolm 1981). Male care for infants is more widespread in primates than in most mammals (e.g., 40% of primate genera: Kleiman and Malcolm 1981), where it is believed to play an important role in protection from infanticide (Palombit 2000). Infanticide is relatively common in primates, where males kill unrelated infants due to the long periods of female lactational amenorrhea that would otherwise limit their reproductive success (van Schaik and Janson 2000).

The evolution of male–female association in response to infanticide risk is supported by several independent lines of evidence in primates. First, a comparative study shows that year-round male–female associations at the group-level did not evolve independently from infant carrying by the mother (as opposed to parking), suggesting that they evolved because males can protect infants transported by their mothers against infanticidal threats from conspecifics (van Schaik and Kappeler 1997). Second, direct observations have shown that male residents attempt to protect infants against infanticidal attacks from strange males in Hanuman langurs (Borries et al. 1999). Third, playback experiments in chacma baboons have shown that males associating with lactating females run towards them for assistance when hearing a combination of their call with the threat vocalisations of a potentially infanticidal male (Palombit et al. 1997). In addition, recent evidence that male–female bonds protect females and juveniles against other forms of harassment by conspecifics (olive baboons: Lemasson et al. 2008; chacma baboons: Moscovice et al. 2009; yellow baboons: Nguyen et al. 2009) further clarifies the benefits of these associations to females.

Much less is understood about the adaptive significance of heterosexual associations to primate males. Males may simply care for their own offspring. This hypothesis is supported by genetic analyses in Hanuman langurs, showing that only the fathers or likely sires of an infant (e.g., males that had mated with a female during her conceptive cycle) attempted to protect it against infanticide (Borries et al. 1999). Yet, particularly cohesive associations or 'friendships', characterised by an enduring proximity and high levels of affiliative behaviour between a lactating female and a particular adult male (Smuts 1985), are frequent in multi-male multi-female societies where promiscuous mating by females lowers paternity confidence. Such friendships have been described in olive baboons (Ransom and Ransom 1971; Smuts 1985; Bercovitch 1991; Lemasson et al. 2008), yellow baboons (Altmann 1980; Nguyen et al. 2009) and chacma baboons

(Seyfarth 1978; Palombit et al. 1997), as well as in other cercopithecines such as Japanese macaques (Takahata 1982), rhesus macaques (Chapais 1986; Mason 1994) and Barbary macaques (Paul et al. 1996; Ménard et al. 2001).

In these species, male caretakers are not always the sires or likely sires of their friend's infant. For instance, male olive baboons may associate with mothers of youngsters that they are unlikely to have sired (e.g., Strum 1984; Smuts 1985), and male Barbary macaques can develop strong relationships with unrelated infants (Paul et al. 1996; Ménard et al. 2001). One possible explanation is that such male friends gain future mating benefits, i.e., females prefer their infant's caretaker as a sexual partner (Smuts 1985; reviewed in van Schaik and Paul 1997; see also Ménard et al. 2001); although, in Barbary macaques, males may also use unrelated infants to regulate their social relationships with other males (Paul et al. 1996). However, in yellow baboons, friendships do not appear to serve either in paternal care (most male friends have not sired their protected infants or even mated with the mother at the time of conception) or in future mating success (friendships do not predict future sexual access to females; Nguyen et al. 2009). Here, males may trade infant protection against services that are not yet identified (Nguyen et al. 2009). Similarly, in chacma baboons, although females preferentially associate with fathers, they also form friendships with former mates if the fathers have died or disappeared (Moscovice et al. 2009). This indicates that the costs of helping unrelated infants may be low compared with the costs of refusing aid to a potential offspring (Moscovice et al. 2009). Taken together, these studies suggest that females preferentially associate with their infant's sire in some, but not all, species. This may reflect inter-specific differences in either the motivations of males or their ability to reliably identify their own offspring.

Two studies suggest that male primates can track their paternity, even in promiscuous mating systems. In yellow baboons, males preferentially support their genetic offspring in agonistic encounters (Buchan et al. 2003). In chimpanzees, males spend significantly more time playing with their own than with unrelated offspring (Lehmann et al. 2007). However, the proximate mechanisms underlying paternity discrimination remain obscure. Two non-exclusive hypotheses have been proposed (reviewed in Widdig 2007). First, males might rely on their past mating history with the infant's mother, remembering whether they have mated or not, at what frequency and at which stage of the female's cycle. This could account for observations in Hanuman langurs (Borries et al. 1999) and chacma baboons (Moscovice et al. 2009), where male caretakers are not only the genetic fathers but also the males who mated with the mother at the time of conception. However, as these studies show, this indirect mechanism leads to substantial and potentially costly, recognition errors.

Such costs could be avoided through the use of a second direct mechanism based on distinctive cues (Johnstone 1997). In this case, males might assess their paternity by comparing the infant's phenotype to their own ('phenotype matching': Lacy and Sherman 1983). Such a mechanism could account for observations made in yellow baboons where males can distinguish between related and unrelated offspring even if they have mated with the mothers of the latter (Buchan et al. 2003). Evidence that paternal care is adjusted in response to male-offspring phenotypic similarities has recently been documented in fish (through olfactory cues: Neff and Sherman 2005) and in humans (facial and olfactory cues: Alvergne et al. 2009), but the possibility that non-human primates can also use direct paternity cues has not previously been investigated. A likely candidate would be the perception of body odour similarities, a significant cue for kin recognition in various mammals, from rodents (e.g., Todrank et al. 1998; Mateo 2002) to humans (Alvergne et al. 2009). Body odour is influenced by the major histocompatibility complex (MHC) (reviewed by Penn 2002; see also Willse et al. 2006; Kwak et al. 2008), a highly polymorphic genetic system which plays a crucial role in vertebrate immunity by recognising and presenting pathogens to immunocompetent cells. Each individual has a unique MHC genotype, and MHC has been proposed to act as a genetically based system of kin recognition (Brown and Eklund 1994). Evidence that MHC similarities are used as a kin label has been documented in mice in a parent–progeny recognition context (Manning et al. 1992; Yamazaki et al. 2000) as well as in humans, where MHC similarities are thought to play a role in inbreeding avoidance (reviewed by Havlicek and Roberts 2009). Thus, individual MHC genotype, through its influence on body odours, might act as a paternity cue in non-human primates.

This study has two goals. First, we explore the adaptive significance of friendships to males by assessing the genetic bonds between males and their female friend's infants. If friendships represent a form of true paternal care, we expect males to associate with the mother of their offspring. Secondly, we investigate whether the establishment of friendships is compatible with the use of MHC similarity (possibly perceived through body odours) as a paternity cue. Under this hypothesis, we expect that male–infant MHC similarity predicts the establishment of friendships better than or as well as male–infant relatedness.

Methods

Study site and subjects

We studied a wild population of chacma baboons living on the edge of the Namib Desert in Namibia at Tsaobis

Leopard Park (for details on this site and population, see e.g., Cowlishaw 1999). Data were collected during two field seasons (June 2005 to December 2005, May 2006 to January 2007) from two groups. In October 2006, these groups comprised nine adult or subadult males, 16 adult females and 32 juveniles for the larger group (Troop J) and seven adult or subadult males, nine females and 16 juveniles for the smaller group (Troop L). All subjects were fully habituated to observers on foot and adults were individually identifiable.

Both groups were captured during the study to obtain a variety of morphometric measures and biological samples, including the tissue samples necessary for MHC genotyping taken in the form of small ear biopsies. Briefly, troops were captured using cages (one for each individual) baited with maize. Cages were set at dusk to capture the baboons at dawn the following morning. A wildlife vet anaesthetized the animals using 100 mg/ml of tiletamine–zolazepam (Zolatil™ Virbac Australia Ltd, NSW, Australia) at a dose rate of 5 mg/kg administered intramuscularly by darting them, and each baboon was under anaesthesia for about 45 min. Infants were not anaesthetised, but a local anaesthetic (lidocaïne) was used during tissue sampling. Baboons were kept under continuous observation and in the shade (using sheets or natural shade) from capture to release and were all processed within a day in order to release the baboons together the following morning, when fully awake. Dental data were also collected under anaesthesia to estimate age: tooth eruption schedules were used to assign age up to the eruption of the molars (e.g., Kahumbu and Eley 1991), beyond this point age was estimated on the basis of molar wear (Huchard et al. 2009).

Behavioural observations

Adult dominance ranks were established using ad libitum or focal observations of agonistic and approach–avoid interactions. The dominance hierarchy was always linear ($N = 1{,}190$ interactions in Troop L, $N = 1{,}173$ in Troop J; Landau's linearity index h, $p < 0.05$ in both cases), with adult males outranking adult females. Dominance rank was described as proportional rank, expressed from 0 to 1 (i.e., absolute rank/number of same sex animals in group) to control for differences in group size. Male ranks remained stable, except for minor changes due to the emigration of four (non-alpha) males in Troop J, but this did not affect the hierarchy among the remaining males. Male ranks were analysed as a binary variable (the alpha male, 1; all other males, 0) and thus unaffected by such fluctuations.

Twenty lactating females and 21 unweaned infants (nine mother–infant dyads in the smaller group where one female gave birth twice during the study and 12 mother–infant dyads in the larger group) were followed during 3 months

after birth. All females who gave birth to a live infant (surviving more than 48 h) were included, provided that DNA was available for their infant (21 of 22 births). Behavioural data were collected using 1-h focal animal sampling periods (Altmann 1974) spread equally across the day (split into four 3-h time blocks) for each individual. Observations interrupted during the first 30 min were excluded from the analysis. The choice of a focal individual was randomised, and the same individual was sampled no more than once per half day. Each lactating female was followed for at least 13.7 h (mean±SD=18.2±2.8 h, N=20). The following measures were used to quantify variation in heterosexual relationships and to identify 'friends' dyads.

Proximity

The duration that each focal female spent in proximity of males was measured by recording both the time that the focal subject approached to within a given distance of an individual and the time that it or the other individual moved away. Distance of 0–1 and 1–5 m were used to define close and intermediate proximity, respectively.

C-score and identification of friendships

Following previous studies (e.g., Smuts 1985; Palombit et al. 1997; Lemasson et al. 2008), measures of proximity characterising heterosexual dyads were used to derive a composite proximity measure or "C-score" in a group using the equation $C = 2(T_{0-1m}) + 1/3(T_{1-5m})$ where $T_{0-1\,m}$ is the percentage of time that the members of the dyad spent within close proximity, and $T_{1-5\,m}$ is the percentage of time they spent in intermediate proximity. For a given female, a discontinuous distribution of C-scores with resident males reflects the existence of a 'special relationship' or 'friendship' involving the female and one or two males. Males whose C-scores were separated by at least three score intervals from other males were identified as 'friends' of the female.

Maintenance of close proximity

The responsibility for the maintenance of close proximity (within 1 m) between the two members of a dyad was assessed using 'Hinde's index', which is calculated here as the percentage of close approaches due to the female subtracted by the percentage of close leaves due to the female (Hinde and Atkinson 1970; Hinde and Proctor 1977). The index varies from −100 (complete male responsibility for maintaining close proximity) to +100 (complete female responsibility). Hinde indices were calculated only for dyads for which there were at least 20 approach–leave interactions (Hinde and Proctor 1977; Smuts 1985).

Allogrooming

The cumulative duration of 'female grooms male' and 'male grooms female' was initially assessed. The symmetry in grooming interactions between friends was then expressed as a percentage of grooming due to one partner relative to all grooming exchanged between those partners in that dyad.

Infant handling

Male handling of infants may include holding the infant ventrally or carrying it underneath while moving, often accompanied by the mother. During these events, neither the mother nor infant look distressed. The occurrence of infant carrying and holding by males was systematically recorded. Following Smuts (1985), those instances that occurred on rare occasions during an agonistic interaction between males were not included.

Genetic analyses

Genotyping

All males, females and infants were genotyped at 16 microsatellite loci and MHC-DRB using tissue samples, with the exception of one adult male (JM34) and one infant (JM35; DNA extracted from hair plucks in both cases, genotyped for 16 and 12 microsatellite loci, respectively, but not for MHC-DRB). Full details regarding DNA sampling and genotyping for microsatellites are provided in electronic supplementary materials (ESM; see S1 and S2 in ESM).

With respect to MHC-DRB typing, 23 distinct MHC-DRB sequences (Genbank accession numbers DQ339722-DQ339737 and EU244816-EU244822) were identified. These were non-randomly associated within individuals, defining haplotypes (i.e., combination of sequences inherited together). Each individual possesses one (homozygote) or two (heterozygote) distinct MHC-DRB haplotypes. Fifteen haplotype configurations were identified, each carried by 1 (0.025%) to 52 (26%) individuals and comprising 1–4 MHC-DRB sequences so that each individual possessed 2–8 MHC-DRB sequences (mean±SD=5.38±1.60, N=199 individuals). A given sequence can be found in several haplotypes. Full details regarding MHC-DRB genotyping and haplotype determination are provided in Huchard et al. (2006, 2008).

Estimates of pairwise relatedness

Pairwise coefficients of relatedness (r) based on microsatellite typing similarity were calculated between all males and females, using a triadic likelihood estimator of

relatedness (TL) based on a likelihood method that uses the genotypes of a triad of individuals to estimate pairwise relatedness (Wang 2007). Pairwise relatedness coefficients ranged from 0 to 0.80 (median=0.02; mean±SD=0.07± 0.12, N=21,945 dyads across six baboon groups for 210 individuals, see S1 and S3 in ESM for details). Using relatedness coefficients, the mean (±SD) value of pairwise relatedness in the observed mother–offspring pairs was found to be 0.48±0.08, CI 95%=[0.44; 0.51].

MHC similarities between individuals

Parent–offspring pairs systematically share at least one *MHC-DRB* haplotype in our study sample (number of haplotypes shared by 16 father–offspring dyads: mean±SD= 1.25±0.44), in contrast to unrelated individuals (number of haplotypes shared by adult males and unrelated infants born in their group: mean±SD=0.86±0.68, N=78 dyads across the two study groups). *MHC-DRB* similarity between a male A and an infant B was quantified using two different estimators. First, we calculated F_{AB} as the absolute number of *MHC-DRB* sequences shared by A and B. Although F_{AB} is an intuitive and widely used measure of MHC similarity, it might not be ideal in species with a highly variable number of sequences per individual. For instance, if A and B have perfectly similar genotypes in the form of two shared sequences ($F_{AB}=F_A=F_B=2$, with F_A and F_B the number of sequences of A and B, respectively), they will be assigned the same similarity score as a dyad where $F_A=F_B=6$, but with only two sequences in common ($F_{AB}=2$). To overcome this potential problem, a second index D_{AB} of MHC similarity has been proposed as $D_{AB}=2 \ F_{AB}/(F_A+F_B)$ (Wetton et al. 1987). Because the mechanism linking MHC genotype to body odours is still poorly understood (e.g., Willse et al. 2006; Yamazaki and Beauchamp 2007), it is difficult to determine which estimator is the most coherent with respect to odour similarities. We therefore ran our analyses using both.

Genetic determination of paternity

Likelihood-based paternity analysis was carried out using two different software packages: Cervus 3.0 (Kalinowski et al. 2007) and COLONY (Wang 2004). The criteria for inclusion of candidate parents and the parameters used for analysis are also provided in the ESM (S1). A candidate father was considered assigned when he was identified as the most likely father in both analyses. The results from both Cervus and COLONY analyses were in total agreement. Paternity was established for 19 of the 21 (90%) infants included in this study. In this sample, the mean (±SD) value of pairwise relatedness between father–offspring pairs was r=0.50±0.12, CI 95%=[0.44; 0.55],

N=19. Paternity could not be assigned for two juveniles (JM28 and JM32) in both analyses, although no mismatches could be detected between their genotypes and their mother's. In both cases, there were at least three mismatches between their genotype and that of the father identified as most likely by Cervus (although with a very low confidence threshold). These defaults of assignments might have resulted from incomplete father sampling or unresolved genotyping errors.

Statistical analyses

Our first hypothesis states that a female's male friend is the father of her infant. Paternity was established for 19 (of 21) infants, including 17 (of 18) whose mother had a male friend, allowing us to test two (non-independent) predictions: that (1) females establish friendships with their infant's father more often than with males randomly drawn from their group and (2) male friends are more related to their friend's infant than males randomly drawn from the group. To test prediction (1), the number of male friends that had sired their friend's infant was compared to a random distribution, generated by randomly allocating adult males to lactating females in heterosexual friendships. To test prediction (2), the mean relatedness coefficient between males and their friend's infants was compared to a random distribution generated in the same way. In each case, the p value was computed as the proportion of cases out of 10,000 that displayed a higher or equal value than the observed one.

Our second hypothesis states that the infant's MHC genotype (perceived through body odour) is used either by females to select their male friend or by males to decide whether to tolerate a female friend. Under this hypothesis, the MHC similarity between a male and his friend's infant is expected to be a reliable indicator of relatedness. Moreover, if baboons use MHC similarity to assess relatedness between males and infants, male–infant MHC similarity is expected to be interchangeable with male–infant relatedness in predicting the establishment of a friendship. We ran two models testing the effects of MHC similarity (indexed by F_{AB} or D_{AB}) and relatedness of a male–infant dyad on a binary response variable: the presence/absence of a friendship between an adult male and the infant's mother. We also used two indices to estimate male–infant relatedness: paternity/non-paternity (a binary variable) and the quantitative r coefficient. Both models had the same structure. In each case, all the adult male-lactating female dyads within each group were considered, which resulted in 94 dyads including 19 females (20 infants) and 12 males. Additional (control) explanatory variables included group membership and female social rank. Due to the reproductive monopoly of alpha males, a male's social rank was not independent of

his average relatedness to infants recently born in his group (Mann–Whitney test: $W=20$, $N=12$ males, $p=0.03$) and so was not included in the models. Both models were analysed using a mixed-model approach (mixed modelling procedures in R: Pinheiro and Bates 2000), where female identities were treated as random effects to correct for multiple appearances in the dataset; one female can appear in multiple male–female dyads. Male identity was similarly fitted as a random effect, crossed with female identity. The significance of variables was tested using the full models to avoid problems associated with stepwise model selection procedures, such as biased parameter estimation and risks of false positives (Mundry and Nunn 2009). The significance of the fixed quantitative factors was evaluated using χ^2 tests calculated according to the principle of marginality, testing each term after all others (i.e., comparing two models differing only in the presence of the tested fixed effect). All analyses were carried out using software R 2.5.1 (R Development Core Team 2008).

Results

Behavioural patterns of male–female associations

Spatial proximity between males and females and identification of friendships

Of the 21 infants monitored, the mothers of 18 infants established friendships with one or two resident males whose C-scores are clearly segregated from those of other males from the group (Fig. 1). On average, 32 intervals (SE= 27; range, 7–77; $N=21$ dyads) separated the C-scores of male friends from other males (Table 1). Four females had more than one friend. In three cases, females possessed two friends simultaneously (Table 1). In the last case, one female gave birth twice during the study and associated with one to two friends each time. Following Palombit et al. (1997), her consecutive friendships were analysed separately since they were separated by more than a year.

Seventeen females (with 18 infants) of all dominance ranks and ages formed 21 friendships with seven different males (Table 2). The alpha males were involved in ten out of 21 (48%) friendships. Both natal and non-natal males were chosen as male friends (see Table 2 plus S4 and S5 in the ESM for determination of male origin in Troop J). Females spent more time near their friend (selecting that friend with whom females spent less time in proximity for those involved in two friendships) than near the non-friend male with whom they shared the most time in proximity (Wilcoxon paired rank test, close proximity, $T=171$, $p< 0.001$; intermediate proximity, $T=171$, $p<0.001$, $N=18$ females; Table 1).
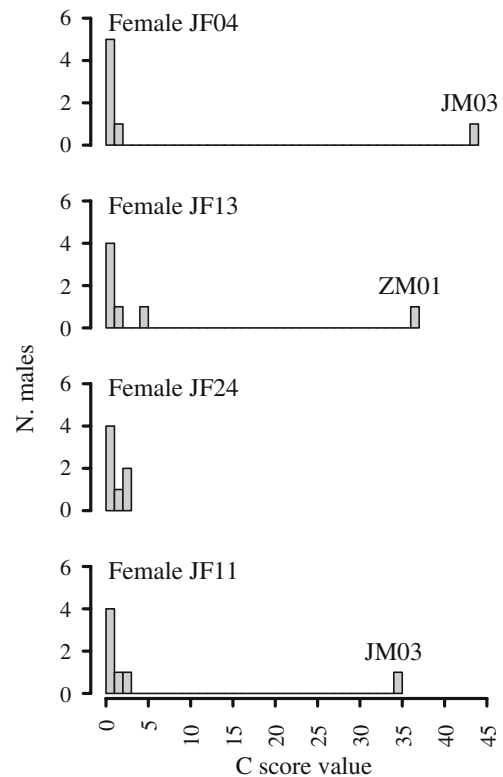

Fig. 1 Distribution of composite proximity scores (C-scores) for four representative lactating females in the larger group. The number of males in the group (y-axis) with a C-score falling within the range indicated on the x-axis is shown for each female. A four letter name code is provided for each male who was identified as a friend on the basis of the distribution of C-scores. Note that no male friend could be identified for female JF24

Responsibility for the maintenance of close proximity between friends

Hinde indices, available for 18 of the 21 friendships, were positive in all but two cases (Table 1), suggesting that females were primarily responsible for the maintenance of proximity (range: [−6.2; +70.8], mean±SD=28.1±20.7, CI 95%=[17.8–38.4], $N=21$).

Patterns of grooming between friends

The majority of lactating females involved in friendships (17 of 21 cases) were never observed grooming any male other than their friend (Table 1). Females exchanging grooming spent an average of 3.8% (SD=4.0%) of observation time grooming their friend, which represented 17.5% (SD=14.0%) of the time spent at close range (within 1 m) of their friend. Females who groomed non-friends ($N= 3$) never did so with more than one other male and spent an average of only 0.1% (SD=0.06%) of observation time grooming him (Table 1). Where friends exchanged grooming,

Table 1 Patterns of spatial proximity and grooming characterizing friends in comparison to non-friends

Infant[a]	Friendship		C-score with friend [mean±SD for non-friends]	Hinde index [number of approaches-withdrawal interactions]	% time spent within 1 m of friend [mean±SD for non-friends]	% time spent within 5 m of friend [mean±SD for non-friends]	% time spent grooming with friend [mean±SD for non-friends]
	Female	Male					
JF28	JF13	ZM01	37.0 [1.4±1.9]	5.5 [99]	15.9 [0.3±0.9]	31.3 [2.5±2.2]	1.3 [0.1±0.0]
JF29	JF17	JM01	61.3 [0.3±0.5]	22.9 [98]	26.1 [0.0±0.1]	53.6 [0.8±1.1]	4.9 [0.0±0.0]
JF30	JF04	JM03	43.3 [0.9±0.8]	37.2 [199]	15.8 [0.1±0.1]	50.9 [2.5±2.2]	1.7 [0.0±0.0]
JF31	JF05	JM03	9.9 [1.8±1.3]	25.8 [62]	3.0 [0.2±0.6]	14.7 [2.9±2.0]	0.0 [0.0±0.0]
JM31	JF18	JM03	45.3 [2.2±3.0]	43.2 [88]	19.9 [0.9±1.6]	36.6 [2.2±4.0]	1.8 [0.0±0.0]
JM33	JF11	JM03	34.2 [0.9±1.1]	34.9 [77]	16.3 [0.0±0.1]	21.3 [2.5±3.1]	0.0 [0.2±0.0]
JF32	JF14	JM03	10.0 [1.6±1.8]	17.3 [32]	3.5 [0.5±0.6]	12.6 [2.5±2.3]	0.3 [0.0±0.0]
JM32	JF22	JM03	23.9 [4.3±4.1]	26.8 [40]	12.0 [1.8±1.8]	11.4 [4.1±4.6]	1.0 [0.0±0.0]
JM27	JF01	JM34	9.9 [0.9±1.2]	NA [15]	4.4 [0.2±0.3]	7.6 [1.9±2.3]	0.2 [0.1±0.0]
JM35	JF12	JM34	79.1 [1.1±0.2]	28.5 [101]	34.3 [0.1±0.1]	65.8 [3.0±1.1]	6.8 [0.0±0.0]
JM30	JF25	JM34	57.5 [2.7±2.6]	11.1 [85]	24.4 [0.3±0.5]	50.3 [6.6±8.3]	10.0 [0.0±0.0]
LM11	LF04	HM08[b]	9.3 [0.3±0.3]	−6.2 [49]	4.3 [0.1±0.1]	6.3 [0.5±0.4]	0.6 [0.0±0.0]
LM12	HF16	HM08[b]	15.7 [0.1±0.0]	−4.6 [23]	7.4 [0.0±0.1]	9.9 [0.4±0.0]	2.3 [0.0±0.0]
LM12	HF16	HM23	10.2 [0.1±0.0]	57.6 [30]	4.1 [0.0±0.1]	10.1 [0.4±0.0]	1.4 [0.0±0.0]
LF17	HF22	HM08[b]	9.6 [1.1±1.6]	NA [13]	4.4 [0.2±0.3]	6.9 [2.5±3.5]	1.5 [0.0±0.0]
LF20	HF24	HM08[b]	28.3 [0.2±0.0]	7.0 [86]	12.4 [0.1±0.0]	23.2 [0.4±0.0]	5.2 [0.0±0.0]
LF20	HF24	HM23	8.6 [0.2±0.0]	43.2 [80]	1.4 [0.1±0.0]	15.2 [0.4±0.0]	0.0 [0.0±0.0]
LF18	HF11	HM23	98.3 [1.9±2.5]	47.3 [90]	37.6 [0.9±1.3]	53.8 [1.2±1.1]	11.6 [0.0±0.0]
LF21	HF11	HM08[b]	9.5 [0.6±0.4]	NA [13]	4.3 [0.0±0.0]	6.9 [1.2±1.0]	0.0 [0.0±0.0]
LF21	HF11	HM23	50.6 [0.6±0.4]	38.3 [108]	21.2 [0.0±0.0]	45.4 [1.2±1.0]	5.4 [0.0±0.0]
LM10	HF26	LM04	102.2 [0.3±0.4]	70.8 [124]	43.8 [0.0±0.1]	69.7 [0.6±0.8]	12.1 [0.0±0.0]

NA indicates that the Hinde index was not available because the number of approaches-withdrawal interactions was too low (<20). For the same reason, mean values of Hinde indices were not available for non-friend dyads

[a] The second digit of individual identification codes indicates sex (*M* males, *F* females)

[b] Male friends who were not the genetic father of a given offspring

their contributions were uneven: females groomed males for 83.0±26.3% of the total grooming time (Wilcoxon paired rank test, $T=28$, $N=17$, $p<0.001$).

Behavioural aspects of male–infant relationships

Infant handling

Male care through handling behaviour was not observed for the three infants whose mothers failed to form friendships. Among the 18 infants whose mothers did form friendships, male handling occurred at very low frequency in four of them and was exclusively performed by the mother's male friend (carrying, mean±SD=0.06±0.05 incidences per infant per hour, $N=9$ occurrences involving four infants and three males; holding: 0.08±0.07 incidences per infant per hour, $N=9$ occurrences involving three infants and two males).

Infant mortality and report of an infanticide

Of the 24 infants born during the study period, 18 (75%) survived over a year. Of the remainder, two infants were only 2–3 months old at the end of the study, two others died within 48 h of their birth after being noticeably weak and unable to suckle properly, one died at 9 months of age after showing signs of physical weakness and delayed growth, and one was killed during an infanticidal attack at 3 weeks of age.

The infanticide victim (JM35) was the infant of a female (JF12) who developed a friendship with her infant's father (JM34; Table 1). The infanticidal attack was initiated by the alpha male (JM03), who reached his alpha status at least 5 months before the infant's conception. The infant's father attempted to protect him from the attack by ventrally carrying him during a prolonged chase. The two males ran out of sight for a couple of minutes where the infant was evidently caught by the alpha male. The latter re-appeared

Table 2 Characteristics of partners involved in friendships

Identity					Social rank[a]		Age (years)		Origin of male friend
Infant	Group	Mother	Genetic father	Male friend	Mother	Male friend	Mother	Male friend	
JF28	J	JF13	ZM01	ZM01	89	44	16	15	non-natal
JF29	J	JF17	JM01	JM01	78	78	9	16	natal
JF30	J	JF04	JM03	JM03	94	80	11	11	natal
JF31	J	JF05	JM03	JM03	33	80	8	11	natal
JM31	J	JF18	JM03	JM03	39	89	7	10	natal
JM33	J	JF11	JM03	JM03	6	89	7	10	natal
JF32	J	JF14	JM03	JM03	22	80	16	11	natal
JM28	J	JF24	Unknown	None	17	–	15	–	–
JM32	J	JF22	Unknown	JM03	11	89	10	10	natal
JM27	J	JF01	JM34	JM34	72	30	16	15	non-natal
JM35	J	JF12	JM34	JM34	50	60	7	15	non-natal
JM30	J	JF25	JM34	JM34	83	30	15	16	non-natal
LM11	L	LF04	HM23	HM08	18	50	7	19	natal
LM12	L	HF16	HM23	HM23	0	83	13	10	non-natal
	L			HM08		50		19	natal
LF17	L	HF22	HM23	HM08	27	50	15	19	natal
LF20	L	HF24	HM23	HM23	55	83	10	10	non-natal
	L			HM08		50		19	natal
LF19	L	HF12	HM23	None	45	–	15	–	–
LF16	L	LF01	HM23	None	82	–	15	–	–
LF18	L	HF11	HM23	HM23	91	83	12	10	non-natal
LF21	L	HF11	HM23	HM23	91	83	13	11	non-natal
	L			HM08		50		20	natal
LM10	L	HF26	LM04	LM04	10	33	7	19	non-natal

[a] Social status is expressed as the percentage of all same sex adults dominated in a group, and calculated at the time of the friend's infant birth for males

carrying the apparently dead infant in his mouth, dismembering the body before discarding it. Examination of the body revealed deep canine punctures in the skull as well as wide lacerations to the abdomen. The infant's father did not display any obvious wounds. The infanticidal male mated with the female when she resumed cycling (about 45 days after her infant's death) during a 48-h mate-guarding period.

Genetic aspects of male–infant relationships

Relatedness between males and their friend's infants

Out of 17 infants with known paternity whose mothers were involved in friendships, 15 were sired by a mother's friend. This value is higher than that expected by chance alone (mean±SD=4.82±1.72, $p<0.001$). Moreover, the mean relatedness between the 17 infants and their mother's main friends (0.42±0.20) stands close to the average relatedness of mother–infant dyads (0.40±0.08) and is higher than that generated under the null hypothesis (0.24± 0.04, $p=0.001$).

One male (HM08) was found to be involved in five friendships without having sired the female's infant (Table 2). This male was a relatively old natal male (Table 2) and the former alpha male. As a consequence, four of the five infants of his friends were related to him ($0.19<r<0.37$, mean±SD=0.26±0.08). One was his maternal grandchild while his relationship with the other three could not be established. However, his average relatedness did not statistically differ between the infants of his friends (0.21±0.13, $N=5$) and those of non-friends (0.13±0.12, $N=4$; Mann–Whitney test, W=13.5, $P=0.46$). In any case, these data indicate that all but one of the friendships identified (95%) involved a male who was genetically related to his friend's infant. Interestingly, male friendships that involved their own offspring seemed stronger than those involving other related infants: the proximity scores in non-father male associations appeared lower

(mean±SD=14.5±8.2, CI 95%=[7.3; 21.7], N=5) than those involving the genetic father (42.6±31.1, [27.4; 57.8], 16), and the two negative values of the Hinde indices were similarly found in dyads involving HM08 (HM08 dyads: mean±SD=−1.2±7.2, CI 95%=[−9.4; 6.9], N=5, genetic father dyads: 34.0±17.3, [25.6; 42.5], 16). However, the non-independence of HM08 dyads precluded a statistical test of these differences and calls for a cautious interpretation of such patterns.

Male–infant MHC similarity and friendships

Our first index of MHC similarity (F), the mean number of shared *MHC-DRB* sequences, does not significantly differ between 16 father–infant dyads (mean±SD=3.25±1.12, CI 95%=[2.70; 3.80]) and 78 unrelated male–infant dyads (2.76±2.16, [2.28; 3.24], Mann–Whitney test: W=720.5, p=0.32). It is also not significantly correlated with r (Spearman test: r_s=0.18, N=94 dyads, p=0.08). Our second index of MHC similarity (D), the proportion of shared sequences, is higher for father–infant dyads (mean±SD=0.73±0.11, CI 95%=[0.62; 0.84]) than for unrelated male–infant dyads (0.48±0.08, [0.39; 0.55], Mann–Whitney test: W=872, p=0.01) and is moderately correlated with r (Spearman test: r_s=0.27, N=94 dyads, p=0.01). This suggests that only one measure of *MHC-DRB* similarity is a reliable predictor of relatedness. Similarly, male–infant *MHC-DRB* similarity does not explain the presence of friendships between males and females, but fatherhood and quantitative coefficients of relatedness are good predictors (Table 3). These results suggest that *MHC-DRB* similarity is not a primary cue used by male baboons for kin discrimination.

Discussion

We examined the behavioural and genetic nature of the friendships occurring between male and lactating female baboons. We have described the behavioural patterns that characterise these associations and established that the males have usually fathered their friend's infant. However, friendships were not predicted by male–infant *MHC-DRB* similarity.

Behavioural aspects of friendships and their potential benefits to females

As commonly reported in cercopithecines (e.g., Takahata 1982; Smuts 1985; Chapais 1986; Paul et al. 1996), heterosexual partners in our study population spent a great deal of time in close proximity and formed exclusive grooming partnerships. Furthermore, females were consistently responsible for maintaining proximity, confirming previous observations on chacma baboons (Seyfarth 1978; Palombit et al. 1997), but in contrast to olive baboons (Smuts 1985; Lemasson et al. 2008). This difference may reflect the fact that infanticide is less common in olive baboons (Palombit 2003). However, females may also derive additional benefits from their friends, such as protection against non-lethal forms of conspecific aggression (Lemasson et al. 2008; Moscovice et al. 2009), particularly harassment by dominant females which regularly involves rough handling of the infant (Nguyen et al. 2009).

Genetic aspects of friendships and their benefits to males in the study population

At least two sorts of benefits could motivate males to protect females with infants: increasing the probability of their offspring's survival or increasing future mating opportunities (Smuts 1985; van Schaik and Paul 1997). By showing that 95% of males were related to their friend's infant and by clarifying the genetic relationships linking the infant killed to both his attacker and his caretaker, our results help to explain male willingness to protect their

Table 3 Results of the binomial mixed-effect models explaining the establishment of heterosexual friendships (N=18 dyads with 14 females and six males genotyped for *MHC-DRB*) among 94 male-female dyads involving 19 females and 12 males

Sample	Fixed effect	Estimate±SE	X_1^2	p	AIC
Model including all friendships (N=18 dyads with 14 females and six males)	Group[a]	1.75±1.08	2.41	0.12	88.29
	Mother's dominance rank[a]	−0.62±0.91	0.46	0.50	
	Paternity[b]	18.86±9.52	34.99	<0.0001	55.30
	Male–infant relatedness (TL)[b]	9.22±2.66	19.49	<0.0001	70.80
	Number of shared *MHC-DRB* sequences F[b]	0.30±0.22	1.92	0.16	88.36
	Index of *MHC-DRB* similarity D[b]	2.26±1.21	3.58	0.06	86.71

[a] Estimates and p values are calculated before the introduction of additional variables (i.e., in a model containing only group identity and mother's dominance rank as fixed effects)

[b] Estimates and p values are calculated after the introduction of the considered variable in a model containing only group identity and mother's dominance rank as fixed effects

friend's infant. Males, by discouraging or countering infanticidal attacks against their own infant, increase their own fitness. Paradoxically, a single male (HM08) was involved in five friendships without being the infant's father. These associations still mostly involved related infants (including a maternal grandson), but the lower degree of relatedness seemed to be matched by a correspondingly less intense friendship. It is, thus, possible that a minimum degree of relatedness may occasionally motivate females to engage in friendships with non-father males, for instance, when social access to the father is limited by female–female competition (Palombit et al. 2001). This hypothesis is supported by the fact that all infants protected by HM08 had been sired by the alpha male, whose friendship was generally highly solicited. Alternatively, these patterns may simply reflect the idiosyncrasies of this particular male.

Male adaptive value of friendships from a wider perspective

Our finding that most males involved in friendships had sired their friend's infant confirmed results from an earlier behavioural study on chacma baboons from Moremi (Palombit et al. 1997), which noted that virtually all males involved in friendships had probably fathered their friend's infant. But these results contrast with patterns of paternity reported by two recent studies, on chacma baboons from Moremi (Moscovice et al. 2009) and on yellow baboons from Amboseli (Nguyen et al. 2009), where the proportion of friends who were fathers was much lower (i.e., ~25% and ~48%, respectively).

At Moremi, the frequent absence of fathers (~65%, which was exceptionally high in this particular cohort) made them unable to protect their infants. If most fathers had still been present, the proportion of males who had sired their friend's infants might have been nearer that observed at Tsaobis (the Moremi study also focused on juveniles until 2.5 years of age, which increased their chances to be orphaned compared to the newborns targeted by our study). However, this does not explain why males form friendships with mothers of unrelated infants. It has been suggested that males, in a context of low paternity confidence, adjust their behaviour to the costs of recognition errors. If the cost of caring for unrelated juveniles (acceptance errors) is lower than the cost of refusing help to related offspring (rejection errors), males might tolerate friendships from mothers of infants that they might have sired (even if this probability is relatively low; Moscovice et al. 2009), especially in the absence of the most likely (or of a more likely) sire (Clarke et al. 2009). Males might even adjust their paternal investment in relation to their paternity certainty for each infant. For instance, a male might be willing to protect a potentially unrelated mother–infant dyad against harassment by other group members (often

females or immatures), which likely incurs only moderate costs (since adult males outrank females and immatures), but be unwilling to enter a dangerous fight with an infanticidal male unless his paternity confidence was high. Such flexibility is clearly plausible but would prove difficult to demonstrate since it would require the quantification of male paternity certainty and a test of male motivation to incur varying degrees of costs in the protection of corresponding mother–infant dyads.

An alternative explanation is required to elucidate the involvement of non-father males in friendships at Amboseli, where past mating history (i.e., mating with female at the time of conception) failed to predict the establishment of friendships (Nguyen et al. 2009). In this case, even if protection against infanticide might have initially favoured the emergence of long-term heterosexual associations, friendships might have been secondarily retained in the absence of high infanticide risk (like in yellow and olive baboons: Palombit 2003) in response to other benefits. Friendships could indeed help males gain future matings with the mother (Smuts 1985) or with other females who observe their caring behaviour (van Schaik and Paul 1997; Nguyen et al. 2009) since males who care for their offspring seem to be more attractive than others in some primates (cotton-top tamarins: Price 1990). It has also been proposed that males may trade grooming in exchange for the protection of unrelated infants (Nguyen et al. 2009). These hypotheses might also explain why male olive baboons appear to play a more active role in maintaining friendships (Smuts 1985; Lemasson et al. 2008) than male chacma baboons (Palombit et al. 1997, this study).

MHC similarity and the assessment of paternity

Our establishment of the genetic relationships linking males and infants suggests that both females and males in friendships know the father's identity. However, the mechanism responsible for this information is unknown. Although males could rely on indirect cues, such as mating history, this would necessarily involve a significant rate of errors. Alternatively, males might use a more direct recognition mechanism, such as phenotype matching through male–infant odour similarities potentially influenced by *MHC-DRB* similarities. However, our analyses indicate that while *MHC-DRB* similarity can predict paternity, it does not predict the establishment of friendships.

A number of hypotheses might explain this negative result. First, establishing MHC similarity at a single region (such as MHC Class II–*DRB*) might be insufficient to accurately estimate the odour similarity shared by related individuals. To overcome this problem, future studies might estimate odour similarities directly from the chemical signal itself (e.g., Charpentier et al. 2008). Ideally, a realistic

assessment of odour similarities should also take into account the perception of the signal by the animals. This would require behavioural assays where odour similarity is judged by the baboons themselves. However, this is probably difficult (although not necessarily impossible) to achieve, even in captivity. Second, olfactory cues may not be so important for kin discrimination by anthropoid primates, since the increasing importance of trichromatic vision during primate evolution may have reduced their reliance on smell (e.g., Gilad et al. 2004). As a result, anthropoid primates may rely on alternative phenotypic cues, such as visual or auditory cues (Widdig 2007).

Alternatively, paternal recognition of offspring based on indirect mechanisms, such as contextual cues, might be accurate enough to keep the rate of recognition errors relatively low. For instance, it is possible that males remember the frequency and timing of copulations in relation to their partner's fertility during the conceptive cycle. While this hypothesis was not supported in yellow baboons (Nguyen et al. 2009), it was compatible with patterns at Moremi (Moscovice et al. 2009). Although not testable in this study (the necessary data were not available), a male's contextual assessment of his paternity would have been facilitated by the long duration of mate-guarding consortships in chacma baboons (lasting up to 13 days in our population, unpublished data, see also Bulger 1993; Weingrill et al. 2003). During these consortships, a male secures exclusive access to his partner and can presumably obtain detailed information about her physical and hormonal state (and thus, conceptive ability) by combining olfactory and visual cues obtained at close range over an extended period (Higham et al. 2009). An ability to detect and remember such cues would be consistent with the cognitive abilities of baboons to keep track of complex social relationships (e.g., Cheney and Seyfarth 2007).

Our study clarifies the nature of some evolutionary benefits gained by male chacma baboons through heterosexual associations and adds to existing evidence that animals can discriminate their paternal relatives (Widdig 2007). But these results also outline the need for further research in at least two important directions. First, a comparative perspective, made possible by recent work in different populations (Moscovice et al. 2009, this study; Nguyen et al. 2009), highlights intriguing variation in the pattern of friendships in relation to paternity. This variation might reflect a multiplicity of benefits to males and/or great flexibility in the males' ability to manipulate the cost/benefit balance of their investment according to context. A better understanding of male decisions regarding investment in friendships will thus probably require the combination of long-term (and large-scale) behavioural datasets with genetic data to disentangle the complexity of factors at play. Second, the proximate mechanisms underlying kin discrimination by males remain mysterious and future studies might usefully investigate the use of alternative paternity cues.

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