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# Paternity alone does not predict long-term investment in juveniles by male baboons

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**Abstract** Adult male chacma baboons (*Papio hamadryas ursinus*) form preferential associations, or friendships, with particular lactating females. Males exhibit high levels of affiliative contact with their friends' infants and defend them from potentially infanticidal attacks (Palombit et al. 1997). Little is known about males' associations with juveniles once they have passed the period of infanticidal risk. We conducted an observational, experimental, and genetic study of adult male and juvenile chacma baboons in the Moremi Reserve, Botswana. We identified preferential associations between males and juveniles and used behavioral data and a playback experiment to explore whether those associations have potential fitness benefits for juveniles. We determined whether males preferentially invest in care of their own offspring. We also determined how often males invest in care of their former friends' offspring. The majority of juveniles exhibited preferential associations with one or two males, who had almost always been their mother's friend during infancy. However, in only a subset of these relationships was the male the actual father, in part because many fathers died or disappeared before their offspring were weaned. Male caretakers intervened on behalf of their juvenile associates in social conflicts more often than they intervened on behalf of unconnected juveniles, and they did not appear to differentiate between genetic offspring and unrelated associates. Playbacks of juveniles' distress calls elicited a stronger response from their caretakers than from control males. Chacma males may provide care to unrelated offspring of former friends because the costs associated with such care are low compared with the potentially high fitness costs of refusing aid to a juvenile who is a possible offspring.

**Keywords** Paternity · Caretaking · Juvenile · Chacma baboon · *Papio hamadryas ursinus* · Playback experiment · Interventions

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## Introduction

Male chacma baboons (*Papio hamadryas ursinus*), like males in other baboon subspecies, form close preferential associations, or friendships, with lactating females that coincide with infant birth and terminate abruptly if the infant dies (Palombit et al. 1997, 2000). Chacma infants face higher rates of infanticide than East African conspecifics, and male friends can have a significant impact on infant survival (Palombit et al. 2000; Weingrill 2000). Behavioral and experimental studies indicate that chacma males are more willing to protect female friends than non-friends when threatened by potentially infanticidal males (Palombit et al. 1997). During periods of high infanticidal risk, lactating females with a male friend exhibit a reduced stress response compared with lactating females without a

male friend (Beehner et al. 2005; Engh et al. 2006), underscoring the importance of friendships as infanticide deterrents from the female's perspective.

There has been little research on chacma males' relationships with immature baboons after their female friends resume cycling, when offspring are no longer at high risk of infanticide. In yellow baboons (*Papio hamadryas cynocephalus*) co-residency with male caretakers has important short- and long-term fitness implications for juveniles. Males aid their offspring in aggressive disputes significantly more often than they aid unrelated juveniles (Buchan et al. 2003). Furthermore, the presence of a father during the juvenile period significantly accelerates the age of maturation for both males and females (Charpentier et al. 2008). These studies suggest more extensive and long-term paternal care than has previously been reported in Old World monkeys (e.g., Stein 1984, Taub and Redican 1984).

It remains unclear how males determine the recipients of their caretaking behavior. Yellow baboon males appear to distinguish genetic offspring from unrelated juveniles, even when they mated with the mothers of unrelated juveniles during their conceptive cycles (Buchan et al. 2003). Such discrimination is consistent with phenotypic matching, but it could also result from behavioral cues—for example, memory of the proportion of a female's consort days that the male monopolized, or a previous friendship with the juvenile's mother.

We designed a study to examine male chacma baboons' relationships with juveniles once they have passed the period of high infanticidal risk. Chacma baboon friendships are characterized by high levels of affiliative contact between males and their friends' infants, including frequent infant carrying (Busse and Hamilton 1981; Palombit et al. 1997). These close associations may promote a long-term bond between a male and the offspring of his female friend that continues after the female resumes cycling and no longer associates closely with her former friend (Palombit et al. 1997).

If male–female friendships facilitate long-term bonds between males and particular juveniles, males should invest in their former friends' offspring regardless of their genetic relatedness to them. Because male chacma baboons typically form friendships with previous consort partners (Palombit et al. 2000; Weingrill 2000; Moscovice et al., manuscript in preparation), investment in the juvenile offspring of former friends should then also frequently result in paternal care. Alternatively, males might provide preferential care only to their genetic offspring, irrespective of their previous friendships with particular females. This outcome would be consistent with patterns of male care of juveniles in yellow baboons and would offer further support for phenotypic matching.

In this paper, we identify preferential associations between males and juveniles and examine whether male caretaking behavior is directed preferentially toward genetic offspring. We also compare male–juvenile associations with males' previous associations with the juveniles' mothers during lactation to test the hypothesis that males may use behavioral cues from previous friendships to determine patterns of investment in juveniles. Finally, we use behavioral data and a playback experiment to explore whether associations with male caretakers have potential fitness benefits for juveniles.

## Materials and methods

### Study site and population

Subjects were members of a group of wild chacma baboons living in the Moremi Game Reserve in the Okavango Delta of Botswana. The group has been observed since 1978 and has been the subject of intensive behavioral observation since mid-1992. All births and deaths, as well as immigration and emigration, are noted daily and matrilineal relatedness of all individuals is known (Cheney et al. 2004). Female baboons usually attain a rank similar to their mothers by sexual maturity, at around 5–6 years. Males typically emigrate from their natal group between 8 and 11 years (Cheney et al. 2004), although some males remain in their natal group into adulthood. Males form linear dominance hierarchies based primarily on fighting ability (Bulger 1993; Kitchen et al. 2003). The highest ranking, or alpha, male has priority of access to females and achieves the highest mating success (Bulger 1993). However, chacma males exhibit high levels of instability in the adult hierarchy, and males at the Moremi site have an average alpha tenure of only 6.5 months (Palombit et al. 2000). During the study period, group size ranged from 62 to 73 individuals, including seven to nine adult males, 20–22 adult females, 11–14 subadult males, five to six subadult females, and 19–22 immature animals who did not yet exhibit signs of puberty.

For the purposes of this study, it is important to differentiate between two periods in immature baboons' development: the period when their mothers were still lactating and they were at high risk of infanticide (Palombit et al. 2000) and a later stage after their mothers had either resumed cycling or died and they were at reduced or negligible risk. Animals in the former period were classified as infants and those in the latter period as juveniles. This study focuses on 17 immature baboons ranging from 0.6 to 2.5 years of age (median=1.3 years), whose mothers had either resumed cycling ($N=13$) or died ($N=4$). We examine these juveniles' relationships with the

eight adult males who were resident for a minimum of 3 months during the study period. Seven of these males were immigrants; one (NA) was a natal male who emigrated during the study. Tenure length for the seven immigrant males ranged from 1.3 to 9.3 years at the completion of the study (median=3.1 years). The males' estimated ages ranged from 11 to 19 years.

The adult male hierarchy remained relatively stable during the entire study, with a single male (BY) maintaining the alpha position throughout. The other seven males occupied descending positions from two to nine (during one brief immigration event, the lowest ranking male in this study was ninth ranked) and exhibited only minor changes in rank (±1 position).

Identifying caretakers

Between July 2006 and June 2007, two to three observers conducted 10-min focal animal samples (Altmann 1974) on all adults. Each female was observed for a mean of 34.0 (±1.1) h and each male for a mean of 22.6 (±7.9) h. The greater variability in male observation time was due to deaths, immigration, and emigration.

During focal animal sampling, we recorded all social interactions between the subject and any group member classified as a juvenile or older. We used two measures of affiliative behavior to identify caretakers: tolerated approaches and nearest neighbors. A tolerated approach was defined as an approach to within 2 m of another animal that did not immediately result in aggression or a supplant to >2 m. Nearest neighbors were all individuals located within 5 m of the focal subject at the end of a focal. We focused on these measures rather than other social behaviors (e.g., grooming), since these measures may be less susceptible to age- or sex-biased variation.

For each juvenile, we determined the total number of tolerated approaches that it shared with any adult male. We then calculated the proportion of each juvenile's total tolerated approaches that involved each male, correcting for differences in the amount of time each juvenile and male were co-resident in the group. We also calculated the proportion of male point samples when each juvenile was a nearest neighbor. A caretaker relationship was identified when a male–juvenile dyad shared a proportion of tolerated approaches and a proportion of time as nearest neighbors that was at least twice as high as the same measure for that juvenile and its next closest male affiliate.

To determine who was responsible for the maintenance of close associations in caretaker relationships, we calculated the Hinde Index for caretaker–juvenile dyads with ≥20 combined tolerated approaches and leaves. The Hinde Index measures the percentage of approaches to a male initiated by the juvenile subtracted by the percentage of its leaves from the same male (Hinde and Atkinson 1970; Hinde 1977). The index varies from −100–+100, with more positive scores indicating that the juvenile is more responsible for initiating contact with its caretaker than vice versa.

We also calculated the hourly rate of friendly approaches between males and juveniles' mothers to determine whether current male caretaker relationships reflected current male–female associations. To examine whether males' caretaker relationships with particular juveniles were based on their former friendships with the juveniles' mothers, we used long-term behavioral records to identify the primary male associates, or friends, of the juveniles' mothers during infancy (Moscovice et al., manuscript in preparation).

Measuring investment in juveniles: interventions and playback experiments

Because support in disputes has been used as the primary measure of male paternal care in baboons (Buchan et al. 2003), we recorded all occurrences of interventions by a third party during aggressive acts. An aggressive act occurred when one individual threatened an unambiguous target with at least one of the following behaviors: threat grunts, head bob and ground slaps, lunges, chases, and/or bites. Interventions occurred when a third individual aided the recipient of an aggressive act by threatening the original antagonist. We calculated each male's average monthly number of interventions on behalf of a juvenile by dividing the male's total number of interventions to that juvenile by the number of months the male and juvenile co-resided in the group. We also examined the proportion of interventions that each juvenile received from three categories of potential helpers: male caretakers, other unconnected adult males, and close maternal relatives (mothers and siblings). To facilitate direct comparison with Buchan et al. (2003) results, we also calculated the total number of interventions that each juvenile received from all adult males and then measured the proportion of aid to each juvenile that each male was responsible for, considering only the time period when he and the juvenile were both present.

To evaluate a male's willingness to aid a juvenile in distress, we supplemented behavioral data with a playback experiment. We opportunistically recorded screams of juvenile baboons involved in aggressive disputes using Sennheisser ME88 microphones and Marantz digital recorders. Digital sound files were saved in .wav format and edited with CoolEdit software (Syntrillium, Phoenix AZ, USA). Each scream bout used in a playback experiment consisted of between 4 and 6 (mean=5.2±0.8) screams, in most cases originating from one recording of

a naturally occurring scream bout. The mean duration of each playback sequence was 4.4 (±0.5)s. All scream bouts were similar in amplitude and matched the amplitude of naturally occurring screams (60–70 db recorded at approximately 5-m distance).

Calls were broadcast from a Bose Roommate II loudspeaker hidden in vegetation between 10 and 12 m from the male at roughly a 90° orientation to him. In all cases, the caller, the caller's mother, and all other adult males were out of sight and separated by at least 50 m from the playback location. We used a Sony DCR-TRV25 digital video camera to record any changes in the male's orientation relative to the speaker for 10 s before and 1 min after playback. We measured a male's strength of response by his latency to respond to the call and the duration of time spent looking in the direction of the speaker. We then followed the male for 15 min to determine whether he subsequently interacted with the caller.

Playback experiments followed a matched-pair within-subject design. In trials separated by at least 1 day, six males heard either the screams of their juvenile associate or the screams of a same-aged control juvenile. Control juveniles had been conceived when the male was present in the group but did not exhibit preferential associations with him. We attempted to test every male with calls from each of his juvenile associates, counter-balanced with tests involving an age-matched control. One male emigrated from the group before we were able to test his response to the screams of any control juveniles. We were not able to complete playback experiments for four juveniles with identified male caretakers, either because we did not record a high-quality scream (two juveniles), the juvenile died before we were able to conduct the playback experiment (one juvenile), or the playback experiment could not be scored because the male subject was distracted by an interaction with another baboon immediately after the playback (one juvenile). If a male had more than one juvenile associate and appeared as a subject in more than one playback, we calculated his mean response latency and duration to derive a single figure for statistical analyses.

To increase our sample size for the within-subject comparison, we also included as subjects two recent immigrant males who did not exhibit preferential associations with any juveniles but who had been resident in the group long enough to father the infants of females with whom they now maintained a friendship. These two males heard the screams of their female friend's infant matched with the screams of a non-friend's infant.

We also conducted a between-subject analysis in which we compared the response of a male caretaker with the response of an unconnected control male to the same juvenile's screams. Unconnected males had all been resident in the group when the juvenile was conceived—and thus were possible fathers—but did not exhibit preferential associations with the juvenile. Unconnected males had dominance ranks within two positions of the caretaker's rank. As much as possible, we attempted to ensure that each male was included in the role of caretaker and control in the same number of playback experiments. Again, if a male appeared as a subject or control in more than one playback trial, we calculated a mean response measure for statistical tests.

Genetic analyses

Genetic samples were collected from 75 individuals, including all 17 juveniles, eight infants, their mothers, and 25 candidate fathers. Candidate fathers included all adult and sub-adult males aged ≥7 years who were present when the immature baboon was conceived. In most cases, four fecal samples were collected per individual and stored in RNA Later at −20–+10°C for between 1 and 3 years before extraction at the Molecular Anthropology Laboratory, New York University. Samples were extracted using the QIAamp DNA Stool Mini Kit (Qiagen, Valencia, CA, USA), following the protocol for isolation of DNA from human stool, but with the following modifications: (1) Feces were agitated in ASL buffer at 10°C for between 12 and 24 h before extraction; (2) half of an InhibitEx pellet was used per sample; (3) for the final elution step, 75 μL of elution buffer were applied to the extraction column, and the buffer was allowed to remain on the column for 20–30 min. For two individuals, tissue samples were recovered after death, and DNA was extracted using the DNeasy Tissue Kit (Qiagen).

Samples were genotyped using polymerase chain reaction (PCR) at nine to ten human-derived MapPairs microsatellite marker loci found in initial screenings to amplify reliably and to be variable in this baboon population. PCR amplifications were multiplexed using QIAgen Multiplex PCR kits with between one and five loci run in a single PCR reaction, following the manufacturer's protocol, with the exception that PCR reactions were run in a total volume of 10 μL rather than 50 μL. PCR product separation was run via capillary electrophoresis on an ABI 3730 automated DNA analyzer. GeneMapper 3.5 software was used to assign fragment size and to make preliminary allele calls, which were verified by A.D. Heterozygous allele calls at each locus were confirmed with a minimum of two independent PCR replicates, and homozygous allele calls were confirmed with a minimum of four independent PCR replicates. Maximum likelihood-based paternity was assigned using the software Cervus 3.0

(Marshall et al. 1998). Known mothers for all immature baboons were assigned maternity with >95% confidence in likelihood-based analyses; in no case did offspring mismatch from their putative mothers at any loci. For the final paternity assignment, Cervus paternity simulations were run assuming a pool of 20 candidate fathers for each offspring (which we presumed to represent 95% of total possible candidate fathers), 95.7% of all loci typed, and a conservative genotyping error rate of 0.05 (the actual estimated genotyping error rate was less than 0.002). The confidence levels associated with paternity assignments were obtained by simulating parentage for 100,000 offspring based on allele frequencies derived from the study population.

Paternity was assigned with 95% confidence for all 17 juvenile baboons. For 16 individuals paternity was unambiguous, since one male could not be excluded at any of the loci and all other sampled males were excluded at one locus or more. For one remaining juvenile (SB; Table 1), two candidate fathers were excluded at a single locus, and all other males were excluded at multiple loci. A sub-adult male JL was assigned as the most likely father of this juvenile. However, the next most likely father was an adult male, HA, who held the alpha position when SB was sired and who behaved as the caretaker of SB. We compared SB

and both putative fathers at four additional loci but were unable to resolve his paternity. Due to the exclusion of both candidate fathers at one locus and the discrepancy between the cervus assignment and our behavioral observations, we did not assign a father to SB and did not include him in paternity analyses.

To determine possible genetic relatedness between caretakers and fathers, we used the software GenAlEx version 6.2 (Peakall and Smouse 2006) to evaluate the pairwise relatedness ($r$) values among group members using the estimator of Queller and Goodnight (1989). Values of r range from $-1$–$+1$, with negative values indicating that two individuals are less closely related than two individuals drawn at random from the population. We included all genotyped members of the troop, based on samples collected between 2001 and 2007 ($n=138$ unique individuals, including 40 males and 98 females).

Statistical analyses

Due to small sample sizes and violations of normality, we used non-parametric statistics for all analyses (SPSS 16.0 Software, Chicago, IL, USA). All tests were two-tailed. When making multiple comparisons between groups, we used the Bonferroni correction to control for family-wise

**Table 1** Attributes of juveniles and their male caretakers

| Juvenile | Sex | Age when research began (month) | Cervus least likelihood father (number of trio loci genotyped/number of loci excluded at) | Status of father | Status of mothers' former friend(s) | Male caretaker(s) | Is caretaker sire? | Was caretaker friend of juvenile's mother post-parturition? |
|---|---|---|---|---|---|---|---|---|
| BM | F | 21 | EL (10/0) | Present | Present | EL | Yes | Yes |
| JT | F | 16 | EL (10/0) | Present | Present | EL | Yes | Yes |
| IA | M | 30 | EL (10/0) | Present | Present | EL | Yes | Yes |
| XA | M | 14 | EL (10/0) | Present | Present | EL/LO | Yes/No | Yes/No |
| SF | F | 6 | LO (10/0) | Present | Present | HA | No | Yes |
| SB | M | 9 | JL/HA (10/1)[a] | Present (?) | Present | HA/FT | Yes (?)/No | Yes/Yes |
| BX | M | 12 | SP (10/0) | Absent | Present | NA | No | Yes |
| VV | M | 12 | SP (10/0) | Absent | Present | RY | No | Yes |
| LP | F | 14 | SP (10/0) | Absent | Present | EL | No | Yes |
| PE | F | 14 | SP (10/0) | Absent | Present | EL | No | Yes |
| FA | M | 19 | BG (10/0) | Absent | Present | EL | No | Yes |
| DD | M | 23 | MU (9/0) | Absent | Present | None | n/a | n/a |
| CB | F | 16 | SP (10/0) | Absent | Absent | FT | No | No |
| KT | F | 24 | MU (10/0) | Absent | Absent | FT | No | No |
| PP | F | 26 | WO (10/0) | Absent | Absent | LO | No | No |
| HP | M | 16 | SP (10/0) | Absent | Absent | None | n/a | n/a |
| KH | M | 14 | SP (10/0) | Absent | Absent | None | n/a | n/a |

[a] Two candidate fathers were both excluded at a single locus, while all other males were excluded at multiple loci (see "Materials and methods"). JL was a sub-adult when SB was conceived. HA was the alpha male

error rate. These tests are designated by $\alpha^*=\alpha/c$, where $\alpha$ equals 0.05 and $c$ equals the number of comparisons performed. For all other tests, alpha was set at 0.05. Results are presented as median and ranges, unless otherwise stated.

## Results

### Preferential associations between adult males and juveniles

We identified 16 caretaker relationships involving 14 (82%) juveniles and six (75%) adult males (Table 1). Twelve juveniles had one male caretaker, and two juveniles exhibited similarly high levels of association with two male caretakers. All six of the males who had been resident in the group when juveniles were conceived were caretakers of between one to seven juvenile associates (median=2). Caretakers held ranks from two to nine during the study period. The only males who were not caretakers of juveniles were the two most recent immigrants, who had not been present when any of the juveniles were conceived.

Juveniles and their male caretakers shared 63.2% of the juveniles' total tolerated approaches with any male (range= 18.6–100%), while juveniles and their next closest male associate shared 10.7% of the juveniles' total tolerated approaches (range=0–21%) (Wilcoxon, $T^+=105$, zero ties,
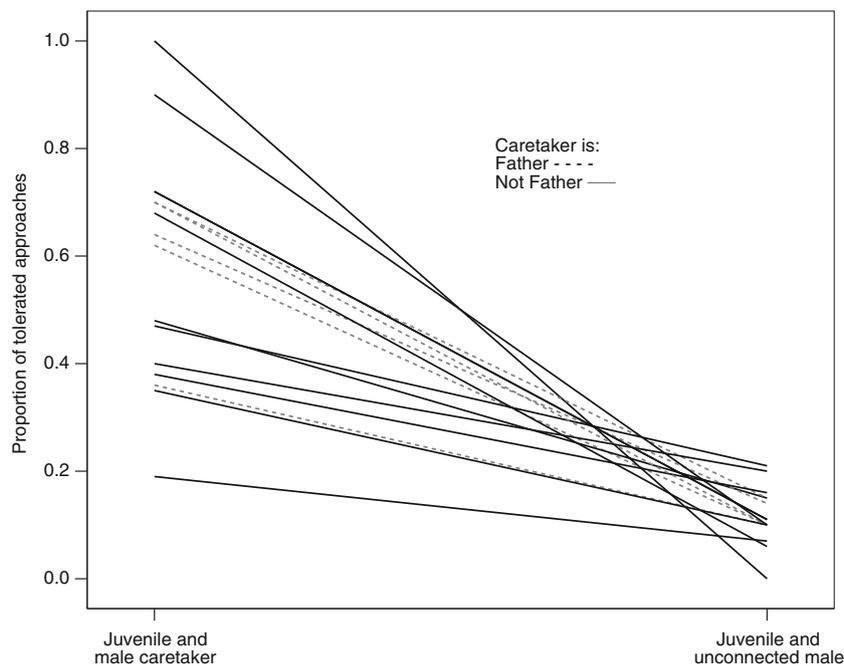
$N=14$, $P=0.001$; Fig. 1). Juveniles and their male caretakers were nearest neighbors during 6.5% (range=1.5– 37.5%) of male focals, while juveniles and their next closest male associate were nearest neighbors during 2.5% (range=0.8–5.0%) of focals (Wilcoxon, $T^+=103$, zero ties, $N=14$, $P=0.002$).

There were 13 male–juvenile dyads with sufficient data to calculate Hinde indices. In all cases, the Hinde indices were positive (median score=31.3, range=5.0–49.9), indicating that juveniles were more responsible for initiating contact with males than for breaking contact, while males were more responsible for breaking contact with juveniles than for initiating contact.

### Relationship between caretaking, paternity and previous friendships

Only five of 16 juveniles (31%; excluding SB; see "Materials and methods" and Table 1) had fathers still residing in the group at the time of this study. Four of these juveniles had the same father (EL), who, in all four cases, was both the current caretaker and also the former friend of the juvenile's mother. In the fifth case, the father was neither the current caretaker nor a former friend.

Twelve (71%) of the 17 juveniles co-resided with the male or males who had been their mother's friend during their infancy (the mother of one juvenile had had two friends during his infancy). In 11 of these cases, the



**Fig. 1** Proportion of tolerated approaches between juveniles and their male caretakers and juveniles and unconnected males. *Gray thatched lines* indicate caretakers who were the fathers of their juvenile associates. *Black solid lines* indicate caretakers who were unrelated to their juvenile associates
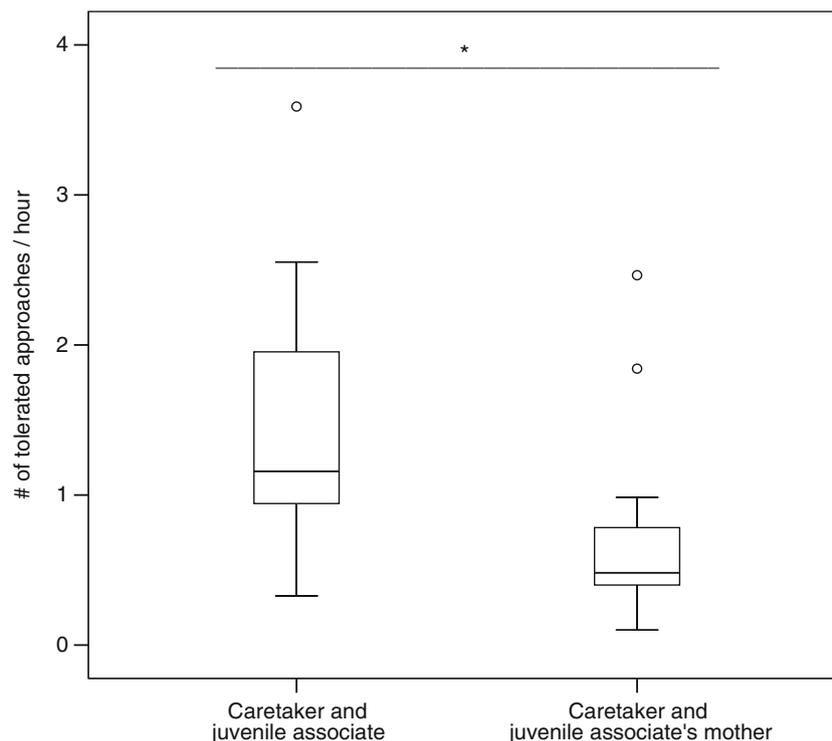
juvenile's current male caretaker (or caretakers) was its mother's former friend (binomial, $N=12$, $P=0.006$). One of these juveniles had a second caretaker who had not been his mother's friend. One juvenile did not exhibit preferential associations with any male, despite the fact that his mother's former friend was present. Finally, five juveniles (29%) did not co-reside with their mother's former friend or with their fathers because those males had either died or emigrated. Nonetheless, three of these juveniles had male caretakers.

Males who were caretakers of unrelated juveniles had not previously shared a close bond with the juveniles' biological fathers. Male chacma baboons rarely groom one another or form coalitions, and their relationships are largely competitive (Bulger 1993; Kitchen et al. 2003). Long-term records suggest that males seldom immigrate to the same group as their brothers or other close relatives (Cheney and Seyfarth, unpublished data). The relatedness analysis confirmed that fathers and caretakers were no more closely related, on average, than random male pairs. The mean $r$ among all male dyads ($n=40$ males, 780 dyads) was $-0.002$ (SD=0.200), while the mean $r$ among the subset of ten father–caretaker dyads where the father was not also the caretaker was $-0.024$ (SD=0.199). The father–caretaker dyad with the highest degree of relatedness shared an $r$ value of only 0.150 (LO and HA).

In summary, a previous friendship with the juvenile's mother appeared to be the primary factor motivating male caretaking behavior. In contrast, genetic relatedness appeared to be neither a necessary nor a sufficient determinant of male caretaking behavior. Most of the juveniles' biological fathers had died or emigrated from the group before this study began and thus did not have opportunities to provide paternal care. Of fathers present during the study, only those who had formed friendships with their offspring's mother post-parturition exhibited preferential associations with their juvenile offspring.

Relationship between caretakers and mothers of juvenile associates

Twelve (71%) juveniles co-resided with both their mothers and their male caretakers. Only two (17%) of these mothers, however, currently exhibited a preferential association with their juvenile's caretaker, based on tolerated approach rates. These females also had the two youngest juveniles in the study. In all other cases, females either did not currently exhibit a preferential association with any male or they exhibited a preferential association with a male other than their juvenile's caretaker (usually because they had a new infant and had formed a friendship with a different male). Male caretakers and their juvenile asso-



Fig. 2 Rates of tolerated approaches between juveniles and their male caretakers and the juveniles' mothers and the same males. *Box plots* indicate median values and second and third quartiles. *Error bars* represent minimum and maximum values. *Circles* above or below the *box plots* represent outliers. A *single asterisk* denotes *p* values less than 0.05. A double asterisk denotes *p* values less than 0.01

ciates shared a higher rate of tolerated approaches than did the same males and their juvenile associates' mothers [1.2 approaches/hour (range=0.3–3.6) vs. 0.5 approaches/hour (range=0.1–2.5); Wilcoxon, $T^+=65$, zero ties, $N=12$, $P=0.041$; Fig. 2]. Thus, male associations with juveniles did not reflect current associations between males and the juveniles' mothers.

Interventions

Adult males intervened on behalf of juveniles in 52% of all interventions to juveniles ($N=88$). Of these, 74% were by the juveniles' caretakers, with confirmed fathers contributing 12% (17% if likely father HA is included; see Table 1) of the total interventions by caretakers ($n=34$). Caretakers intervened when juveniles were in conflicts with other adult males (38%), with subadult males and females (23%), with adult females (21%), and with other juveniles (18%). Males made 0.3 interventions/month (range=0–1) on behalf of their juvenile associates, compared with 0.01 interventions/month (range=0–0.1) on behalf of unconnected juveniles (Wilcoxon, $T^+=15$, one tie, $N=6$, $P=0.043$).

Although the sample size of confirmed fathers was small, there was no evidence that males discriminated between their genetic offspring and their unrelated juvenile associates. Of the one likely and two confirmed fathers, only one male (HA, the likely father) provided as great a proportion of interventions to his genetic offspring as he did to his unrelated juvenile associates. However, all three males aided their unrelated juvenile associates more than they aided unconnected juveniles. Indeed, all caretakers (both the three fathers and the three caretakers without any genetic offspring) provided a significantly greater proportion of aid to their unrelated juvenile associates than they did to unconnected juveniles [80.1% (range=0–100%) vs. 2.5% (range=0–15%), Wilcoxon, $T^+=15$, one tie, $N=6$, $P=0.042$].

There were differences in the proportion of interventions that juveniles received from male caretakers, close maternal relatives, and other adult males (Friedman, $\chi^2=7.128$, $N=12$, $P=0.028$). Juveniles received more support from caretakers than from other, unconnected adult males (post-hoc Wilcoxon, $T^+=54$, two ties, $N=12$, $\alpha^*=0.017$, $P=0.007$) and juveniles received, though not significantly, more support from caretakers than from close maternal relatives (post-hoc Wilcoxon, $T^+=54$, one tie, $N=12$, $\alpha^*=0.017$, $P=0.059$). Juveniles received similar levels of support from maternal relatives and from unconnected males (post-hoc Wilcoxon, $T^+=16.5$, six ties, $N=12$, $\alpha^*=0.017$, $P=0.207$; Fig. 3). Male caretakers were also more likely to support their juvenile associates in conflicts involving the members of higher ranking matrilines. Considering only the subset of interventions where the aggressor was ranked within the female hierarchy, interventions on behalf of juvenile associates in conflicts with members of higher ranking matrilines made up 61% ($N=11$) of male caretaker interventions ($N=18$). In contrast, such interventions made up only 19% ($N=3$) of maternal kin interventions ($N=16$).

Playback experiments

Regardless of whether they were confirmed or probable fathers ($N=4$) or unrelated to their juvenile associates ($N=5$), caretakers responded to playbacks of their associates' screams for a significantly longer duration than unconnected control males (Mann–Whitney, $U=12$, $N_1=N_2=9$, $P=0.011$; Fig. 4). There were no differences between male caretakers and unconnected males in the latency to look toward the speaker (Mann–Whitney, $U=39.5$, $N_1=N_2=9$, $P=0.931$). Neither male caretakers nor unconnected males tended to interact with the juvenile caller in the 15 min immediately following the playback (Mann–Whitney $U=40.5$, $N_1=N_2=9$, $P=1.0$).

For the within-subject comparison, we combined the responses of five male caretakers tested with juvenile associates and control juveniles with the responses of two additional males tested with the screams of their female friends' infants and control infants. Males spent more time looking toward the speaker in response to the calls of their juvenile or infant associates than to the calls of age-matched control juveniles or infants (Wilcoxon, $T^+=20$, one tie, $N=7$, $P=0.046$; Fig. 5). Again, this difference was not driven by confirmed or probable fathers, who accounted for only three of the seven caretakers tested. There were no differences in the latency to look toward the source of the calls (Wilcoxon, $T^+=18$, one tie, $N=7$, $P=0.116$).

**Discussion**

Our research, in combination with recent findings in yellow baboons (Buchan et al. 2003; Charpentier et al. 2008), confirms that, even in primate species with promiscuous mating systems, short-term and variable heterospecific bonds, and high levels of paternity uncertainty, males provide long-term care to juveniles. During social conflicts, juveniles received the greatest proportion of support from their male caretakers, and male caretakers were more likely than maternal relatives to defend juveniles against aggressors from higher ranking matrilines (see also Pereira 1989). Thus, while support from maternal relatives is important in reinforcing existing dominance hierarchies (e.g., Cheney 1977; Datta 1988; Pereira 1989; Cheney and Seyfarth 1990; Chapais et al. 1997, 2001), support from male caretakers
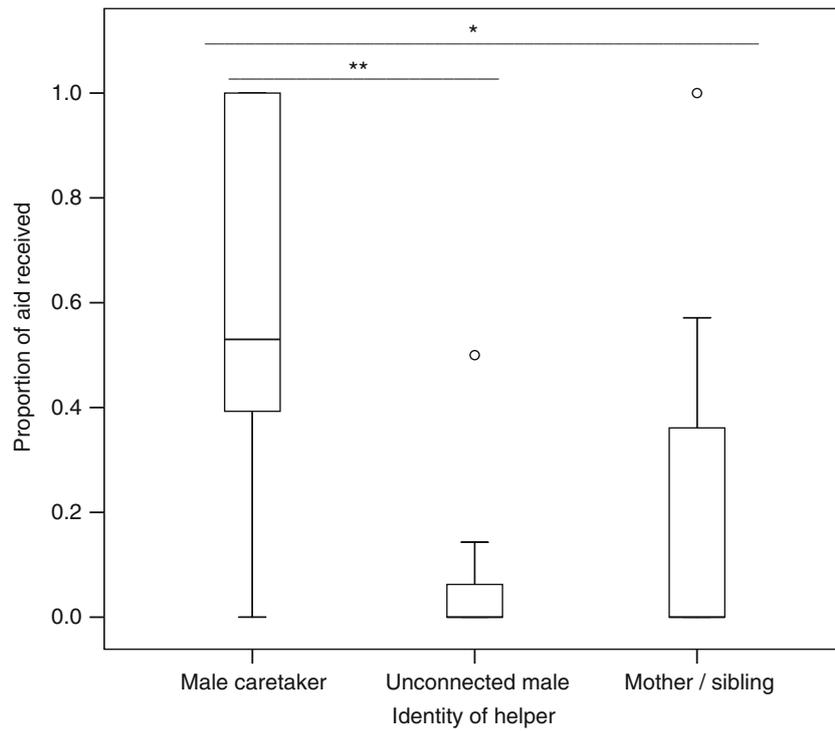
**Fig. 3** The proportion of total interventions received by juveniles from caretakers, unconnected males, and close maternal relatives. Legend as in Fig. 2
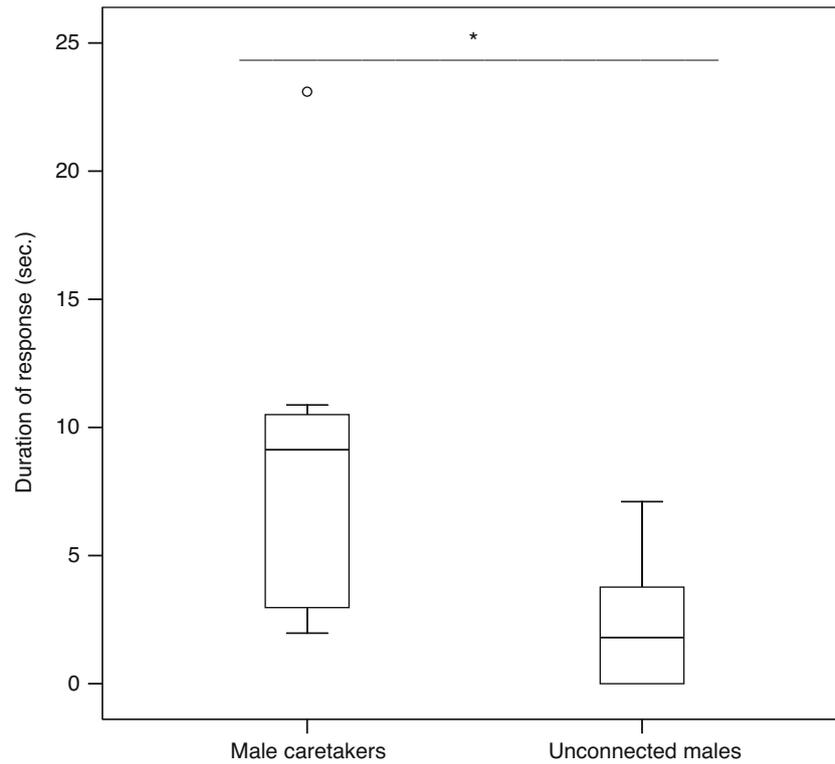


**Fig. 4** The duration of response by male caretakers and unconnected males to playbacks of juveniles' screams. Legend as in Fig. 2
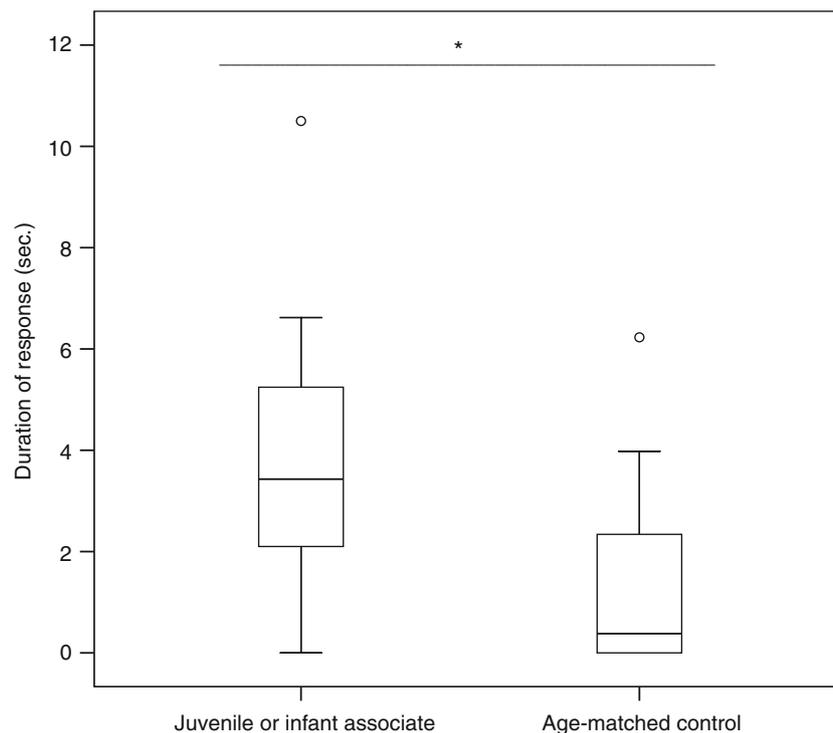
**Fig. 5** The duration of response by male caretakers to playbacks of their juvenile or infant associates' screams compared to the screams of unconnected juveniles or infants

may be an important factor in rare cases in which juveniles attain ranks above their maternal relatives (e.g., Pereira 1989).

In addition to support in aggressive interactions, long-term male caretaking behavior has many other potential fitness benefits for immature baboons that deserve further study, including increased foraging efficiency, access to high quality foods, and protection from predators. During our study, juveniles were often found in close proximity to their male caretakers at water crossings, where predation risks are high, and also immediately following an attempted or successful predation event. There is anecdotal evidence for a role of putative fathers in protection of infants from predators at the same study site (Hamilton 1984).

Male chacma baboons provided preferential aid to the juvenile offspring of their former female friends regardless of whether they were the fathers of these offspring. Indeed, although the two confirmed and one likely father in this study aided their juvenile associates at higher frequencies than they aided unconnected juveniles, they did not appear to differentiate between their genetic offspring and their unrelated juvenile associates. This evidence is similar to patterns of male–infant associations in olive baboons where "…the existence of a friendship with the mother is a necessary and sufficient condition for the existence of an affiliative relationship between him and the female's

infant…" (Smuts 1985: 183). In contrast, in the study of Buchan et al. (2003) of yellow baboons, males provided a greater proportion of interventions to genetic offspring than to both unrelated juveniles they could not have sired and unrelated juveniles they might have sired. However, because Buchan and colleagues did not differentiate between offspring of former friends and non-friends, the unrelated juveniles in the latter category likely included "unconnected" offspring of non-friends. This leaves open the possibility that males might not have differentiated their genetic offspring from unrelated offspring of former friends. Indeed, Buchan et al. (2003) suggest that males may rely in part on behavioral cues to identify their offspring. Additional studies of both yellow and chacma baboons are clearly needed to determine the exact behavioral and/or phenotypic cues that males use to identify their offspring.

Although males in our study invested primarily in juveniles whom they might have fathered, for the most part, these associations involved non-offspring. Only 35% of immature baboons aged 0.6–4 years had fathers present, and these fathers represented only 25% of the adult males residing in the group. In comparison, in the study of Buchan et al. (2003), 50% of juveniles had fathers present at 3 years of age. The relative lack of opportunity for long-term paternal investment in the Moremi population may

reflect the high predation rates at this site (Cheney et al. 2004). The median length of time that fathers remained in the group following the birth of their offspring was only 0.9 years (range, 0–7.4 years; $N=48$ individuals born from 1997 to 2007 whose fathers could be identified, excluding individuals with fathers still present in the group). Indeed, 20% of the 59 individuals with known fathers were born after their fathers had disappeared from the group. These disappearances were most often the result of death due to illness or predation rather than emigration; 12 (80%) of the 15 known fathers who disappeared from 2002 to 2007 died either of illness or confirmed or strongly suspected predation. The high proportion of absent fathers during this study period may also have resulted in part from stochastic events. In the 2 years before the onset of this study, two alpha males had died suddenly, leaving nine unweaned or as yet unborn infants, representing 53% of the juveniles in this study. In the 13 prior years, no male had ever disappeared while holding the alpha position. It therefore seems likely that a higher proportion of juveniles at this site typically have fathers available as potential caretakers.

The majority of lactating females formed friendships with males whether the father of their offspring was present or absent (Moscovice et al., manuscript in preparation). When fathers were present, females formed friendships primarily with these males, who had typically monopolized matings during the females' last conceptive cycle. When fathers were absent, females formed friendships with the male who had monopolized the greatest proportion of her consort days of the males still present in the group. It seems likely that, in both chacma and yellow baboons, females' and males' choices of friends are linked to reliable cues of paternity, such as previous mating effort, and that males rely on these cues to determine their investment patterns (Palombit et al. 1997; Lemasson et al. 2008). The frequency with which this strategy results in true paternal care should depend on the extent of co-residency of fathers and offspring over time. When fathers are present, they will likely become caretakers of their own offspring. When fathers are absent, the most probable father among the remaining available males will likely become the caretaker.

Most forms of male caretaking behavior, including support of juveniles during social conflicts, may represent relatively low-cost activities for males. The majority of caretaker interventions in social conflicts occurred against female, sub-adult, or juvenile opponents who posed minimal threat to males, and the subset of interventions against adult males rarely resulted in direct fights and never resulted in injuries to the caretaker. Ultimately, male baboons may provide care to unrelated juvenile offspring of former friends because the costs associated with such care are relatively low compared with the potentially high fitness costs of refusing aid to a juvenile who is a possible offspring.

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