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Friendships between males and lactating females in a free-ranging group of olive baboons (*Papio hamadryas anubis*): evidence from playback experiments

A. Lemasson · R. A. Palombit · R. Jubin

Abstract Close association between an anoestrous female at the time of lactation and adult male(s) is relatively rare in mammals, but common in baboons (*Papio hamadryas* subsp.). The functional significance of these "friendships" remains unclear, however. In chacma baboons (*P. h. griseipes*), friendships are a counter-strategy to infanticide by immigrant males. Experimental playback of female distress calls in chacma baboons revealed that male friends are more motivated to protect females and infants than are control males. Olive baboons (*P. h. anubis*) also exhibit friendships, but infanticide is rare, suggesting that friendships provide females with protection from non-lethal aggression (anti-harassment hypothesis) or serve to promote male–infant bonds that later benefit the maturing juvenile (future male caretaker hypothesis). We replicated these playback experiments on a group of olive baboons to test between these hypotheses and to evaluate if the lower costs of non-lethal harassment lessens male protective responsiveness relative to protection from (more costly) infanticide. Spatial data revealed that most lactating females had one to four friend males. Relative to non-friends, friend dyads were characterized by higher rates of allogrooming and infant handling, but less agonism. Female rank was correlated with the number of male friends. Just as in chacma baboons, playback of female screams elicited stronger responses from male friends than control males in support the anti-harassment hypothesis. Compared to the chacma baboon, male olive baboons appeared to exhibit similarly high levels of protective solicitude for female friends although they protect against non-lethal harassment rather than infanticide.

Keywords Friendship · Infanticide · Lactation · Playback · Olive baboons

Introduction

The coevolution of male and female social and reproductive strategies has received increasing attention of late (e.g., Arnqvist and Rowe 2005). One area of special interest concerns the evolution of cohesive bonds between the sexes that persist into a female's anoestrous period. Darwin's (1871) sexual selection theory predicts that if post-copulatory association generally limits a male's sexual access to additional mates and is irrelevant to antecedent female choice, such association should be rare. The rarity of relationships between males and anestrous females in the mostly polygynous mammals largely supports this view. Yet, enduring bonds between anoestrous females and males do occur. Durable "pair bonds" were originally viewed as typical of monogamous systems with high paternity certainty and biparental care (Trivers 1972). This argument has been challenged on two grounds. First, avian studies have demonstrated that social monogamy, paternity certainty, and male care are not invariably linked (Birkhead and Møller 1992; Avise

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1996; Møller and Cuervo 2000). Second, "bonds" between anoestrous females and males have evolved in some polygynous systems.

For example, affiliative bonds between adult males and lactating females are widespread in baboon (*Papio hamadryas* subsp.) societies. Olive baboons (*P. h. anubis*) live in polygynous, multi-male, multi-female groups characterized by male migration and stable matrilineal kinship structure (Melnick and Pearl 1987). Births occur throughout the year and are followed by a period of lactational amenorrhea averaging 407 days (Smuts and Nicolson 1989). After parturition, a lactating female and her infant are frequently in proximity to unrelated adult male(s) who interact peacefully with them (Smuts 1985). These "friendships" have also been described in yellow baboons (*P. h. cynocephalus*; Altmann 1980; Collins 1986), gray-footed chacma baboons (*P. h. griseipes*; Palombit et al. 1997), and Cape chacma baboons (*P. h. ursinus*; Seyfarth 1978; Anderson 1983; Weingrill 2000).

The adaptive significance of friendships to females is addressed by at least three alternative hypotheses. The anti-infanticide hypothesis posits that males shield their friends' infants from risk of sexually selected infanticide (Busse and Hamilton 1981; see also van Schaik and Dunbar 1990). The anti-harassment hypothesis suggests that males protect mothers and/or infants from non-lethal harassment from conspecifics (Altmann 1980; Smuts 1985). Finally, the future male caretaker hypothesis posits that there are no immediate protective benefits from friendships, but a female's friendship promotes development of a bond between her infant and particular male(s). The fitness benefits of this bond accrue later to the independent, maturing juvenile, and may include enhanced access to food, accelerated socialization, retrieval from predators, and/or agonistic support in competition with other juveniles (Ransom and Ransom 1971; Seyfarth 1978; Altmann 1980; Burton 1972).

For the chacma baboons, several independent lines of evidence—demography, playback experiments, behavioral observations, and hormonal profiles—support the anti-infanticide hypothesis over rival models (reviewed by Palombit 2008). Infanticide by newly immigrant alpha males is not only common, but the primary cause of infant mortality among chacma baboons of the Okavango Delta, Botswana. A key question is whether friendship status enhances a male's tendency to invest in costly defense against infanticidal attacks. Palombit et al. (1997) addressed this question partly through playback experiments, which revealed that male friends responded significantly more strongly to simulated female distress than did non-friend control males of similar dominance rank. In summary, in this social system in which an alpha male's attack sometimes resulted in the death of an infant, a female's male associate responded more strongly to her screams than did other resident males.

In contrast to the chacma populations, infanticidal attacks are rare among east African olive baboons and not clearly part of male reproductive strategies (Henzi and Barrett 2003; Palombit 2003). However, olive baboons have long been known to form strong friendships (Smuts 1985). This situation offers an opportunity to replicate audio playback experiments of Palombit et al. (1997) to evaluate the functional significance of friendships for females and to assess the effect of reduced infanticide risk on male responsiveness to vocal signals of female distress.

Results of playbacks address the functional hypotheses in two ways. First, in light of the rarity of infanticide, the anti-harassment and future male caretaker hypotheses are arguably more likely adaptive explanations of female friendship behavior in olive baboon. As argued by Palombit et al. (1997), experimental playbacks can help to test between these two alternatives: The former hypothesis predicts significant differences in male response to female screams at the time friendships exist, but the future male caretaker hypothesis does not (as the proposed benefits of friendships do not lie in immediate protection but rather in male–infant bonds developing later). Thus, one aim of this study was to test experimentally the contrasting predictions of these alternative explanations for the first time in olive baboons.

Second, application of the same controlled playback protocol additionally allowed us to evaluate whether male olive baboons differ from male chacma baboons in their "solicitude," i.e., their tendency to protect female friends. Contrasting costs of lethal vs non-lethal aggression provide a rationale for such a test. In "infanticidal" chacma baboons, variation in a male's reaction to female distress potentially carries high fitness consequences—infant survival versus death. Palombit et al. (1997) argued that this situation adaptively intensifies male friend responsiveness to female screams. Conversely, in olive baboons, the comparatively lower fitness costs of non-lethal harassment to females predict that the response of male friends to playback screams may be weaker or more variable. We examined this possibility by evaluating the potential of the playback experiments to differentiate friend vs non-friend male responses.

A final goal was to assess the generality of friendship behavior in *Papio hamadryas anubis*. Since Smuts's (1985) ground-breaking research, no studies have applied the same quantitative methods to evaluate male–female relationships in other olive baboon groups.

Materials and methods

Study site and subjects

The research was conducted as part of an ongoing study of olive baboons (*P. h. anubis*) in the Laikipia District of

Kenya. Observations were made in the vicinity of Segera Ranch (36°50′ E, 0°15′ N) whose 20,250 ha join with neighboring landholdings to constitute a large conservation area. The study group (TDM group) is one of two olive baboon groups studied by RAP and colleagues since 1999. Subjects were fully habituated to observers on foot and individually identifiable. The study group comprised 100–110 individuals, including 19 to 23 adult males, 25 adult females, and their immature offspring.

Behavioral observations

Data presented here derive from approximately 489 contact hours with TDM group from February to July 2004. Behavioral data were collected via 10-min focal animal samples ($N=766$ evenly distributed among individuals) and ad libitum observations (Altmann 1974) of the adult males and adult females (14 of which were lactating during the study period). Observations were recorded onto a Psion Organizer handheld computer.

Male–female and male–infant social relationships were derived from spatial and social measures previously used to identify "friend dyads" in chacma baboons (Palombit et al. 1997):

Close proximity All approaches (movements within 2 m) and withdrawal (movements beyond 2 m) involving the focal animal were continuously recorded.

2- to 6-m Range The identities of all individuals within 2–6 m of the focal individual were recorded at 2-min intervals.

C score The above two spatial measures were used to calculate the "C score", following Smuts (1985): $C = 1(T_{0-2m}) + 0.25(T_{2-6m})$ where T_{0-2m} is the percentage of time that the members of a given dyad spent within close proximity and T_{2-6m} the percentage of time they spent in the 2- to 6-m range. For each lactating female, C scores were calculated for all adult males. A discontinuous distribution of C scores reflects the existence of a "special relationship" involving the female and particular males (Smuts 1985). Palombit et al. (1997) defined a "friend" as a male whose C score isolated him from the scores of other males by at least three intervals (Fig. 1).

Maintenance of close proximity The responsibility for maintenance of close proximity between the two members of a friendship dyad was determined using the Hinde's index (Hinde 1977). It is the percentage of approaches by the female subtracted by the percentage of withdrawals by the female. Its value varies from −100 (suggesting complete male responsibility for proximity maintenance) to +100 (suggesting complete female responsibility). Hinde indices were calculat-

ed for dyads with a sample of at least 20 approach–withdrawal interactions (Smuts 1985; Palombit et al. 1997).

Allogrooming The onset and termination times of hetero-sexual grooming involving the focal individual were recorded continuously during focal sessions. To assess how allogrooming varied with friendship status, we calculated the percentage of a female's close proximity time with each individual male devoted to grooming him. For each female, we then compared the total percentage for all male friends (divided by the number of male friends she had) with the corresponding quantity for non-friend males in the group. The analogous comparison was done for males grooming lactating friends vs non-friend females.

Agonism The following agonistic interactions were recorded continuously during focal sessions to yield a rate per unit time in close proximity: submission (e.g., the grimace or "bared-teeth" display, the "tail-up" display; Busse 1984), contact aggression (e.g. biting, slapping).

Infant-oriented behaviors We scored the frequency of several social behaviors involving infants and adult males: (1) "visual examination" occurred when an adult male in close proximity (2 m) to a lactating female and infant oriented his head toward the infant, to look at it closely or smell it, without touching the infant; (2) "handling" occurred when a male touched or manipulated the infant or carried it a short distance of 2–10 m; (3) allogrooming exchanged between infants and adult males; (4) "maternal intolerance" occurred when a male approached or reached for an infant but its mother immediately picked up the infant or repositioned her body to prevent the male from touching the infant.

Dominance The dominance status among all adult group members was assessed through data on supplants, the directionality of decided status-related displays (e.g., grimace), and the outcomes of aggressive interactions. A dominance index was estimated as the percentage of same-sex individuals dominated.

Non-parametric tests were used to compare the frequency of interactions (for the aforementioned categories) between a given lactating female and her friend vs non-friend males.

Experimental methodology

We performed playback experiments of females' calls to different male subjects and compared their reactions. Gouzoules et al. (1984) and Cheney and Seyfarth (1990) argue that one function of distress calls in cercopithecines is to recruit aid from potential allies when being attacked by conspecifics. Individual recognition of one another by voice (Bergman
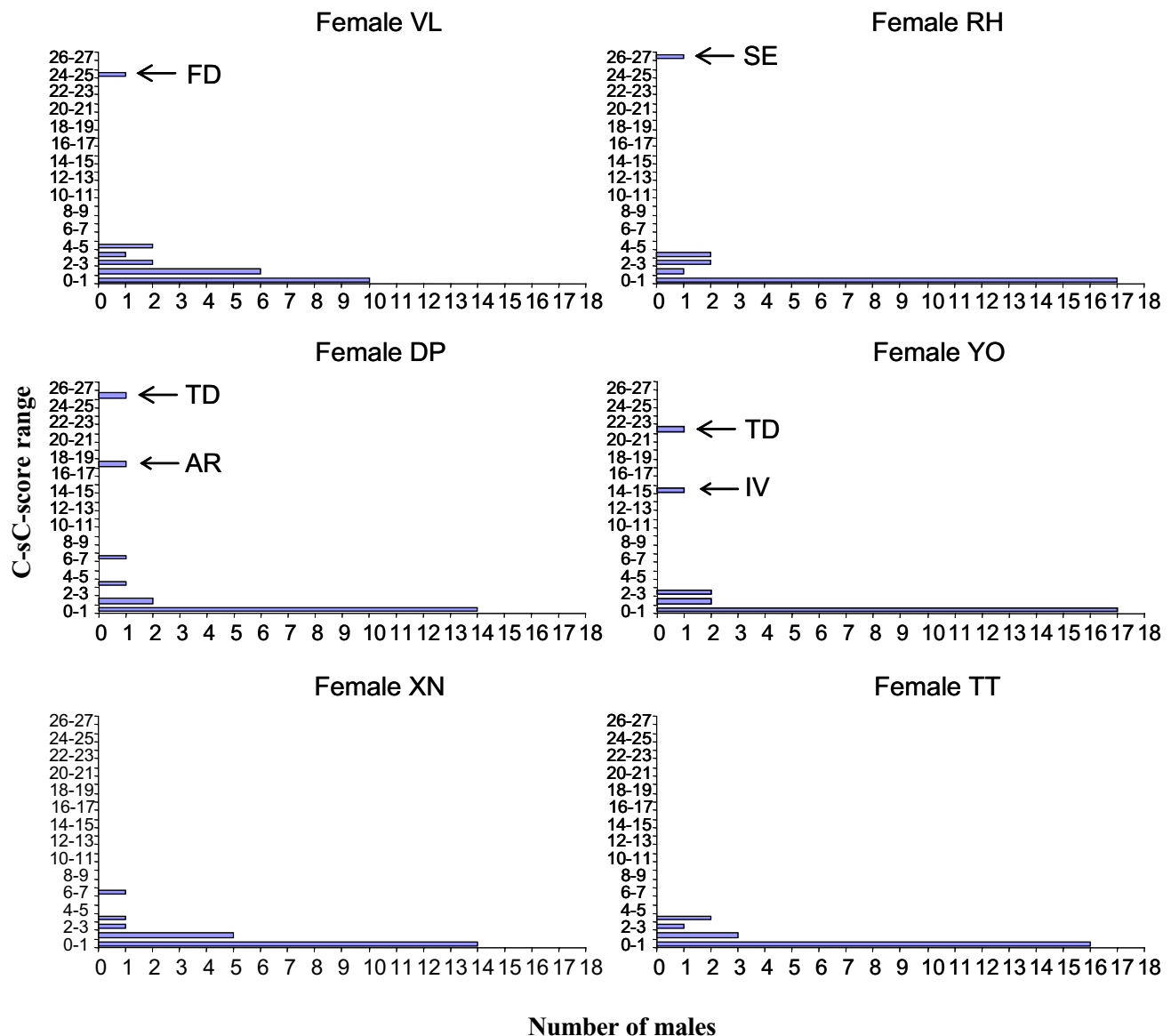
Fig. 1 Distribution of composite proximity score (*C* score) for six representative lactating females. The number of males in the group (*X*-axis) with a *C* score falling within the range given (*Y*-axis) is shown for each female. A two-letter name code is provided for any male who was designated a friend based on the distribution of *C* scores. In the examples illustrated here, VL and RH possessed a single friend, DP and YO possessed two friends, and XN and TT possessed no friend

et al. 2003) potentially facilitates this aid. The immediate response of baboons to naturally occurring screams is typically visual orienting (Palombit et al. 1997), which presumably reflects an effort by the listener to obtain information about the circumstances surrounding the signaler's current situation (Marler et al. 1992). In some cases, a listener provides actual support to the signaler through direct intercession in the conflict (Smuts 1985). We investigated whether friend and non-friend males differed in their responses to the screams of a lactating female.

Playback stimuli were distress calls (screams) recorded from known adult females in natural conditions during observations. Screams were responses to an attack by a male or a higher ranking female. Stimuli were recorded with a Sony WM-D6C recorder and a Sennheiser MZS6 microphone, subsequently digitized and isolated for playback using Cooledit Pro™ (version 2) software. Screams used as stimuli had an average duration of 1.59 ± 0.28 s ($N=7$). Playback amplitude was chosen to deliver a "natural" sounding scream, as previously judged by an observer at the distance of 15 m from the speaker, and was held constant in playbacks within each pair of experimental and control males.

The subjects were different pairs of adult males, classified either as a "friend" (i.e., the male presenting the highest *C* score value) or a control "non-friend" of the female whose scream was played back. A control male held comparable status in the male hierarchy as the corresponding friend male (± 2 rank positions) and possessed at least one

lactating female friend at the time of the experiment. Friend and control males in paired comparisons were presented with the same stimulus scream(s).

Following Palombit et al. (1997), several conditions were controlled in the experimental design to improve comparison of friend vs control male reactions: (1) the subject was spatially isolated (by 50 m) from other group members; (2) the female whose call was played was not visible to the subject and had not interacted affiliatively with him in the preceding 10 min; (3) friend and control male subjects in paired comparisons were engaged in the same activity (resting or eating the same food); (4) microhabitat visibility was qualitatively similar for both paired trials; (5) no intergroup encounters had occurred in the preceding 30 min; (6) no screams by any female or infant occurred in the previous 10 min.

During experiments, one observer (R.J.), typically visible to the subject, played the digitized stimulus from an I-pod™ A1040 connected to a Nagra-Kudelski™ DSM loudspeaker concealed in vegetation. Another visible observer (A.L.) videotaped the subject before and after playback using a digital video camera recorder Sony DCR-TRV 33.

The following precautions were observed to minimize habituation: (1) no more than two playbacks were conducted per day; (2) a particular stimulus was never played more than once per day; (3) a minimum of 72 h separated trials on a given subject; (4) frequent "mock" experiments were conducted in which observers and equipment were positioned as in actual experiments, but no stimulus was broadcasted. We performed the two matching tests (for a given female) as close as possible in time to avoid infant age effects [a mean of 12.6 days (SD=11.5, $N=7$) separated the two tests].

The screams of seven females were used as stimuli in playbacks. The order of presentation to friend vs control male was randomized. Following playbacks, an experienced observer "blind" to the particular treatment later reviewed videotapes and scored subjects' responses along the following variables: (1) duration of orienting in the direction of the speaker in the 20 s after playback minus the duration of orienting in the same direction in the 20 s before playback (following Palombit et al. 1997); (2) directionality of any movements in relation with the loudspeaker (walk/run towards or away the playback speaker). Subjects never responded vocally.

Results

Identification of friendship dyads and characteristics

Friendships

The distribution of C scores for the 14 lactating females were examined for patterns suggesting friendships. For three females, a lack of discontinuities in the distribution of C scores suggested the absence of a conspicuous male friend (AS, TT, XN). The remaining 11 females participated in a total of 19 friendships. The average number of C score intervals separating any male friend from the group of non-friend males in the next closest C score interval was 11.8 ± 5 (range 5–23, $N=19$). Six females possessed a single friend, while five females had several (one to four) friends (Fig. 1). For the latter five females, we found a particular friend characterized by a very high C score and several "weaker" friendships whose C Scores were still higher than those of the "mass" of non-friend males.

Among the resident adult males, 11 (48%) were never observed in friendships with lactating females, seven (30%) were involved in friendships with a single friend, and five (22%) participated in friendships with multiple (two or three) females simultaneously. The average C score of friendship dyads was 19.7 ± 5.8 (range 7.2–26.2, $N=19$).

Temporal development of friendships

The highest C score male friend was observed in close proximity with their associated female very soon after parturition (i.e., the same day, $N=5$ one day postpartum $N=1$, or 4 days postpartum $N=1$). The onset of "weaker" friendships was more variable, typically falling 9 ± 10 days after birth (range 0–27, $N=6$).

Factors influencing the number of friends possessed by a lactating female

Table 1 summarizes broad features of male–female friendships observed during the study period. Both multiparous and primiparous mothers of infants of both sexes were represented among observed friendships. A female's dominance rank was positively correlated with the number of simultaneous male friends she was observed to have (Spearman $N=14$, $r=0.63$, $p=0.02$).

Male–female interactions

Maintenance of close proximity

Friends spent $18.9\pm6.2\%$ (range 6.3–27.4, $N=19$) of their time in close proximity (2 m) to one another. For nine friendships dyads, the sample of approach–withdrawal interactions was large enough to calculate the Hinde index. In five of these friendships (56%), the male appeared more responsible than the female for close proximity maintenance, whereas the converse characterized three other friendships; in one friendship, partners appeared to contribute more or less equally to proximity maintenance (Fig. 2).

Table 1 Descriptive characteristics of friendships

Female	Male friends	Sex of infant	Infant age at time of playback	Female dominance index	Parity
EU	PY	M	265	88.9	M
YO	TD IV	M	95	87.5	M
FL	WT FD IA	M	57	85.7	P
PH	LY	F	55	66.7	M
RH	SE	F	115	50	M
DP	TD AR	F	60	37.5	M
CA	WT	M	45	30	P
KT	LY JI	F	No PB	100	M
NO	AR	F	No PB	75	M
VL	FD	M	No PB	72.2	M
BE	TD AR EG BO	F	No PB	66.7	M
TT	x	F	No PB	28.6	M
XN	x	F	No PB	20	M
AS	x	F	No PB	0	M

This table lists for each friendship: the infant's sex and age (in days) at time of playback (we averaged "the age at time of playback performed with the friend male" and "the age at time of playback performed with the control male", *No PB* No playback performed); the female's dominance index (percentage of females dominated); the female's reproductive parity (*P* Primiparous, *M* multiparous)

Allogrooming

Lactating females devoted a greater proportion of their close proximity time with male friends to grooming them than they did with male non-friends (two-tailed Wilcoxon signed-ranks test, $T=1$, $N=11$, $p=0.01$, Fig. 3). Similarly, more of an adult male's close proximity time with a female friend was committed to grooming than occurred during his close proximity with other lactating females (Wilcoxon $T=4$, $N=11$, $p=0.05$).
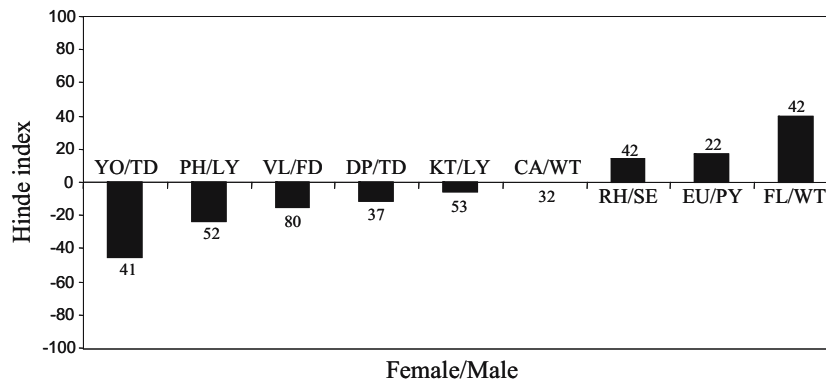
Agonism in close proximity

We focused on one type of mild heterosexual agonistic interaction (maternal intolerance) and two types of more intense heterosexual agonistic interactions (submissive display performed by the female and aggression performed

by the male). There was no statistically significant difference in rates of maternal intolerance directed at friend and non-friend males (two-tailed Wilcoxon signed-ranks test: $T=6$, $N=11$, $p=0.69$). Intense agonistic behaviors (submission and aggression), however, were less often observed among friends (0.33 ± 0.54) than among non-friends (3.33 ± 3.66; two-tailed Wilcoxon signed-ranks test: $T=4$, $N=11$, $p=0.03$).

Male–Infant interactions

Visual examination and handling of infants by males

The rate of visual examination of infants was similar for friend and non-friend males (0.99 ± 0.70 per hour of male–female close proximity; two-tailed Wilcoxon signed-ranks test: $T=7$, $N=11$, $p=0.24$). A significant difference existed in rates of infant handling behavior, however, which was

Fig. 2 Hinde indices for close proximity between males and female friends. The number of approach–withdrawal interactions used for the index calculation is given on the *top* of the histograms with the code name of the corresponding female. Positive (negative) Hinde indices suggest a female (male) responsibility for proximity maintenance
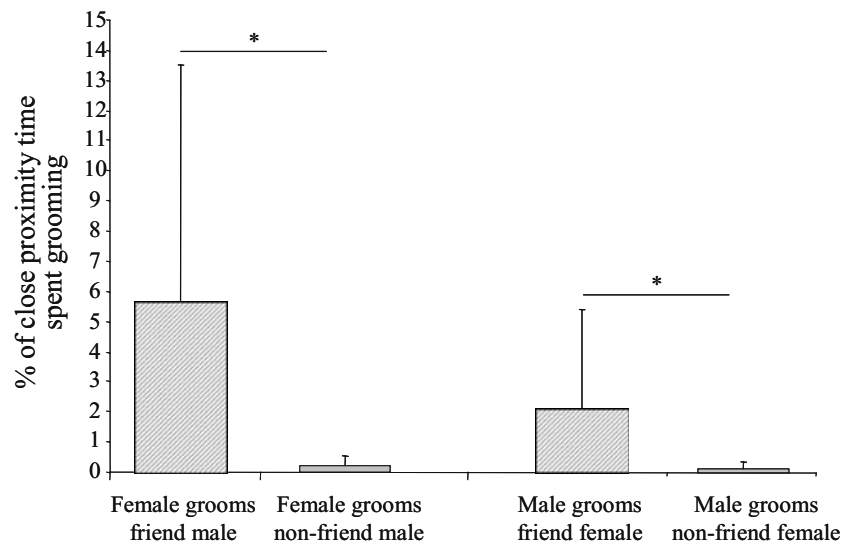
Fig. 3 Proportion of close proximity time spent grooming from female to male friend vs non-friend and male to female friend vs non-friend. Statistically significant differences are indicated by *asterisks* (Wilcoxon signed-ranks: $p \leq 0.05$)

three times higher for friend males than for non-friend males combined ($T=9$, $N=11$, $p=0.03$). This behavior occurred among friends at the rate of 1.85±1.51 per hour of male–female close proximity. All infants were seen to be handled by at least one male.

Allogrooming

Fourteen male–infant grooming interactions were recorded, of which, 13 involved a friend male but only one a non-friend male. Ten grooming bouts were directed by the male towards the infant, and four were directed by the infant towards the male. The average duration of these grooming bouts was 61.7±62.8 s.

Results of audio playback experiments

Visual-orienting response

Female screams elicited significantly stronger responses from male friends than from (non-friend) control males (two-tailed Wilcoxon signed-ranks test: $T=0$, $N=7$, $p=0.02$; Fig. 4). No statistically significant correlation was found between the duration of the male visual response and the age of the infant for either friends (Spearman correlation: $N=7$, $r=0.27$, $p=0.56$) or control males ($N=7$, $r=-0.50$, $p=0.25$). In addition, no statistically significant correlation was found between the relative magnitude of the response (estimated by the friend gaze duration minus the control's
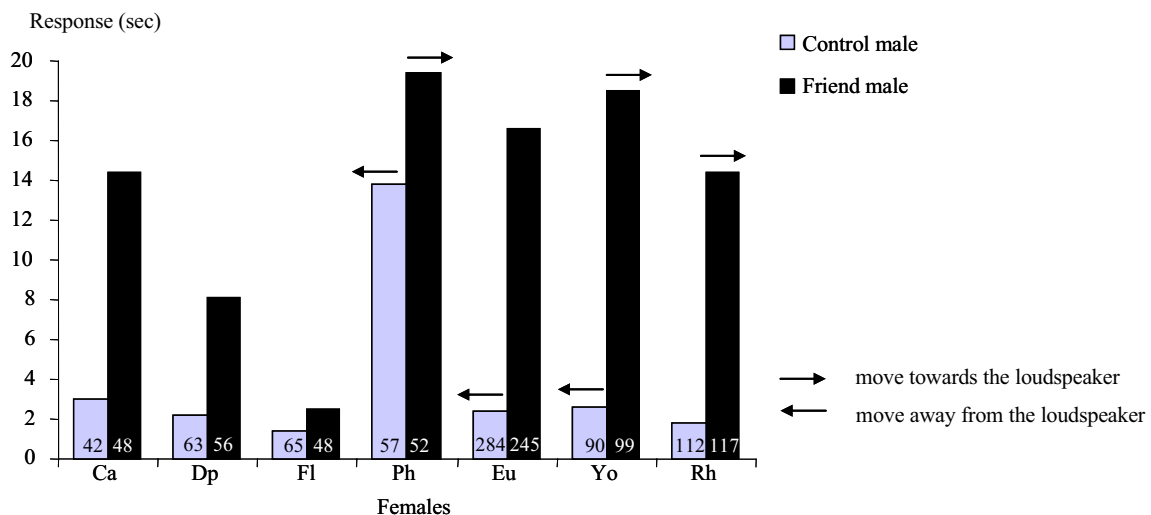
Fig. 4 Duration of visual-orienting responses and description of other behavioral responses by males to playback of females' screams. The age of infant when the test was done is written into the histograms

gaze duration to the same scream) and the age of the infant of the female whose call was played (Spearman correlation: $N=7$, $r=0.64$, $p=0.12$), or the strength of the friendship (as reflected by C score: $N=7$, $r=-0.32$, $p=0.48$), or responsibility for close proximity maintenance (as reflected by the Hinde index: $N=7$, $r=-0.29$, $p=0.54$) or the dominance status of the female ($N=7$, $r=0.36$, $p=0.43$).

Movement response

Movement toward the loud speaker followed audio playback for three (42.9%) friend males (all of whom reached the simulated conflict area within 20 s) but for no control males (Fig. 4). Conversely, playback elicited movement away from the loud speaker in three (42.9%) control males but in none of the friend males.

Discussion

This study provides new data supporting the widespread generality of "friendships" between adult males and anoestrous females in baboons in general and olive baboons in particular. Using methods similar to those of other studies (Smuts 1985; Palombit et al. 1997), we found that a substantial majority of lactating females (80%) engaged in close affiliative relationships with at least one adult male in the group. Among males, a smaller majority (52%) participated in friendships during the study period. Although these summary statistics derived from 6 months' observation may change as more data for this and other study groups are analyzed (Palombit 2006; Palombit, unpublished data), they nevertheless underscore the important distinctions Smuts (1985) originally drew between "friend" and "non-friend" males: Relative to non-friend dyads, friends are characterized by conspicuous spatial proximity initiated by both partners, high rates of grooming, and low rates of agonism. Lactating females were much more tolerant of male friends handling their infants than other males. We similarly found that female olive baboons commonly maintain multiple male friends at the same time. The number of male friends a female had was found to correlate positively with her dominance status. As higher rank may be associated with greater reproductive success (Smuts and Nicolson 1989; but see Cheney et al. 2004), this result may reflect the greater attractiveness of higher ranking females to multiple male associates (Stein 1984; Smuts 1985). Alternatively, high-ranking females may competitively exclude lower ranking rivals from social access to male friends (Palombit et al. 2001).

Playback of a female's distress call elicited significantly stronger responses (visual orienting and movement) from her male friend than from a control male of similar rank and friendship status. These results support the anti-harassment

hypothesis and are less consistent with the future male caretaker hypothesis. The greater solicitude of friends suggests that a primary benefit of friendships to female olive baboons is male protection. We believe that this protection is most likely to function in the context of support against conspecific harassment. Of course, olive baboons also confront allospecific danger, such as predation, which may also influence male protectiveness, and hence, the adaptive significance of heterosexual friendships. Potential predators in the Segera study area include lions (Panthers leo), leopards (Panthera pardus), spotted hyenas (Crocuta crocuta), wild dogs (Lycaon pictus), and feral dogs (Canis familiaris).

Risk of infanticide is a less likely female incentive for protective friendships. With the possible exception of the Gombe population (Collins et al. 1984), evidence for male infanticide is limited in olive baboons, and its patterning is much less consistent with the sexual selection hypothesis than is the case for chacma baboon infanticide (Palombit 2003). For example, only one case of male infanticide has been observed in 7 years in our study groups (Matsumoto-Oda and Palombit, unpublished data). Thus, although infanticidal behavior is certainly part of the behavioral repertoire of baboons generally, it is arguably demographically less important in olive baboons than in chacma baboons.

Nevertheless, the prediction that less lethal forms of aggression would dilute male responsiveness to vocal signals of female distress was not supported by our data. The playbacks suggested that male olive baboon friends are more strongly predisposed to supportive responses to female distress in a manner highly reminiscent (both qualitatively and quantitatively) of male chacma baboons in "infanticidal contexts." Thus, friendship status in olive baboons seems to similarly enhance male interest in defending lactating females (and infants) even from non-lethal forms of harassment that are ostensibly less costly to female fitness than infanticide.

The possible benefits of friendships to males are addressed by three general, but not mutually exclusive, set of hypotheses (reviewed Palombit 2000). The parental effort hypothesis proposes that males are the fathers of their female friends' infants (Palombit et al 1997; Weingrill 2000). Alternatively, the mating effort hypothesis posits that friendship with a particular female increases the chances of siring *future* offspring with that female in her following estrus period (Smuts 1985; van Schaik and Paul 1996). A final set of strategies emphasize indirect reproductive benefits of friendships to males, such as the use of infants as "agonistic buffers" or of females as "social tools" facilitating immigration.

Our data do not directly support these different alternatives. The comparatively greater infant handling rates by male friends is consistent with one version of the social tool hypothesis, but the generally peaceful contexts of such

handling episodes did not suggest an "agonistic buffering" function (sensu Stein 1984; Collins 1986). Genetic paternity analyses are required to address conclusively the parental effort and mating effort hypotheses, and these analyses are underway for the study population.

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