The adaptive value of 'friendships' to female baboons: experimental and observational evidence

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Abstract. Lactating female baboons, *Papio cynocephalus*, often maintain close associations with particular males. There are at least three proposed benefits of 'friendships' to females: (1) male protection against potentially infanticidal males; (2) male protection against harassment by dominant females; (3) male attachment to an infant that develops into future care of juveniles. These hypotheses were examined in a population of chacma baboons, *P. c. ursinus*, in which male infanticide accounted for at least 38% of infant mortality. Almost all mothers of young infants formed strong bonds with one or two males with whom they had copulated during the cycle in which they conceived their infants. Females were primarily responsible for maintaining friendships during lactation, but they terminated these relationships if their infants died. In playbacks of females' screams, male friends responded more strongly than control males. They also responded more strongly to the screams of female friends than to the screams of control females. Following an infant's death, however, male friends responded less strongly than control males to the same females' screams. Finally, male friends responded more strongly than control males to playback sequences in which female screams were combined with the threat vocalizations of a potentially infanticidal alpha male, but not when female screams were combined with the threat calls of a non-infanticidal male or the alpha female. Both observations and experiments suggest that the benefits of friendships to females derive from the protection of their infants against infanticide.

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Savannah baboons, *Papio cynocephalus*, are characterized by particularly high rates of association between anoestrous females and certain adult males (e.g. Ransom & Ransom 1971; Seyfarth 1978; Altmann 1980; Smuts 1985; Bercovitch 1991). These male companions are typically unrelated to females (i.e. non-natal males) and may hold any rank in the male dominance hierarchy. Although these long-term bonds, called 'friendships' (Strum 1974), have been widely described, the reproductive benefits and costs that they confer upon the male and female participants are poorly understood.

In this paper, we consider the adaptive advantages of friendships to females using data collected on a group of free-ranging chacma baboons, *P. c. ursinus*, in southern Africa. Friendships have received less empirical attention in chacma

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baboons in southern Africa than in East African populations, but research has confirmed their existence in multi-male groups (Seyfarth 1978). Several hypotheses have been suggested to explain the benefits of friendships to female baboons (Smuts 1985). The 'anti-infanticide' hypothesis proposes that females benefit from the protection that male friends provide against attacks by infanticidal males. The inhibitory effect of lactation on female ovulatory cycles establishes a potential for sexually selected infanticide in baboons (Altmann et al. 1978). Only in the chacma baboons of southern Africa, however, have reports emerged that repeated infanticidal attacks by newly immigrant males that have attained the alpha position in the dominance hierarchy appear to be relatively common (Busse & Hamilton 1981; Collins et al. 1984; Bulger & Hamilton 1987; Tarara 1987). The occurrence of infanticide among chacma baboons may result from the restriction of mating opportunities in these populations. Not only are alpha males apparently more successful at excluding

other males from copulating (Bulger 1993), even occasionally to the point of sometimes defending uni-male breeding units (Hamilton & Bulger, 1993) but they also appear to hold their alpha positions for far shorter periods of time than do their East African counterparts (Collins et al. 1984). These factors may favour infanticide as a male reproductive strategy. Several distinctive aspects of chacma baboon social behaviour have been interpreted as adaptively linked to male infanticide, including the relatively short alpha male tenure (Bulger & Hamilton 1987), the regular occurrence of copulation calls (O'Connell & Cowlishaw 1994), social interactions between females and immigrant males (Busse 1984a), and bonds between males and infants (Busse & Hamilton 1981; Anderson 1992).

In contrast, the 'female harassment' hypothesis suggests that male friends protect females from aggressive interactions with higher-ranking females. Postpartum harassment of mothers potentially occurs when dominant females handle other females' infants roughly or even kidnap them for variable lengths of time (e.g. Altmann 1980; Wasser 1983; Wasser & Starling 1988). Altmann (1980, 1983) suggested that mothers of young infants may avoid female harassment and/or mitigate the costs of feeding competition during lactation by associating with a male companion.

Finally, the 'male caretaker' hypothesis suggests that there are no immediate, protection-related benefits of friendships to females. Rather, a female establishes a friendship with a particular male to promote the development of an attachment between her infant and that male (e.g. Ransom & Ransom 1971; Seyfarth 1978; Nicolson 1982; Stein 1984; Smuts 1985; Collins 1986; Strum 1987). The proposed benefits of this attachment to infants include occasional carrying (Anderson 1992), vigilance, defence from predators (Altmann & Altmann 1970; Packer 1980), increased access to food (Altmann 1980; Packer 1980), accelerated socialization and attainment of independence (Burton 1972; Altmann 1980) and access to a potential 'adoptive' step-parent should the mother die (Smuts 1985).

Our goal was to examine these hypotheses by supplementing systematic behavioural observation with playback experiments. Our focus was on the proposed benefits of friendships to females.

PART I:
BEHAVIOURAL OBSERVATIONS

Methods

Study area and subjects

Research was conducted in the Okavango Delta, a seasonal wetlands formed by the expansion of the Okavango River in a large flat depression in semi-arid, northwestern Botswana. The study site is in the Moremi Game Reserve along a floodplain between the main channel of the Boro River and the western edge of Chief's Island (23°02′E, 19°31′S). The habitat is a mosaic of grasslands interspersed with wooded 'islands' ranging from less than one hectare to hundreds of hectares (e.g. Tinley 1966; Buskirk et al. 1974; Hamilton et al. 1976).

The study group (C) comprised 60–70 individuals, including 4–8 adult males, 22–25 adult (cycling) females and their immature offspring. The group had been studied more or less continuously from 1977 to 1991 by W. J. Hamilton III and colleagues (e.g. Hamilton et al. 1976; Busse & Hamilton 1981; Hamilton & Bulger 1990; Bulger 1993) and since 1991 by D. Cheney, R. Seyfarth and colleagues (e.g. Cheney et al. 1995, 1996). Because of this long history of observation, maternal relatedness of all females and natal males was known. All subjects were fully habituated to observers on foot and individually identifiable.

In chacma baboons, both males and females are organized into linear dominance hierarchies in which all females are subordinate to males (even, usually, immature males) (Bulger 1993). The average tenure of alpha males during this study was five months ($N=4$), which corresponded with the median tenures reported previously for the same population and study group (Collins et al. 1984; Hamilton & Bulger 1990).

In addition to the multiparous females chosen as focal subjects, two young (6.5-year old) females were observed to maintain friendships with males following primiparous births. These relationships were sufficiently obvious to be noted in ad libitum observation, but they did not persist long enough (due to infant deaths) to allow systematic study. Thus, although these infants are included in assessing the rate and causes of infant mortality, the friendships their mothers maintained with males are not included in the quantitative analysis.

Behavioural observations

We observed the study group for over 1400 contact hours from June 1993 to June 1995. Behavioural data were collected in 10-min focal animal samples ($N=3454$) and ad libitum observations (Altmann 1974) of 20 adult, multiparous females and 11 adult males.

The following measures were used to quantify variation in heterosexual social relationships and to identify 'friend' dyads.

Close proximity. The duration that each subject spent in close proximity (within 2 m) of others was measured by recording the time that the subject approached to within 2 m of a given individual and the time that it or the other individual moved more than 2 m away (withdrew).

2–6 m range. Time spent within 2–6 m of others was measured by instantaneously recording the identities of all individuals within this distance of the subject at 2-min intervals during the focal session. If no adults were within 6 m of the subject, then the nearest neighbours of each sex were identified and their distance to the subject assessed.

C score. The above two proximity measures were used to derive a composite proximity measure, or '*C* score' (Smuts 1985) using the equation:

$$C = 1(T_{0-2 \text{ m}}) + 0.25(T_{2-6 \text{ m}})$$

where $T_{0-2 \text{ m}}$ is the percentage of time that the members of the dyad spent within close proximity and $T_{2-6 \text{ m}}$ is the percentage of time they spent in the 2–6-m range. The constants 1 and 0.25 are weighting factors for each spatial category derived from taking the reciprocal of the mid-point of the inner and outer limits of that category. A *C* score was assigned to each female–male dyad. For the calculation of *C* scores, the percentage of time in close proximity was extracted from the same instantaneous samples that generated estimates of time within 2–6 m time.

Maintenance of close proximity. The responsibility for maintenance of close proximity between the two members of a dyad was assessed using 'Hinde's index', which is the percentage of approaches due to the female subtracted by the percentage of withdrawals due to the female (Hinde & Atkinson 1970; Hinde 1977). The index varies from -100 (complete male responsibility for maintaining close proximity) to $+100$ (complete female responsibility). Calculation of Hinde indices excluded supplants, defined as cases when an individual withdrew immediately (within 20 s) from an approacher. Hinde indices were calculated only for dyads for which there was a sample of at least 20 approach–withdrawal interactions (Hinde & Proctor 1977; Smuts 1985).

Allogrooming. Grooming between adult male and female chacma baboons occurs at low rates. Symmetry in grooming interactions between friends were assessed by calculating the cumulative duration of 'female grooms male' and 'male grooms female', expressed as a percentage of all grooming exchanged between partners that were observed to groom one another.

Infant handling. Male baboons often engage in prolonged touching and manipulation of an infant in contact with or near its mother while producing a long series of grunts. We distinguished this behaviour from 'agonistic buffering' (Deag & Crook 1971), in which a male carries an infant (often screaming) away from its mother and towards a nearby, higher-ranking male (Ransom & Ransom 1971; Busse 1984b). By definition, infant handling did not involve movement of the participants or overt interactions with higher-ranking males, and it usually did not obviously distress infants.

Screams. Rate of screaming was estimated by recording the number of screams heard on 135 observation days. The age and sex of the caller was assigned visually or aurally (aural classifications were used only after each observer had acquired 1 year of experience based on hearing/recording vocalizations and on repeated confirmations of age/sex classifications). Assessments of male responses to naturally occurring female screams were made opportunistically on an ad libitum basis.

Results

Infant mortality

During the study period, 21 infants were born, of whom 16 (76.2%) died within 112.2 ± 27.9 days of birth (mean $\pm$ SE). Of the neonates that died,

disease or reduced viability accounted for two (12.5%) deaths, and six (37.5%) were victims of infanticide. Of these six cases, three were observed infanticides, two were instances in which dead infants were discovered with bleeding punctures (canine wounds) to the head immediately after outbursts of female screaming, and one was a disappearance suspected to be caused by infanticide (given that an established infanticidal male was simultaneously discovered with blood on his muzzle).

All observed infanticides were committed by adult males who had recently immigrated into the group and who had achieved the alpha position in the hierarchy; all victims were infants who had been conceived prior to the male's immigration. In infanticidal attacks, the alpha male rushed at a mother with infant, succeeded in seizing the infant, and ran off with the infant (sometimes screaming) in its mouth, thereupon killing it while in the process of running or after moving some distance away. These events were accompanied by repeated screaming by the mother as well as other females in the group. In all cases, the mothers of victims resumed cycling within 2 months and subsequently mated with the male who had killed their infants.

The reported percentage of deaths by infanticide represents a minimum estimate of infanticidal rate during the study, given that eight (50%) infants that died simply disappeared. Of these, five were overnight disappearances of otherwise healthy infants. Most disappearances occurred during 6-week period in 1994 when a newly immigrant alpha male engaged in repeated attacks on females with dependent infants (three attacks were successful infanticides).

Spatial proximity and friendships

Variation in spatial relations between female and resident males was the primary indicator of differences in heterosexual relationships and was used to define friendships. Of the 17 infants who survived beyond 48 h of birth, the mothers of 15 had a discontinuous distribution of C scores with resident males, in which the high scores of one or two males segregated clearly from the low scores of other males. Figure 1 illustrates the distribution of C scores for four typical females. Males whose C scores were separated by at least three score intervals from other males were designated as 'friends' of the particular female. On average, 13

intervals (SD=9, range: 3–37, N=22) separated the C scores of male friends from other males. In no case did a lactating female associate with a recently immigrant alpha male.

C scores provided the basis for identifying 22 friendships involving 12 lactating females and eight adult males. Six females had more than one friendship during the study. In three of these cases, females possessed high C scores for two males simultaneously (Fig. 1). Second, three females gave birth twice during the study and associated with one to two males each time. The consecutive friendships of individual females were analysed separately, since they were disassociated in time (>1 year) and, for two females, involved different adult males. Third, four females switched friends while still lactating. In three cases, the change was preceded by the disappearance or emigration of a current friend from the group. In one other case, it occurred when a higher-ranking mother established a friendship with the same male and effectively 'supplanted' the female from her friend.

Maintenance of close proximity

Friends spent approximately $13.7 \pm 8.3\%$ of their time in close proximity to one another (range=3.9–33.6%, N=22). Hinde indices for the 17 friend dyads with sufficient data were all strongly positive (Table I), suggesting that females were primarily responsible for the maintenance of proximity (two-tailed sign test: x=16, N=17, $P<0.01$). The mean $\pm$ SD index was $+26.0 \pm 16.4$.

Infant handling

Of the 15 infants born to females who formed postpartum friendships, only one infant (who died within 50 days of birth) was never observed to be handled by an adult male. Even after controlling for time spent in close proximity, infants were handled by friends at approximately 2.5 times the rate that they were handled by non-friends (two-tailed Wilcoxon signed-ranks test: T=38.5, N=19, P=0.02). Indeed, of the 14 infants handled by males, nine (64%) were observed to be handled only by their mothers' male friend(s).

Female–male grooming

The percentage of a female's close proximity time devoted to grooming was significantly higher for her friend (mean $\pm$ SE=$7.2 \pm 1.6\%$) than for any other non-friend male with the highest
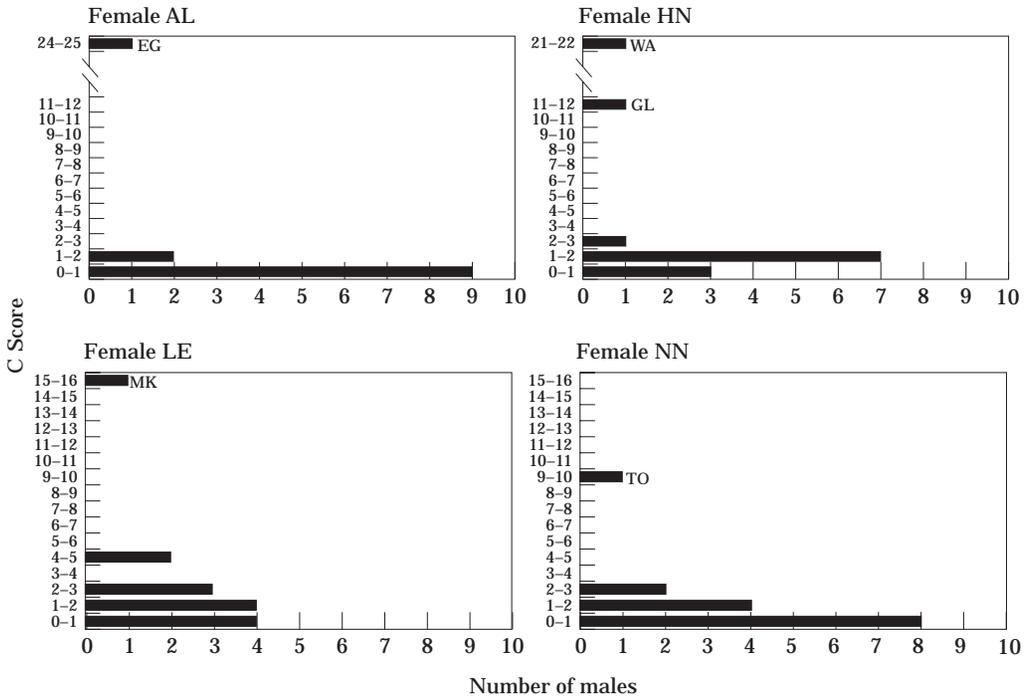
Figure 1 The distribution of composite proximity scores (C scores) for four representative lactating females. The number of males in the group (X-axis) with a C score falling within the range given (Y-axis) is shown for each female. A two-letter name code is provided for each male who was designated a friend based on the distribution of C scores. The number of focal sessions used to derive scores are: 171 (female AL), 214 (female HN), 154 (female LE), 614 (female NN).

grooming time $(1.88 \pm 2.0\%)$ ($T=17$, $N=17$, $P<0.005$). For the majority of females, this difference in grooming behaviour was qualitative, in that the friend was the only male she was ever observed to groom or be groomed by while lactating. No lactating female was ever observed to groom or be groomed by more than one other non-friend male. Grooming between heterosexual friends, therefore, was greater than between non-friends, even after correcting for the fact that friends were more often near one another.

Within friendships, grooming was not equally distributed between the sexes. Female grooming of the male accounted for $87.6 \pm 3.5\%$ of all grooming exchanged between friends, a significantly larger contribution than that of the males ($T=0$, $N=11$, $P=0.003$).

The characteristics of friendships

Females of all dominance ranks and ages formed friendships (Table II). The males participating in

Table I. Hinde indices for close proximity between male and female friends

| Friendship | | Hinde | |
Female	Male	index	N
SY	GL	+4.8	63
BT	WA	+13.8	80
	WA	+19.0	46
HN	WA	+53.8	53
	GL	+34.5	30
SH	NP	+7.1	27
SS	EG	+37.5	54
	GL	+26.4	48
LE	MK	+25.0	20
NI	EG	+45.5	54
	WA	+36.0	105
	WA	−1.5	36
NN	TO	+33.6	40
AL	EG	+13.8	77
OL	NP	+10.2	28
HN	WA	+33.5	128
CD	TN	+49.6	27

Females are listed in order of dominance rank. N=number of approach–withdrawal interactions.

**Table II.** Attributes of females and males that formed 'friendships'

Female	Male friend	Female dominance rank (% females dominated)	Female age (years)	Did male have alpha rank during friendship period?	Was male a former alpha male?	Did male reside in group when female conceived?	Did male copulate with female during conception cycle?
SY	GL	92	11.7	Temporarily	Yes	Yes	Yes
BT	WA	83	15.0	Temporarily	Yes	Yes	Yes
	WA	83	16.0	No	Yes	Yes	Yes
HN	GL	63	7.9	Temporarily	Yes	Yes	Yes
	WA			No	Yes	Yes	?
SH	NP	58	16.0	No	No	Yes	Yes
SS	EG	48	9.9	No	No	Yes	Yes
	GL			No	Yes	Yes	Yes
LE	MK	43	8.7	No	Yes	Yes	Yes
NI	WA	38	7.6	No	Yes	Yes	Yes
	EG	35	9.1	No	No	Yes	?
	WA			No	Yes	Yes	?
NN	TO	30	14.8	No	No	Yes	?
AL	TN	17	13.9	No	Yes	Yes	Yes
	WA			No	Yes	Yes	Yes
	EG	13	15.1	No	No	Yes	Yes
	TO			No	No	Yes	?
OL	NP	8	19.5	No	No	Yes	Yes
	GN			No	No	Yes	Yes
	TO			No	No	Yes	?
JN	WA	5	8.1	No	Yes	Yes	Yes
CD	TN	0	8.4	No	Yes	Yes	?
				19 (86%) No	13 (59%) Yes	22 (100%) Yes	15 (68%) Yes

these relationships were all fully adult, non-natal individuals of various dominance ranks (from the highest- to lowest-ranking male). The current alpha male was rarely a friend of a female. Both of the males who did occupy alpha status while maintaining a friendship fell in rank during the period of the friendship. On the other hand, 13 (59%) friend dyads involved males who had formerly been alpha males. Regardless of rank, all males had been resident in the group during the cycle in which their (future) female friend conceived her current infant. Moreover, in 15 (68%) cases, the male friend had been observed to copulate with the female during her conception cycle (in the other seven friendships, gaps in the observation record prevented confirmation of copulation between friends). One male, WA, is represented in seven of the 22 dyads listed in Table II, possibly because, of the males listed, he was the only one to reside in the group during the entire study period (and thus we had more opportunities to observe him involved in friendships).

Temporal patterning of friendships

Friends spent significantly more time near one another in the 2 months following the birth of infants compared with the 2 months preceding birth ($T=0$, $N=13$, $P=0.002$ for both close proximity and 2–6 m comparisons; Fig. 2a).

During gestation, there was little evidence of special relationships between females and the males who subsequently became friends. The C scores for postpartum friends were substantially lower during gestation (median=1.3, range= 0.2–4.1) than during lactation (median=13, range=4.3–38.9; $T=0$, $N=17$, $P<0.001$). Male friends' C scores during gestation were also significantly lower than the maximum score observed among non-friend males at the time ($T=12$, $N=17$, $P=0.02$), in contrast to the postpartum period. Of 11 females for whom C scores were available during gestation, eight (73%) had no male partner whose score was high enough to constitute a friendship, two (18%) associated most with a male different from the one who subsequently became a friend, and only one associated with the same male during both gestation and lactation. Even in this last case, the female's C score with her friend rose dramatically following the birth of her infant.
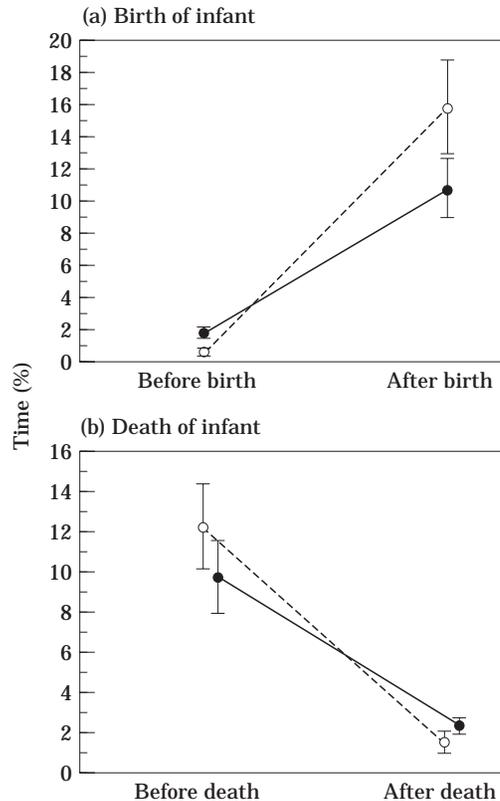
Figure 2 Mean ± SE temporal changes in the time that heterosexual friends spent within close proximity (open circles) and in the 2–6 m range (closed circles). (a) Spatial relations in the 2 months preceding and following the birth of infant ($N=13$); (b) spatial relations in the 2 months preceding and following the death of infant ($N=12$).

The absence of spatial evidence of friendships during gestation derived in part from a greater dispersion of females from males in general. Pregnant females spent significantly more time over 25 m from all males in the group (median=57.5%) than did lactating females (median=30.3%; $T=0$, $N=12$, $P=0.002$). Pregnant and cycling (but non-consorting) females did not differ in this measure ($T=4$, $N=12$, $P>0.05$).

Conversely, an infant's death was accompanied by a sharp decline in the time that friends spent within 0–2 m of one another (two-tailed Wilcoxon signed-ranks test: $T=0$, $N=12$, $P=0.002$) and 2–6 m ($T=1$, $N=12$, $P=0.004$; Fig. 2b). This decrease typically followed within hours following
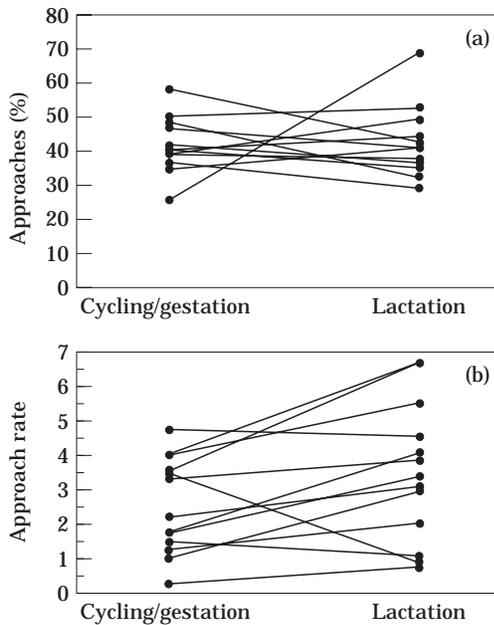
Figure 3 Approach–withdrawal interactions of 12 sub-ordinate females with dominant females. Interactions are divided according to whether the subordinate was pregnant/cycling or lactating. (a) The percentage of dominant females' approaches that resulted in an avoidance response by the subordinate; (b) the rate (number/h) at which subordinate females approached dominant females.

an infant's death. As was the case during gestation, after an infant's death C scores no longer differentiated friends clearly from other males.

Female–female social interactions

We recorded 2462 incidents involving 12 females in which a high-ranking female approached a lower-ranking female. A female was scored as avoiding the approach if she withdrew from the other female within 20 s of the approach. The reproductive state of low-ranking females did not influence their responses to approaching dominant females: females were just as likely to avoid dominant females when they were lactating as when they were pregnant or cycling ($T=47$, $N=12$, $P>0.10$; Fig. 3a). Similarly, although there was a tendency for subordinate females to approach dominant females at a higher rate when lactating than when pregnant or cycling, this difference was not significant ($T=16$, $N=12$, $P=0.07$; Fig. 3b).

Discussion

Neonatal mortality during the 2 years of this study was approximately 76%, which is considerably greater than the 45% reported for the same study group during 1978–1980 (Bulger & Hamilton 1987), but comparable to the rate (86%) reported over a 4-year period in a desert population of *Papio c. ursinus* (Brain 1992). The level of infanticide in this population, at least 38% of infant mortality, is similar to that found in lions, *Panthera leo* (Pusey & Packer 1994), mountain gorillas, *Gorilla gorilla*, *Alouatta palliata*, (Watts 1989), and howler monkeys (Clarke & Glander 1984). These data contribute to the growing empirical evidence suggesting that infanticide is a significant source of infant mortality and a potentially important selective force in the evolution of social behaviour among baboons (Busse & Hamilton 1981; Collins et al. 1984).

In accordance with previous research on chacma baboons (Seyfarth 1978), significant discontinuities in the distribution of males' close proximity, grooming and infant handling with particular females differentiated friendships from other heterosexual relationships in the group. All females formed friendships with males who had some probability of having fathered their infants. Fifty-nine per cent of the friendships observed in this study were formed by males who had occupied the alpha position when their female friends had conceived and who were therefore very likely to have been the infants' father (Bulger 1993). Mothers' interactions with other males were not just less common but typically negligible.

Because allogrooming in non-human primates appears to be a primary mechanism for establishing and maintaining social relationships (Seyfarth 1983; Dunbar 1988; Harcourt 1988), its distribution is often interpreted as an indicator of the 'value' that individuals place on the relationship (Kummer 1978; Seyfarth & Cheney 1984; Simpson 1991). Similarly, patterns of close proximity are significant not just because they may reflect affinity (Carpenter 1945; Rowell & Olson 1983), but also because proximity increases the probability of additional social interactions (Altmann 1965). Data on two potentially reciprocal interactions suggest that females invested more in friendships than did males. First, Hinde indices indicated that females were more responsible than males for the maintenance of

close proximity. Second, females groomed male friends considerably more than vice versa. These sex differences, therefore, implicate a greater female contribution to establishing and maintaining the interactions that constitute a friendship.

What are the possible benefits of friendships to females? One answer is suggested by the changes that occurred in friendships upon the births and deaths of infants. In general, the consistent and pronounced proximity between male and female friends was established by the female only immediately after the birth of her infant. Similarly, the death of an infant was followed by a rapid disintegration of the association. Thus, the most obvious behavioural manifestation of friendships in chacma baboons coincided closely with the presence of infants.

This observation contrasts with reports of some East African baboons, where friendships typically intensified following the birth of an infant, but were nevertheless sufficiently strong and stable enough during gestation to be discernible (Altmann 1980; Smuts 1985; but see Collins 1984). The relatively strict temporal conjunction of friendships with neonates in chacma baboons suggests not only that females may incur costs of maintaining close relationships with males, but also that the benefits of friendships are related to infant viability and survival.

Because females are primarily responsible for the maintenance of close proximity between friends, they reveal little about the male's investment in the friendship. Males do, however, occasionally form alliances with their friends when they are threatened by others. Playback experiments potentially provide a means for systematically examining males' willingness to aid their friends during aggressive interactions, and for evaluating more rigorously the hypothetical advantages of friendships to females. These experiments are discussed below.

PART II: FIELD EXPERIMENTS

Monkeys that are under attack from conspecifics often utter loud screams that appear to function in part to recruit the aid of others (Gouzoules et al. 1984; Snowdon 1986; Cheney & Seyfarth 1990). Male baboons will sometimes, but not always, come to the aid of females who have screamed (Seyfarth 1978; Smuts 1985).

In the study group, screams by adult females occurred approximately once per 50 min ($\bar{X} \pm$ SD hourly rate of screams by adult females: 1.3 ± 0.7; by adult males: 0.1 ± 0.1; by subadults: 0.5 ± 0.5; by immatures: 4.4 ± 2.3). The response of adult males to naturally occurring screams varied. In 61% of observed cases, males oriented to female screams ($N=95$ scream episodes, $N=7$ adult males). When they did orient, the average duration of response was 4.2 ± 4.5 s (range$=0.5$–20 s; $N=58$).

This variation in the duration of male responses established a rationale for experiments in which the screams of females were played to males. As Marler et al. (1992) argued, the orienting and visual-scanning response elicited by some vocalizations can be interpreted as the listener's attempt to obtain cues about the circumstances under which the signaller has called. Having heard a scream, the listener can presumably then decide whether to aid the signaller. Rowell & Olson (1983) also noted that visual scanning of conspecifics is highly predictive of imminent changes in behaviour. Our playback experiments posed the question, does the response of a male to a female's distress call vary systematically with his relationship to that individual?

Methods

General protocol

In these experiments, we assumed that baboons can recognize individual females by voice alone, which seemed warranted given previous experiments on this same group (e.g. Cheney et al. 1995) and observations of naturally occurring screams. The playback stimuli consisted of vocalizations tape-recorded from known individuals using a Sony TCD5PRO cassette recorder and Sennheiser 3K-U microphone with ME 80 microphone head. The female screams used as playback stimuli had been originally recorded when the signallers were being attacked by higher-ranking, unrelated residents of the study group.

The subjects for all experiments were adult males residing in the study group. Subjects were classified as friends or controls based on the various measures described in Part I.

We performed experiments only when the following conditions were met: (1) the activity of the subject was the same for both control and experimental trials (usually resting, but occasionally

feeding); (2) no baboon was within 2 m of the subject; (3) the subject could not see the individual whose call was played; (4) the individual whose call was played had not groomed the subject in the previous 10 min; (5) we had heard no naturally occurring screams of females or infants in the previous 10 min; (6) no inter-group encounters had occurred in the previous 30 min. All experiments were conducted within or on the edge of wooded islands where the loudspeaker could be easily concealed. Playback levels of the loudspeaker were adjusted to deliver a normal-sounding call (as judged by a listener standing a standard distance of 20 m from the loudspeaker). We used the same amplitude settings on the loudspeaker within trials for both experimental and control males.

During each experiment, one observer played the playback stimulus from a tape-recorder connected via a 6-m extension cord to a Nagra Kudelski DSM loudspeaker that was concealed in vegetation approximately 25–30 m from the subject. The loudspeaker was usually in the same direction as the individual whose call was being played. Another observer videotaped the subject before and after playback of the stimulus using a Sony Hi-8 videocassette camera. We reviewed videotapes later to extract the primary measure of response, which was the duration of orienting towards the loudspeaker in the 20 s after playback minus the duration of orienting in the same direction in the 20 s before playback. We also noted movements of the subject relative to the position of the loudspeaker when they occurred.

To prevent habituation to the playback protocol, we conducted no more than two playback experiments on any day, and at least 72 h separated trials for the same subject. We also conducted mock experiments, in which observers and equipment were positioned as in actual experiments but no stimulus was played. These were performed at three times the rate of genuine playback experiments.

Experiment 1: Playback of female screams to friend and control males

In this experiment, a female's scream was played to her male friend and a control male of similar rank (± 1 position in the dominance hierarchy) and friendship status (i.e. a long-term resident who currently had a friendship with another female). Because the same scream was played to two males, the playback stimulus acted as its own control.

Experiment 2: Playback of the scream of a friend and a control female

In this experiment, subjects were played the scream of either a female friend or a control female of similar rank and reproductive state (i.e. a female with an infant). With this protocol, each male acted as his own control. Playback amplitude for each of the two screams used in these trials was adjusted so that each scream yielded equivalent readings on a sound level meter.

To reduce the risk of habituation to the playback stimuli, we played each male the scream of a given female only once. In experiment 1, a male's response to his friend's scream was compared to the response of a control male. In experiment 2, the same trial was used to compare the male's response to another female's scream. We randomized the order of presentation in both experiments.

Experiment 3: Playback of a female's scream after her infant's death

This experiment had the same design as experiments 1 and 2, but was performed after the death of the female's infant. Within 1–4 weeks of the infant's death, the scream of a female was played to her former friend and, in a separate trial, to a control male.

Experiment 4: Playback of a female's scream accompanied by the threat vocalizations of others

This experiment attempted to simulate an agonistic interaction involving a female friend and another individual. Playback stimuli consisted of a female scream preceded by a series of threat vocalizations given by either (1) a recent immigrant, alpha male (always an established infanticidal male), (2) the beta male in the hierarchy (always a long-term resident) or (3) the alpha female in the hierarchy.

We included the second condition to control the rank. In the first condition, the subject heard the threat vocalizations of an individual higher-ranking than himself, but in the third condition he heard the calls of a female who was lower-ranking
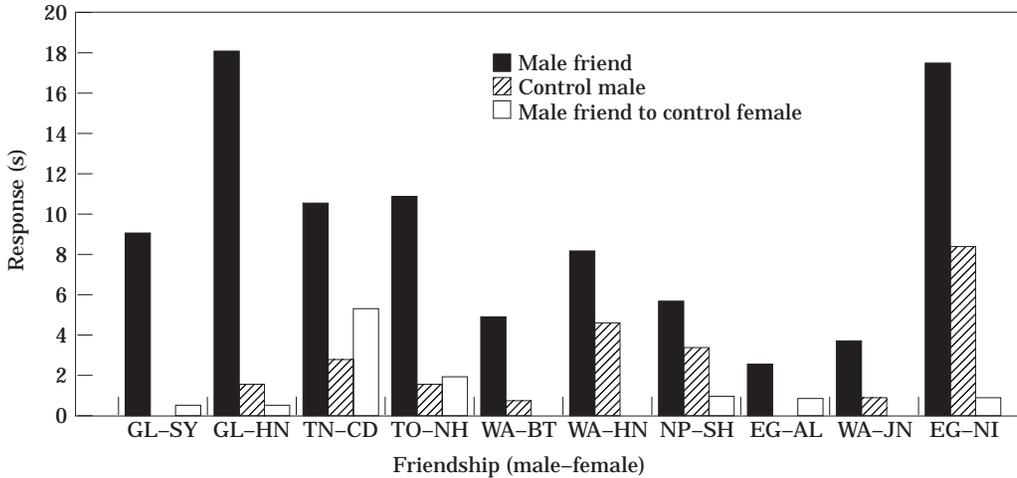
Figure 4 The duration of males' responses to playbacks of females' screams.

than himself. In the second condition, however, he heard the threat vocalizations of an individual who, although higher-ranking than himself, was unlikely to commit infanticide.

We had recorded both the females' screams and the infanticidal male's threat calls during previous attacks by the infanticidal male on the females in question. As with experiment 1, stimuli were played back on separate occasions to either a male friend or a control male. Three male friends and three control males served as subjects, for a total of 18 trials (three trials per subject).

Although trials for experiments 1, 2 and 3 overlapped in time (in randomized order), we did not conduct trials for experiment 4 until well after we had concluded the first three experiments.

Results

Experiment 1

Playback of the same female's scream elicited a significantly stronger response from the friend than from the control male (two-tailed Wilcoxon signed-ranks test: $T=0$, $N=10$, $P=0.005$; Fig. 4). In one case, a male friend responded by running in the direction of the loudspeaker, leaping up and visually scanning the area as he did so.

Experiment 2

Similarly, when males were played either their female friend's scream or the scream of another female, they responded significantly more strongly

to their friend's scream (Fig. 4; $T=0$, $N=10$, $P=0.005$).

Experiment 3

In all cases, male friends showed a sharp decline in their responses to the screams after infants' deaths compared with their responses to the same screams when the infants were still alive (Fig. 5). The difference in the strength of friends' and control males' responses, which was so apparent in experiment 1, reversed itself after the infants' deaths: now, male friends showed significantly weaker responses to playbacks than control males did ($T=20$, $N=6$, $P<0.05$). Finally, in marked contrast to experiment 2, following the death of infants males no longer responded more strongly to their friends' screams than to control females' screams ($T=12$, $N=6$, $P>0.10$).

Experiment 4

This experiment aimed to test the anti-infanticide hypothesis against the female harassment hypothesis. If friendships primarily function to protect the mother of young infants against infanticidal attacks, males should have responded most strongly to playback sequences in which their friends' scream was paired with the threat vocalizations of the infanticidal, alpha male. Male friends should also have responded more strongly than control males to this sequence. Conversely, if friendships function primarily to protect mothers
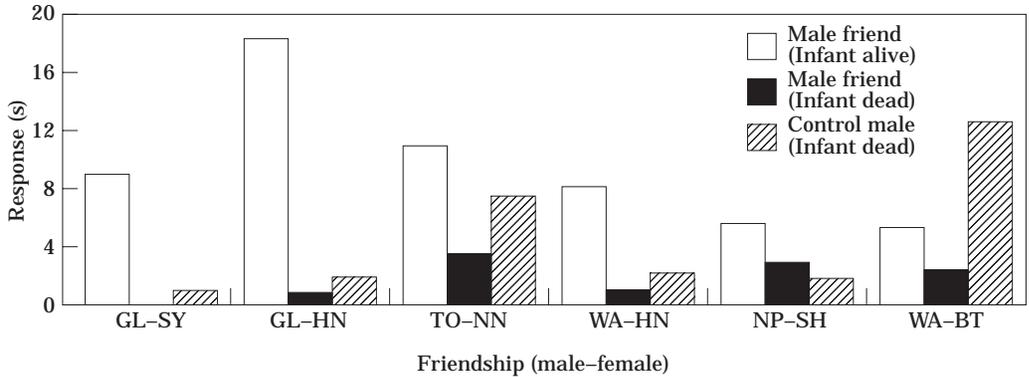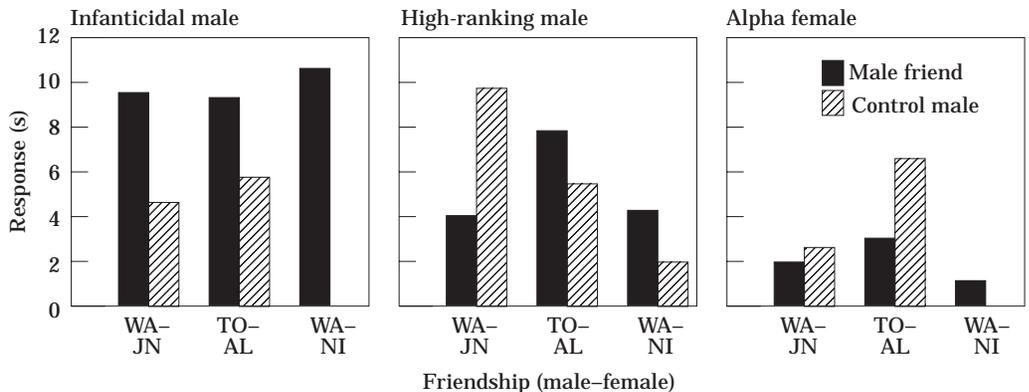
Figure 5 The duration of friend and control males' responses to playbacks of females' screams after the death of infants. For comparison, the responses of male friends to the same screams when infants were alive (Fig. 4) are provided.

from female harassment, male friends should have responded more strongly to the playback sequence that included the threat vocalizations of the alpha female.

This experiment yielded two related but independent results (Fig. 6). First, in all three cases, male friends responded most strongly to trials in which their friend's scream was paired with the threat calls of the infanticidal male (two-tailed Mann–Whitney U-test: $U=0$, $N_1=3$, $N_2=6$, $P=0.02$). This was not true for any of the control males, whose responses in the infanticidal male condition did not differ from either of the two other conditions ($U=7.5$, $N_1=3$, $N_2=6$, $P>0.10$).

Second, all three male friends responded more strongly than did control males to the sequence

that paired their friend's scream with the calls of the infanticidal male (Fig. 6). In contrast, when their friend's scream was paired with the threat calls of the alpha female, only one friend responded more strongly than control males did, and even in this case the friend's response was relatively weak. Intermediate results were obtained when the female's scream was paired with the calls of the beta male: male friends responded more strongly than controls in two of the three cases. Overall, the magnitude of the difference in response between friend and control males in the infanticidal condition was significantly greater than the difference between friends and controls in the other two conditions ($U=0$, $N_1=3$, $N_2=6$, $P=0.02$).

Figure 6 The duration of friend and control males' responses to playbacks of females' screams when paired with the threat vocalizations of the infanticidal alpha male, the beta male and the alpha female.

Discussion

Males responded to playbacks of females' screams either by ignoring the call or by orienting towards the speaker. This result is consistent with our observations of naturally occurring screams, to which males responded on 61% of all occasions. If we assume that the duration of an orienting response reflects the willingness of the listener to intervene on behalf of the signaller, then these playback experiments allow us to examine males' investment in friendships, both when infants are present or absent and when friends appear to be involved in different kinds of aggressive interactions.

Male friends responded more strongly than control males to their female friend's scream (experiment 1), and they also responded more strongly to the screams of their friends than to screams of other females (experiment 2). The strong responses of male friends support the hypothesis (Smuts 1985) that a male's interest in a particular female's distress varies systematically with other measures of his relationship with that female. The results of experiments 1 and 2 are consistent with both the infanticide and the female harassment hypotheses. These results lend less support to the male caretaker hypothesis, which proposes that the benefits of friendships do not lie in the immediate protection of females and their infants but rather in the bonds that form later between males and older infants.

Significant changes in friendships occurred when females' infants died. Within days after an infant's death, males' responses to their former friends' screams declined so sharply that the difference between male friends and control males was now reversed (experiment 3). It seems unlikely that this decline in response occurred simply as a result of increasing infant age (e.g. Stein 1984), because males continued to respond strongly to the screams of friends who had living, older infants. Three trials in experiments 1 and 2 were conducted when female friends had living infants whose ages approximated or exceeded the median age that females' dead infants would have attained when experiment 3 was conducted. In all three trials, male friends oriented longer than control males; they did so in only one of the 12 trials following infants' deaths.

The reduction in males' responses to their former friends' screams after infants' deaths coincided with a sharp decline in spatial associations between friends. Because females played the major role in maintaining spatial proximity between friends, this decline may have been more indicative of the female's than the male's inclination to terminate the friendship. It is not clear whether females who lose infants end friendships because their friends are no longer likely to protect them, or because females no longer benefit significantly from the protection that their friends are still willing to provide. Whatever the cause for the termination of friendships, both the male's and the female's contribution to a friendship declines substantially when an infant dies, suggesting that the function of friendships for both males and females is closely related to the presence of neonates.

Although the infanticide and female harassment hypotheses are not mutually exclusive, the results of this study lend greater support to the anti-infanticide hypothesis. All males who formed friendships were potential fathers of their friends' infants. Had female harassment constituted a threat to their reproductive investment, they should have responded strongly to playback sequences in which their friends' scream was paired with the threat calls of the alpha female. Instead, they responded weakly or not at all to this sequence, but very strongly to the infanticidal male sequence. Male friends, in other words, appeared to perceive that an infanticidal attack was of more potential danger to their friends' infants than was female harassment. The behaviour of mothers themselves also suggests that female harassment and competition were of negligible significance. Females were just as likely to approach dominant females and to withdraw from their approaches when they were lactating as when they were pregnant or cycling. They did not avoid high-ranking females, as would be predicted by the female harassment hypothesis. Moreover, previous observations of the study animals indicate that females are significantly less aggressive to females with young infants than to females without young infants (J. Silk, D. Cheney & R. Seyfarth, unpublished data). Finally, the fact that even the alpha female formed a close friendship with a particular male when she was lactating also suggests that the primary function of friendships was not the avoidance of female harassment.

Evidence that infanticide promotes heterosexual friendships is supported by other aspects of chacma baboon social behaviour. For example,

adult males rarely interact with infants in groups in which the alpha male is a long-time resident. If, however, a new male immigrates into the group and attains alpha status, carrying of infants by resident males substantially increases (Busse 1984b). Although this increase may result partly from the use of infants as 'agonistic buffers' (Deag & Crook, 1971; Smith & Whiten 1988), other features of infant carrying (notably assumed paternity) suggest that infant carrying by resident males constitutes protection against infanticide (Busse & Hamilton 1981). Moreover, females with dependent infants manifest extreme fear of newly immigrant males in the form of long-distance avoidance, screaming and intensive submissive displays (Busse 1984a). More studies are needed to separate the effects of male immigration status and dominance rank. Female counter-strategies, for example, should not be directed at newly immigrant males who fail to acquire the alpha position. Data are unavailable to test this hypothesis, in part because males in the study group typically acquire alpha rank shortly after immigration (Hamilton & Bulger 1990). More data will also help to differentiate between male protection of female friends against infanticidal males in particular versus adult male harassment in general.

Do friendships reduce the risk of death by infanticide? This question is difficult to answer, because few mothers ever fail to form friendships. In this study, two mothers did not form postpartum friendships, even though the alpha male in the group at the time was a recent immigrant. The infant of one of these females survived to weaning. Conversely, only four (21%) of the infants belonging to females who did form friendships survived past the age of 1 year. These observations emphasize that the probability of infant survival is affected by numerous factors. In this study, male–female friendships varied considerably, from the perspective of both females (behavioural measures) and males (responses to playbacks). Future longitudinal research must clarify the reproductive consequences, if any, of this variation, as well as the relative importance of friendships in influencing infant survival.

ACKNOWLEDGMENTS

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