Male parental care, female choice and the effect of an audience in vervet monkeys

ANNE C. KEDDY HECTOR*, ROBERT M. SEYFARTH† &
MICHEAL J. RALEIGH‡

* *Department of Biology, University of California, 405 Hilgard Ave., Los Angeles, CA 90024, U.S.A.*
† *Department of Psychology, University of Pennsylvania, Philadelphia, PA 19104, U.S.A.*
‡ *Department of Psychiatry, Neuropsychiatric Institute, University of California School of Medicine,
Los Angeles, CA 90024, U.S.A.*

Abstract. The parental behaviour of male vervet monkeys, *Cercopithecus aethiops*, was examined to determine whether (1) females respond to the parental behaviour of males and (2) males vary the amount of parental care they provide depending upon the presence of the infant's mother. Eleven males and 11 infants from four groups were observed under dyadic conditions in which the male could or could not see the infant's mother. Males, particularly subordinate males, altered their rates of affiliative and agonistic behaviour towards infants depending upon the perceived presence or absence of the infant's mother. Females varied their affiliative and agonistic behaviour towards males depending upon male dominance status, and the male's behaviour towards the infant.

There is growing evidence that female mate choice is an important evolutionary force in non-human primates (chimpanzees, *Pan troglodytes*: Tutin 1979; brown capuchins, *Cebus apella*: Jansen 1984; baboons, *Papio anubis*: Smuts 1985; vervets, *Cercopithecus aethiops*: Andelman 1985; Keddy 1986), yet there is still controversy concerning the criteria females use to choose mates. Several studies have suggested that females may prefer dominant males (baboons, *Papio cynocephalus*: Seyfarth 1978a, b; macaques, *Macaca* spp.: Robinson 1982; reviewed in Silk & Boyd 1983). There is also evidence that high-ranking females may influence male rank by preferentially socializing with, or aiding particular males in agonistic confrontations (rhesus macaques, *Macaca mulatta*: Chapais 1983; Pigtail macaques, *Macaca nemestrina*: Gouzoules 1980; vervets: Raleigh et al. 1982; chimpanzees: deWaal 1982). Female mating preferences may therefore be determined by more than dominance per se.

Females may also prefer males who provide parental care. In many species of Old World monkeys, males form strong protective relationships with females and their young (baboons: Seyfarth 1978b; Altmann 1980; Johnson 1984; Stein 1984; Smuts 1985). Such relationships may reduce the harassment that the female and her young receive from other members of the group and may decrease competition over food. Bonds between males and infants are often associated

with 'special relationships' between males and females (baboons: Smuts 1983), so that when a female resumes sexual cycling, she is more likely to mate with the male than she might have been otherwise (baboons: Seyfarth 1978a, b; Rasmussen 1980, 1983; Smuts 1985; Japanese macaques, *Macaca fuscata*: Takahata 1982). Whether the male's relationship with the infant's mother is a step towards, or a consequence of, the male's association with the infant is difficult to discern (Whitten 1987). However, researchers have suggested that male–infant affiliation is quite likely to affect subsequent female mate choice (Smuts 1985; Whitten 1987). Therefore, male parental behaviour can potentially be viewed as a strategy adopted by males to influence female mate choice. Parental behaviour might be expected to be particularly strong among low-ranking males who could use this behaviour to counteract their poor competitive abilities (Strassmann 1981).

If females base their mating preferences on traits such as male parental care, then females should alter their behaviour toward males depending upon their past interactions with them. To test this hypothesis, we designed a series of experiments that investigated how prior interactions between males and infants affect subsequent behaviour between the male and the infants' mothers.

The hypothesis that female preferences depend upon traits such as male parental care also predicts

that males will vary the amount of parental care they provide depending upon the social environment. The flexibility of male parental care within a species is already well documented. Among common marmosets, *Callithix jacchus*, for example, males who typically provide care for infants are less likely to do so as the number of helpers increases (Box 1975, 1977). Similarly, among lemurs, galagos and rhesus monkeys, males who typically ignore infants hold, carry and groom infants when caged alone with them (Mitchell et al. 1974; Mitchell 1977; Vogt 1984; also see Snowdon & Suomi 1982).

If the function of male parental care is, in part, to establish bonds with females, and if male parental behaviour is flexible, then males should respond differently to infants depending upon whether the infant's mother is present or absent. To test this hypothesis we investigated the parental behaviour of captive males under conditions in which the male could either see or not see the infant's mother.

METHODS

Subjects and Housing

The vervets used in these experiments were originally obtained from a feral population on St. Kitts, West Indies and were maintained at the Nonhuman Primate Laboratory and the Veterans Administration Hospital in Sepulveda, California. In the wild, vervets live in multi-male groups from which males emigrate to neighbouring groups upon reaching sexual maturity, while females remain within their natal group (Cheney & Seyfarth 1983; Whitten 1983). Andelman (1985) found that free-ranging vervet females frequently reject the sexual solicitations of certain males. Females in captivity also discriminate among males, and experimental evidence indicates that females prefer to mate with dominant males (Keddy 1986). Parental care by free-ranging males is mostly limited to indirect care (Hauser 1986), though in captivity, males will occasionally groom, carry and huddle with infants (personal observation).

Subjects were housed in four groups each containing two–three adult males, three–five adult females, and their immature offspring. Each enclosure consisted of an outdoor area measuring $3 \times 3 \times 5$ m and a nightroom measuring $2 \times 2 \times 3$ m connected to the outdoor area by a series of squeeze cages located inside the nightroom.

In the course of the experiments, we observed 11 males, nine adult females and 11 infants. Social

groups were observed on a regular basis for 15–20 h per week. A linear dominance hierarchy was constructed for adults of each sex based upon approach–retreat interactions (Rowell 1966). Dominance relations remained stable throughout the experimental period. In addition, several new males were added to the groups less than 6 months prior to the start of the experiments. These males were classified as new since they had not yet integrated into the group at the start of this study. Thus males were classified as 'alpha' ($N=4$), 'subordinate' ($N=3$), or 'new' ($N=4$) at the beginning of experimentation.

Experimental Protocol

The social interactions between males and infants were examined in the following manner. First, animals from each group were herded into squeeze cages located inside the nightroom. Next, a preselected male and infant were separated from the group using the squeeze cage doors. The dyad was then released and locked outside under one of the following three treatments.

(1) Plexiglas: the infant's mother was placed behind a Plexiglas partition located inside the nightroom so that males and infants could see the female and the female could see the dyad. No other group members were in sight.

(2) One-way mirror: the infant's mother was placed behind a one-way mirror inside the nightroom so that she could see males and infants but they could not see her. No other group members were in sight.

(3) Metal partition: the infant's mother was placed behind a metal partition within the nightroom such that she could not see males or infants, and males and infants could not see her. No other group members were in sight.

After observing the male–infant pair for 30 min, we released the infant's mother into the outdoor enclosure to join the male and infant, and observed her behaviour for 10 min. At the end of this period, the rest of the group was released.

Infants ranged in age from 6 to 23 months. To minimize the distress to mothers and infants, only infants that readily broke contact with their mothers inside the squeeze cages were used as subjects. Infants were classified as 'young' (less than 12 months) or 'old' (more than 12 months) for the purposes of analysis. Infants were also categor-

ized as high- or low-ranking based upon their mother's dominance rank within the group.

To determine which males fathered particular infants, the date of conception for each infant was determined by counting back 163 days from birth (Cheney et al. 1988). Since alpha males were the only males ever observed copulating in these social groups, we assumed that males who were alpha at the time of conception were the most likely fathers of infants. To maintain genetic diversity in the colony, males were transferred between groups at regular intervals prior to the start of this study. Two out of the four current alpha males had been transferred into their current group at least 1 year earlier. Since they were not group members at the time of conception, they could not be the infants' fathers. These males were classified as alpha, however, since they had been members of the group for at least 6 months.

Table I. Behavioural definition of terms

Behaviour	Definition
Approach	One animal moves within 1 m of another animal and sits down
Leave	One animal gets up and moves away from an animal who is sitting within 1 m
Avoid	One animal quickly moves away from another animal who has moved within 2 m
Groom	One animal separates the fur of another for at least 10 s
Aggress	One animal stares, lunges at, slaps, bites, bares its teeth or chases another animal
Display	An animal rears up on its hind legs exposing chest and genitals. Often accompanied by stares and grunts
Lipsmack	Rapid movement of the lips while facing another individual
Caretake	Dorsal ventral contact between an infant and an adult. Often with arms of adult encircling infant and vocalizations by adult
Huddle	Two animals leaning against one another with substantial body contact between the two
Vocalize	One animal utters a vocal sound towards another individual or towards the environment
Vigilance	One animal sits or stands motionless facing the perimeter of the cage for at least 5 s

Observations were collected between February and October 1986. Table I lists the patterns of behaviour recorded for males, females and infants. All male–infant combinations from the four groups were observed under each experimental condition for a total of 75 trials. The sequence of experimental trials for each male–infant pair was randomized to reduce order effects. Animals from each group were exposed to one-way mirrors several weeks prior to the experiments to minimize novelty effects. Four to six experiments were conducted each week; at least 5 days separated each experiment between a particular male and infant.

Analysis

Since approach and leave behaviours are not independent (Smuts 1985), the Hinde Index (Hinde & Atkinson 1970) was used to measure which member of the dyad was most responsible for maintaining proximity. This index is defined here as the percentage of all approaches initiated by a male minus the percentage of all leaves initiated by a male. It represents a mean value for all the relative dyadic scores of this class. The index varies between -1 and $+1$; it is positive when males are primarily responsible for maintaining proximity to the infants and negative when infants are primarily responsible for maintaining proximity to males. Hinde & Atkinson (1970) suggest that values greater than 0.1 or less than -0.1 are biologically important.

All patterns of behaviour were examined using multi-way ANOVA models to determine the effect of treatment and dominance status on social behaviour (Sokal & Rohlf 1981). In addition, since many of the behaviour patterns were interrelated, principal component analysis was, also used. This reduced a large number of the original social variables into a linear combination of new, uncorrelated components which attempt to explain most of the observed variation (Afifi & Clark 1984).

RESULTS

Male Behaviour Towards Infants

How did males respond towards infants once they were separated from the group? Table II summarizes the approach–leave data for males and infants. Results suggest that both male status and test condition affected the roles played by males

Table II. Approach–leave index for males in male–infant dyadic trials

Test condition	Male status		
	Alpha male	Subordinate male	New male
Plexiglas	−0·43	+0·09	+0·13
One-way mirror	−0·67	−0·52	+0·05
Metal partition	−0·64	−0·40	−0·13

Table III. Principal component analysis for male behaviour in male infant dyads

Behaviour	Principal component 1	Principal component 2	Principal component 3
Approach	0·2797	0·4344*	−0·0675
Leave	0·1920	0·3704*	−0·0349
Avoid	0·0102	0·0338	0·6127*
Groom	0·5321*	−0·2794	−0·0344
Aggression	0·0810	0·1148	0·4453*
Display	−0·0609	−0·0441	0·5765*
Vocalize	−0·2439	−0·2308	−0·2124
Lipsmack	0·5296*	−0·3490	0·0861
Caretake	0·4211*	−0·1587	0·0121
Huddle	0·2685	0·4523*	−0·2502
Vigilance	0·0422	0·4179*	0·2246

* Correlation (r) greater than 0·50.

and infants in maintaining proximity. Infants were responsible for maintaining proximity to alpha males under all trial conditions. Subordinate males, however, were more likely than infants to maintain proximity under Plexiglas conditions (when the mother could see). They were less likely to maintain proximity under one-way mirror and metal conditions (when, from the male's perspective, the mother could not see).

Males also responded directly towards infants. The results of principal component analysis, summarized in Table III, revealed that the original 11 behaviour patterns could be reduced to three principal components which together explained 56% of the total variance in male behaviour towards infants. Grooming, lipsmacking and caretaking were highly correlated with principal component 1 (22% of the total variance), so this

component may be interpreted as a general measure of affiliation. Principal component 2 (17% of the total variance) was highly correlated with variables such as approaching, leaving and vigilance. Finally, behaviours such as aggression, display and avoid were highly correlated with principal component 3 (17% of the total variance), so this component may be interpreted as a general measure of agonistic behaviour.

Based upon the results of principal components analysis and analysis of variance, Table IV summarizes data on the affiliative and agonistic behaviour of males towards infants. Alpha males directed significantly more affiliative behaviour towards infants than did subordinate males or new males ($F = 3·45$, $df = 2,66$, $P < 0·04$) and they were equally affiliative under all experimental conditions regardless of the mother's presence. In contrast, subordinate males were most affiliative under Plexiglas conditions (when they could see the mother) and least affiliative under one-way mirror and metal conditions (when they could not see the mother). New males showed consistently low rates of affiliative behaviour towards infants.

Alpha males also directed more affiliative behaviour towards male infants, while subordinate males and new males directed more affiliative behaviour towards female infants ($F = 3·20$, $df = 2,66$, $P < 0·04$). Subordinate males directed more affiliative behaviour towards the infants of high-ranking females ($F = 3·39$, $df = 2,66$, $P < 0·04$) while alpha males and new males showed no preference towards infants as a function of rank. Finally, rates of male affiliative behaviour towards an infant varied depending on whether current alpha males were likely to have fathered the infant. Alpha males directed more affiliative behaviour towards infants whom they were likely to have fathered. In contrast, subordinate males were more affiliative towards infants not fathered by the current alpha male even though there was a very low probability that they themselves had fathered the infants ($F = 3·60$, $df = 2,66$, $P < 0·03$). Infant age (greater or less than 12 months) had no effect on male affiliative behaviour ($F = 0·05$, $df = 1,68$, $P < 0·95$).

Males also varied in their agonistic behaviour towards infants. Alpha males directed more agonistic behaviour towards infants under one-way mirror and metal conditions (when they could not see the mother) than under Plexiglas conditions (Tukey–Kramer test for unplanned comparisons:

Table IV. Mean ($\pm$SE) social behaviour initiated by males during male infant dyadic trials (rates per half hour)

Behaviour and context	Actor and status		
	Alpha male	Subordinate male	New male
Affiliative behaviour			
Test condition			
Plexiglas	5·88 ± 1·21	6·57 ± 0·92	1·71 ± 0·71
One-way mirror	5·11 ± 1·70	2·57 ± 0·75	3·00 ± 0·67
Metal partition	3·37 ± 1·02	2·33 ± 0·33	1·10 ± 0·29
Infant sex			
Female	3·30 ± 0·59	4·60 ± 0·70	3·71 ± 0·92
Male	6·38 ± 1·06	3·00 ± 0·39	1·26 ± 0·61
Infant status			
High-ranking	4·28 ± 0·90	6·00 ± 1·40	1·69 ± 0·43
Low-ranking	5·50 ± 1·30	1·33 ± 0·65	2·15 ± 0·65
Alpha male			
Father	5·83 ± 1·02	2·36 ± 0·54	1·44 ± 0·46
Not father	2·62 ± 0·60	5·77 ± 0·95	2·17 ± 0·47
Agonistic behaviour			
Test condition			
Plexiglas	4·22 ± 0·81	6·71 ± 0·79	1·14 ± 0·62
One-way mirror	6·22 ± 1·06	8·14 ± 1·60	1·66 ± 0·53
Metal partition	6·26 ± 1·11	6·33 ± 1·50	1·70 ± 0·44

Table V. Principal component analysis for female behaviour during post-dyadic trials

Behaviour	Principal component 1	Principal component 2	Principal component 3
Approach	0·4150*	0·1079	0·4470*
Leave	0·0603	0·0413	0·5984*
Avoid	−0·2102	0·4260*	0·3015
Groom	0·4344*	0·2864	−0·1675
Aggression	−0·3355	0·5469*	0·0963
Display	−0·2404	0·4997*	−0·0816
Vocalize	0·0723	0·2032	−0·3213
Lipsmack	0·3346*	0·2490	−0·1887
Caretake	0·2624	0·2327	−0·3481
Huddle	0·4844*	0·1286	0·2166

* Correlation (r) greater than 0·50.

$msd = 1·87$, $df = 9,73$, $P < 0·05$). Alpha males and subordinate males showed significantly more agonistic behaviour towards infants than did new males ($F = 4·51$, $df = 2,66$, $P < 0·01$). Infant age ($F = 0·01$, $df = 1,68$, $P < 0·95$) infant rank ($F = 0·34$, $df = 1,68$, $P < 0·55$), paternity ($F = 2·28$, $df = 1,68$, $P < 0·13$) and the sex of the infant ($F = 0·24$, $df = 1,68$, $P < 0·62$) had no effect on male agonistic behaviour.

Female Behaviour During Post-dyadic Trials

How did the infant's mother respond to the male once she was released? If female mate choice is at least partially influenced by male parental behaviour, then the females' interactions with each male following her release should have been affected by the male's previous interactions with her infant. Principal components derived for post-dyadic observations of female behaviour explained 53% of the total variance (Table V). Just as with male behaviour, the first principal component for females was a measure of affiliative behaviour (25% of the total variance). The second principal component (14% of the total variance) gave high coefficient values to agonistic behaviour, and principal component 3 (14% of the total variance) gave high values to behaviour such as approach, leave and avoid.

Data on the affiliative and agonistic behaviour of females towards males in post-dyadic trials are summarized in Table VI. In general, females directed more affiliative behaviour towards alpha males after dyadic trials than they did towards subordinate or new males ($F = 17·83$, $df = 2,68$, $P < 0·0001$). There were no differences in the rates at which females directed affiliative behaviour

Table VI. Mean ($\pm$SE) social behaviour initiated by females during post-dyadic trials (rate per 10 min)

Behaviour and context	Recipient and status		
	Alpha male	Subordinate male	New male
Affiliative behaviour			
Plexiglas	$5 \cdot 66 \pm 1 \cdot 73$	$1 \cdot 62 \pm 0 \cdot 92$	$1 \cdot 71 \pm 0 \cdot 89$
One-way mirror	$6 \cdot 44 \pm 2 \cdot 01$	$1 \cdot 85 \pm 1 \cdot 20$	$1 \cdot 11 \pm 0 \cdot 48$
Metal partition	$4 \cdot 22 \pm 1 \cdot 37$	$0 \cdot 40 \pm 0 \cdot 20$	$0 \cdot 72 \pm 0 \cdot 33$
Aggressive behaviour			
Plexiglas	$1 \cdot 33 \pm 0 \cdot 53$	$0 \cdot 62 \pm 0 \cdot 41$	$5 \cdot 28 \pm 0 \cdot 80$
One-way mirror	$1 \cdot 66 \pm 0 \cdot 62$	$5 \cdot 14 \pm 1 \cdot 54$	$4 \cdot 88 \pm 0 \cdot 67$
Metal partition	$0 \cdot 66 \pm 0 \cdot 41$	$1 \cdot 60 \pm 0 \cdot 65$	$1 \cdot 27 \pm 0 \cdot 47$

towards males based upon test condition ($F = 2 \cdot 46$, $df = 2,63$, $P < 0 \cdot 09$).

Infant age ($F = 0 \cdot 77$, $df = 1,68$, $P < 0 \cdot 38$), infant sex ($F = 0 \cdot 26$, $df = 1,68$, $P < 0 \cdot 61$), infant paternity ($F = 1 \cdot 84$, $df = 1,68$, $P < 0 \cdot 17$) and infant social status ($F = 0 \cdot 05$, $df = 1,68$, $P < 0 \cdot 45$) had no effect on female affiliative behaviour. This suggests that females were responding to the behaviour of the males themselves rather then to characteristics or behaviour of their infants. In support of this idea, infants were more likely to approach the partition which separated the mother and infant under conditions in which the infant could not see its mother (one-way mirror and metal) than under conditions in which the infant could see the female (one-way mirror/Plexiglas t-test $= 2 \cdot 95$, $df = 51$, $P < 0 \cdot 05$; metal/Plexiglas $t = 2 \cdot 81$, $df = 49$, $P < 0 \cdot 05$).

Females were also fairly discriminatory in their aggressive behaviour towards males. Females directed more agonistic behaviour towards subordinate and new males than they directed towards alpha males ($F = 12 \cdot 97$, $df = 2,63$, $P < 0 \cdot 0001$). Females also directed more agonistic behaviour towards all males after one-way mirror dyadic trials than after Plexiglas or metal dyadic trials ($F = 3 \cdot 25$, $df = 2,63$, $P < 0 \cdot 05$).

The most interesting result to emerge from the analysis of female agonistic behaviour was that females were more aggressive towards subordinate males after one-way mirror trials (when the subordinate males had been most aggressive towards infants), and less aggressive after Plexiglas trials (when the subordinate males had been the most friendly towards infants; $F = 2 \cdot 62$, $df = 2,68$, $P < 0 \cdot 04$). When the overall rates of female agonistic behaviour (under Plexiglas and one-way mirror

conditions in which the female can see the male and infant) were compared with rates of male affiliative behaviour under the same conditions, a significant negative correlation was found ($r = -0 \cdot 98$, $N = 6$, $P < 0 \cdot 004$). Thus, as male affiliative behaviour increases, female agonistic behaviour decreases.

Females exhibited high levels of agonistic behaviour towards new males under both conditions where they could observe the male's behaviour (one-way mirrors and Plexiglas), but low levels of agonistic behaviour in the conditions when they could not (metal conditions). Infant age ($F = 0 \cdot 00$, $df = 1,68$, $P < 0 \cdot 97$), infant sex ($F = 2 \cdot 99$, $df = 1,68$, $P < 0 \cdot 08$), infant paternity ($F = 3 \cdot 10$, $df = 1,68$, $P < 0 \cdot 08$), and infant social status ($F = 0 \cdot 02$, $df = 1,68$, $P < 0 \cdot 87$) had no effect on female agonistic behaviour.

DISCUSSION

The results of all the experiments are summarized in Table VII. They demonstrate that males vary their affiliative and agonistic behaviour towards infants depending on their own dominance/tenure status, characteristics of the infant, and on whether or not the infant's mother is visible. Females vary their behaviour towards males depending upon the males' dominance/tenure status and on the males' behaviour towards the females' infants.

Male Behaviour

Male parental care in vervets is not as obvious as in many other primate species (Whitten 1987), yet results from this and one other study suggest that male vervets do occasionally care for infants, and

Table VII. Summary of experimental results

Males	
Alpha males	Consistently friendly, more so to male infants and their own offspring. Less aggressive when mother in sight
Subordinate males	More friendly when mother in sight; more friendly to high-ranking infants, female infants, and infants not fathered by the current alpha male. Less aggressive when mother in sight
New males	Consistent low rates of friendly behaviour. Less aggressive when mother in sight
Females	More friendly to alpha males. More aggressive to subordinate and new males. More aggressive to all males after one-way mirror trials

that the amount of care given depends at least partly on the likelihood that the alpha male is the infant's father. Studying East African vervets in the field, Hauser (1986) found that males with a higher probability of paternity responded more strongly than other males to the playback of an infant's distress vocalization. Similarly, alpha males in the present study showed more friendly behaviour towards infants if the infants were likely to be their own offspring (Table IV).

Male behaviour in our experiments was also affected by the male's ability to see the infant's mother. Alpha males in all conditions, and subordinate males in Plexiglas, conditions, were significantly less aggressive towards infants if the mother was in sight than if she was not (Table IV). Given these results, it is possible that males are less aggressive and more friendly in the presence of the female in order to minimize her subsequent aggression. This would be particularly important to increase the subsequent willingness of females to form and maintain relationships with them. A simpler explanation is that male behaviour towards infants was affected merely by the presence of the mother. Similar 'audience effects' have been demonstrated in vervet monkeys where females give more alarm calls in the presence of kin than in the presence of non-kin (Cheney & Seyfarth 1985); in domestic chickens, *Gallus gallus*, where cockerals give alarm calls to a predator if a conspecific is

nearby but not if they are alone or with members of another species (Gyger et al. 1986); and in a variety of ground squirrels and prairie dogs, where animals with kin are more likely than animals without kin to give alarm calls to a predator (Sherman 1977; Hoogland 1983). 'Audience effects' alone, however, may be insufficient to explain why subordinate males differed from alpha and new males in the magnitude of their affiliative response to the presence of females (Table IV).

Female Response To Male Behaviour

Several studies have shown that male behaviour can affect survivorship of infants. While once believed to be an anomaly (Dolhinow 1977), infanticide has now been observed in many non-human primates (see Hausfater & Hrdy 1984; Strusaker & Leland 1987 for reviews). Infants can also be harmed when used by males during agonistic interactions with rival males (baboons: Packer 1980; Stein 1984).

By contrast, males can improve the survivorship of infants by carrying, grooming and protecting them from other group members (baboons: Altmann 1980; Stein 1984). In extreme cases, males have even adopted infants whose mothers have died or disappeared (gorillas, *Gorilla gorilla beringei*: Fossey 1983; rhesus macaques: Berman 1983). This suggests that there are clear evolutionary advantages for females who are sensitive to the behaviour of males.

In contrast to dominant or subordinate males of longer tenure, females have very little information about new males who represent a potential infanticidal threat. In our experiments, females consistently threatened new males regardless of the male's behaviour. This agrees with data from other species where females are intolerant of new males and attack them with little provocation (languers, *Presbytis entellus*: Jay 1963; vervets: Cheney 1981; chimpanzees: Ransom 1981). Such maternal aggression may explain why males often exhibit fear responses towards infants (stumptail macaques, *Macaca arctoides*: Bertrand 1969; Japanese macaques: Alexander 1970; vervets: Lancaster 1975).

Females are less conservative in their response to dominant or subordinate males with whom they have some experience. Here their behaviour is best interpreted as an interaction between the male's relationship with the female and the male's beha-

viour towards the infant. Our results suggest that alpha males show the most affiliative behaviour towards infants whether or not they fathered the infant, and females show the least aggression towards alpha males. This may be a consequence, in part, of advantages obtained by females from affiliative relationships with alpha males. High-ranking males exert a strong influence over group members, and often intervene on behalf of females and lower-ranking individuals (reviewed in Walters & Seyfarth 1987; personal observation). Such intervention may be especially helpful to younger animals. In addition, a number of studies have shown that high-ranking males provide more care for infants than do lower-ranking males (Japanese macaques: Itani 1959; Alexander 1970; baboons: Stein 1984). The importance of such an ally and protector, combined with the generally friendly behaviour of these males towards infants, may further promote affiliative behaviour by females towards alpha males. It seems reasonable that females who may influence male dominance rank, should exhibit the most affiliation behaviour to-wards alpha males.

With subordinate males, female behaviour appears to depend more on what the male actually does. In this respect it is interesting to note that the behaviour of all males, and in particular subordi-nate males seems to have been influenced by their perceptions of whether or not the mothers could observe their interactions with infants. While females show consistently low rates of friendly behaviour towards subordinate males, females are less aggressive when subordinate males are more affiliative towards infants. The low rates of affilia-tive behaviour by females towards subordinate males suggest that while females may be willing to tolerate subordinate males, they are unwilling to initiate any bond-forming behaviour. In contrast, females are intolerant of any aggressive behaviour by subordinate males and will retaliate given provocation.

It is difficult to predict what long-term conse-quences may arise from a single interaction. Indeed, the ontogeny of interactions which lead to the establishment of a relationship between two animals is poorly understood (Kummer 1975; Hinde 1976). Several studies have shown that females occasionally build strong affiliative rela-tionships with subordinate males (baboons: Sey-farth 1978a, b; Smuts 1983, 1985; Strum 1984). It may be that these relationships with subordinate

males do not occur immediately, but are formed gradually, requiring frequent affirmative behaviour on the part of the male before the female will respond positively.

Likewise, although females showed affiliative behaviour towards alpha males, they may be less likely to maintain these relationships with alpha males who continually direct aggression towards infants. It is here that the process of female mate choice may have its greatest effect in species with little sexual dimorphism, as females withdraw their support for one male and build relationships with another. This additional support may then allow subordinate males to safely challenge higher-rank-ing males.

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