

ORIGINAL ARTICLE

Joseph Soltis · Ruth Thomsen
 Kiyooki Matsubayashi · Osamu Takenaka

Infanticide by resident males and female counter-strategies in wild Japanese macaques (*Macaca fuscata*)

Received: 2 September 1999 / Received in revised form: 27 April 2000 / Accepted: 3 May 2000

Abstract Infanticide was observed for the first time in a wild, non-provisioned troop of Japanese macaques on Yakushima Island, Japan. Eight adult resident males attacked unweaned infants in the pre- and early mating season, and one infanticide was observed directly. These attacks were not consistent with the social pathology, side effect of male aggression, cannibalism, or the resource defense hypothesis, but were generally consistent with the sexual-selection hypothesis. First, most male attackers had risen in dominance rank because several high-ranking males had left the troop. Second, in 78% of cases, male attackers had not previously been observed to mate with the mothers of victims. Moreover, analysis of subject animal DNA showed that males did not attack their own offspring. The two mothers who lost their unweaned infants, however, were not subsequently observed to mate. In fact, almost no mating behavior was observed in the troop. This was most likely due to a poor fruiting year. Resumption of mating by females who lost their infants may have been inhibited by an intervening environmental variable which suppressed female reproductive function. These observations contribute to a

growing body of evidence which suggests that sexually selected infanticide can occur in seasonally breeding, multi-male, multi-female primate groups. Female Japanese macaques are known to mate with multiple males. We found evidence that female mating with multiple males inhibits contact aggression towards their infants. Adult males attacked infants eight times more often when they had not previously mated with the mother.

Key words Male infanticide · Female counter-strategies · *Macaca fuscata*

Communicated by S. Boinski

J. Soltis (✉)
 Private Research Institute, Kyoto University

R. Thomsen
 Department of Zoology, LM-University of Munich,
 Luisenstrasse 14, 80333 Munich, Germany

K. Matsubayashi
 Animal Husbandry Center, Primate Research Institute,
 Kyoto University, Inuyama, Aichi, 484-0081, Japan

O. Takenaka
 Department of Cellular and Molecular Biology,
 Primate Research Institute, Kyoto University, Aichi 484-0081,
 Japan

Present address:

Laboratory of Comparative Ethology,
 National Institutes of Health, Box 529, Poolesville,
 MD 20837, USA
 e-mail: soltisj@mail.nih.gov
 Tel.: +1-301-4960835, Fax: +1-301-4960066

Introduction

Infanticide has been observed in numerous animal species (Hausfater and Hrdy 1984; Parmigiani and vom Saal 1994). Potential adaptive explanations for infanticidal behavior include nutritive benefits from cannibalism (Elgar and Crespi 1992), defense of resources by eliminating competitors (Sherman 1981), and manipulation of parental investment, in which parents terminate investment in particular offspring by killing (and sometimes consuming) them (Daly and Wilson 1988; Elgar and Crespi 1992). For non-human primates, the most common adaptive explanation for infanticide has been the sexual-selection hypothesis (Hrdy 1974, 1979), according to which males increase reproductive opportunity by killing unrelated, unweaned offspring, thus hastening the mother's next ovulation, at which time the infanticidal male can mate with her. Alternatively, according to the social-pathology hypothesis, infanticide in primates results from unnatural living conditions such as overpopulation (e.g., Dolhinow 1977; Boggess 1984). Finally, according to the side effect hypothesis, infanticide is an epiphenomenon of overall male aggression (e.g., Sussman et al. 1995).

While the sexual-selection hypothesis remains controversial in anthropological circles (Bartlett et al. 1993; Sussman et al. 1995), most male infanticide in primates is consistent with it (Hiraiwa-Hasegawa 1988; Hrdy et

al. 1995), and is supported by sexually selected infanticide in other taxa (e.g., Perrigo and vom Saal 1994; Pusey and Packer 1994). Infanticide in primates occurs mostly in single-male groups, where intruder males often defeat resident males and take over the group of females, after which they kill unweaned offspring. Infant loss shortens the interbirth interval of mothers, and infanticidal males sometimes mate and produce offspring with the mothers when they resume ovulation (e.g., Borries et al. 1999a).

Compared to one-male groups, the costs of attempting infanticide in multi-male groups may be high because resident males can defend infants, and benefits may be low because resident males must compete for access to females. Nevertheless, infanticide consistent with sexual selection also occurs in multi-male primate groups (e.g., *Alouatta seniculus*: Crockett and Sekulic 1984; *Macaca fascicularis*: de Ruiter et al. 1994; *M. thibetana*: H. Ogawa, personal communication; *Presbytis entellus*: Borries et al. 1999a; *Papio*: Collins et al. 1984; Palombit et al. 1997).

Seasonal breeding is also thought to reduce the likelihood of infanticide because infant loss is unlikely to shorten interbirth intervals (e.g., Hrdy and Hausfater 1984). In cases where females do not give birth every season, however, loss of an infant may increase the probability of giving birth in the subsequent birth season. Under such conditions, infanticide also occurs in seasonally breeding primate groups (*Propithecus diadema*: Wright 1995; *Lemur catta*: Pereira and Weiss 1991; Hood 1994; *P. entellus*: Borries 1997).

If males commit infanticide, then females should develop counter-strategies (Hrdy 1979; Hiraiwa-Hasegawa 1988; Smuts and Smuts 1993; Sterck et al. 1997). Possible female counter-strategies include (1) fighting back, (2) seeking the protection of males who can defend offspring from infanticidal males, and (3) mating with multiple males to confuse paternity. Fighting back often only postpones the male's attempts to kill offspring (e.g., Sommer 1987; Hrdy 1977). There is evidence that former mates, especially high-ranking males, protect females' offspring from infanticidal males (*Papio*: Palombit et al. 1997; *M. fascicularis*: de Ruiter et al. 1994; *P. entellus*: Borries et al. 1999b). While evidence that primate females mate with multiple males is extensive (e.g., Small 1990; Manson 1992; Takahata et al. 1998a; Soltis et al. 1999), evidence that such multiple mating reduces the probability of infanticide is limited to anecdotal reports (e.g., Struhsaker and Leland 1987; Watts 1989).

Japanese macaques are seasonally breeding primates forming multi-male, multi-female social groups, with female philopatry and male dispersal (Pusey and Packer 1987). Infanticide has never been observed in wild, non-provisioned troops, but has been observed twice in provisioned groups (Yoshihiro et al. 1974; Tokida 1976). We observed resident adult males attack unweaned infants, including one case of infanticide, in a wild, non-provisioned troop of Japanese macaques on Yakushima Island, Japan. First, we describe the attacks, and then

evaluate the fit between these observations and the following hypotheses (Hrdy et al. 1995; Sussman et al. 1995): social pathology, side effect of male aggression, cannibalism, resource defense, and sexual selection. We also discuss possible reasons why infanticide has rarely been observed in Japanese macaques. Second, we test the hypothesis that females mate with multiple males in order to confuse paternity and inhibit males from infant attack and infanticide.

Methods

Observations reported here were obtained for the Nina-A troop of Japanese macaques (*M. fuscata yakui*) on Yakushima Island, Japan, (30°N, 131°E; Maruhashi 1982). The Nina-A troop lives in a 2×0.7 km range along the western seashore (altitude 0–220 m above sea level). A single road transects the range. The study area consists of subtropical coastal forest, warm temperate broadleaf evergreen forest, and secondary roadside forest (Maruhashi 1980, 1982). The troop has never been provisioned, but was habituated to human observers from 1994. J.S. and R.T. observed the troop from July 1997 to January 1999. Both observers recognized all adult troop members individually and infants by association with their mothers (Table 1).

Behavioral data were derived from focal sampling and ad libitum observations. J.S. collected behavioral data in the 1997 and 1998 mating seasons during 383 h of female focal samples and ad libitum observations (Soltis 1999). Japanese macaques are seasonal breeders, with the mating season from September to February and the birth season from late March to early July on Yakushima Island (Maruhashi 1982; Maruhashi and Takasaki 1996; personal observations). Japanese monkeys are series mounters (Tokuda 1961), and "mating" in this paper refers to those mounting series culminating in a terminal, ejaculatory mount. R.T. collected data on male aggression towards mothers and their infants and male-male dominance interactions from October 1997 to November 1998 during over 1,200 h of adult male and female focal samples and ad libitum observations. Aggression towards infants included only contact aggression (e.g., bite, hit, slap). Male dominance interactions recorded were displacement (one animal approaches <1 m and the other moves away >1 m) and submission (facial grimace, cower, flee). A total of 1,576 dominance interactions were recorded (median per dyad=8, range=1–143). A matrix was formed with winners on one axis and losers on the other. A few dyads showed bi-directional displacements, and in these cases the highest-ranking male was the male who won the majority of interactions.

The infanticidal attack was observed by J.S. The infant's body was collected and an autopsy performed by K.M. at the Primate Research Institute of Kyoto University (PRI). J.S. and O.T. performed paternity exclusion at the PRI by analyzing microsatellite loci from fecal, urine, blood, and other tissue samples collected

Table 1 Composition of the Nina-A troop at the beginning of the 1997 (values in parentheses) and 1998 mating seasons (*Adult* potentially sexually mature; Takahata et al. 1998b)

	Males	Females	Total
Adult (≥4 years)	(15) 12	(15) 13	(30) 25
Juvenile (1–3 years)	(10) 10	(7) 4	(17) 14
Infant (0 years)	(3) 3	(2) 4 ^a	(5) 7 ^b
Total	(28) 25	(24) 21	(52) 46

^a One of these infants was a victim of infanticide during the mating season

^b Does not include three infants who disappeared before the mating season

from subject animals in the field (for methodological details see Inoue and Takenaka 1993; Takenaka et al. 1993; Soltis et al. 1997; Hayakawa and Takenaka 1999). A non-parametric statistical test was used (Conover 1980; SPSS 10.0) with alpha set at 0.05. Because a directional hypothesis was being tested (see below), a one-tailed test was employed.

Results

Attacks on infants and infanticide

Ten infants were born in the 1998 birth season. Eight resident adult males attacked between one and six unweaned infants each during the pre-mating and early mating season (Table 2). In all, there were 23 separate male-infant dyads involved in such aggression. Most of these males had recently risen in dominance rank because three high-ranking males left the troop before the 1998 mating season, and an additional male left early in the mating season. In 18 of 23 male-infant dyads (78%) involved in aggression, the male was not a former mate of the infant's mother. Moreover, in 22 of the 23 male-infant dyads, the male was excluded as the father of the victim (in one case, paternity was unresolved; Table 2).

Five infants were observed with injuries (Table 2), and four infants died or disappeared. Two of the four were not observed having been attacked by males, and they disappeared along with their mothers. These two infants may have died simply because their mothers died. Another infant which was attacked by males (YGI) disappeared while her mother still lived. This infant may have been a victim of infanticide. The fourth infant (HRS) was killed by an adult male.

The infanticidal male (NM) was observed attacking the victim (HRS) on five occasions previous to the infanticide, twice resulting in visible injury (Table 2). NM was excluded as a possible father of HRS in a paternity exclusion analysis, and he was not observed to mate with the mother during the previous mating season in 1997. In addition, he had risen in dominance rank from 9th of 15 males (42.9% of males outranked) to 5th of 12 males (63.6% of males outranked).

The infanticide occurred on 1 December 1998. HRS was observed with fresh wounds (missing digits on hand, wounds on face). Subsequently, NM was observed to attack her, during which time he persistently bit the infant, until her mother and two other (unidentified) females chased the attacker away. The alpha male also ran toward the scene, but he did not actively defend the infant. The alpha male had mated with the mother in the previous mating season, but he was excluded as the father in a DNA analysis. The infant could not walk well enough to keep up with the troop, and was eventually left behind. She remained motionless, but breathing, until nightfall. The body was confirmed dead the following morning, and was recovered for examination.

Numerous puncture and slash wounds were observed on the body, and three and one-half digits from the right

hand were missing. The body was sent to Kyoto University (PRI), where K.M. performed a routine autopsy. The most likely immediate cause of death was determined to be a strike to the back of the head, where a fracture to the cranium and extensive subdural hemorrhaging were observed. Second, the presence of old and new bite wounds on the legs, arms, and head, as well as subdermal hemorrhaging of the limbs, confirmed a history of repeated attacks. Two nematode parasites were found in the intestines, a single *Trichuris trichiura* and a single *Oesophagostomum aculeatum*, both common parasites in Japanese macaques (Yamashita 1963). The intestines were otherwise healthy, however, so parasitic infection was not considered to be a contributing factor in the infant's death.

No mother who lost her infant was observed to mate after infant loss. In fact, all mating behavior within the troop had ceased early in November, well before the usual cessation of mating in February. No newborns were observed the following birth season.

Female multiple mating and male aggression against infants

We investigated the hypothesis that females benefit from mating with multiple males because such mating reduces the likelihood that males will direct aggression (including infanticide) against their infants. One-tailed tests are justified when a difference in the opposite, unpredicted direction would be considered the same as no trend at all (Kimmel 1957). In such cases, an interpretation of a difference in the unpredicted direction is not deducible from existing theory and is therefore meaningless. We tested the directional hypothesis that males are more likely to attack mother-infant pairs when they have not mated with the mother. The opposite trend (i.e., that males are more likely to attack mother-infant pairs when they have mated) is not interpretable under existing theory and would be treated the same as no trend at all (i.e., that males attack mated and non-mated mother-infant pairs equally).

In this analysis, we used only those males who were both sexually mature and present in the troop at the beginning of both the 1997 and the 1998 mating seasons ($n=11$). For each male, we divided the ten mother-infant pairs into two groups, those in which the male was observed to mate with the mother in the 1997 mating season (mated pairs) and those in which the male was not observed to do so (non-mated pairs). Next, we analyzed male contact aggression towards infants and to mother-infant pairs. We analyzed such data for the pre-mating and early 1998 mating season (26 July 1998 to 1 December 1998), when such aggressive attacks were most frequent. Across the 11 males, the mean aggression rate (\pm SD) toward mated mother-infant pairs was 0.203 ± 0.477 , and the mean rate towards non-mated pairs was 1.693 ± 2.773 (Wilcoxon signed-ranks test, $Z=1.680$, $n=11$ males, $P=0.047$; Fig. 1).

Table 2 Cases of adult male contact aggression against infants and mother-infant pairs in the pre- and early mating season, 1998. The ordinal rank of each male is indicated. Fifteen sexually mature males were in the troop in 1997 and 12 in 1998. Three adult males left the group before the 1998 mating season (ranks 4–6), and AR left the group in the early mating season (20 October 1998). Other males' ranks for 1998 are calculated without AR included. One natal male reached sexual maturity in 1998. A three-letter code is

used to identify the infant victim; *-M* signifies that the mother-infant pair was attacked. Injuries sustained by infant victim: *None* no visible injury; *B* bleeding; *L* limping; *S* swelling; *Killed* victim of infanticide (see text). Prior mating of victim's mother and the male attacker: *X* no mating observed in the previous 1997 mating season; *Yes* mating observed. Results of paternity exclusion analysis: *X* male attacker excluded as the father of the victim at two or more microsatellite loci; *?* paternity for this infant unresolved

	Male	Rank 1997	Rank 1998	Date	Infant	Injury	Mating observed	Paternity
1	SC	1	1	26 July	HRS	None	Yes	X
2				16 September	NMZ-M	None	X	X
3				21 September	TMK-M	None	Yes	X
4	KZ	3	3	13 September	TMK-M	None	Yes	X
5				17 September	SHT-M	None	X	X
6				05 November	YGI	None	X	X
7	AR	7	4	31 August	HRS	None	X	X
8				13 September	SHT-M	None	X	?
9				13 September	SHT	None	X	?
10	NM	9	5	27 July	HRS	None	X	X
11				27 July	TMK-M	None	X	X
12				15 August	HRS-M	None	X	X
13				22 August	SKE	None	X	X
14				27 August	SKE-M	None	X	X
15				31 August	HRS	B	X	X
16				31 August	NRK	None	X	X
17				21 September	SKE	B	X	X
18				25 September	NRK	None	X	X
19				27 September	HRS	B	X	X
20				28 September	SKE-M	None	X	X
21				20 October	TMK	None	X	X
22				05 November	YGI	None	X	X
23				05 November	YGI-M	None	X	X
24				05 November	SKE-M	None	X	X
25				08 November	TMK	None	X	X
26				08 November	NMZ	None	X	X
27				08 November	NRK-M	None	X	X
28				08 November	YGI-M	None	X	X
29				08 November	HRS-M	None	X	X
30				01 December	HRS	Killed	X	X
31	SK	10	6	29 July	SKE	L	X	X
32				20 September	SHT-M	None	X	X
33				26 September	SKE	None	X	X
34				20 October	NMZ-M	None	X	X
35				30 October	NMZ-M	None	X	X
36	MM	11	7	29 September	SKE-M	None	Yes	X
37				05 November	NMZ-M	None	Yes	X
38	BB	12	8	23 November	YGI	None	X	X
39				27 November	YGI	None	X	X
40	JK	14	10	27 July	SKE	None	X	X
41				27 August	SKE	None	X	X
42				29 September	HRS	None	X	X
43				29 September	HRS-M	None	X	X
44				29 September	YGI	None	X	X
45				29 September	YGI	None	X	X
46	Cause of injury unknown ^a			26 July	TMK	L		
47				13 August	HRS	B		
48				22 August	YGI	B,L		
49				22 August	NRK	B		
50				01 September	NRK	S		
51				20 September	HRS	B, L, S		
52				19 October	YGI	B		
53				27 November	HRS	B		

^a For cases 46 to 53, the infant was observed with visible injuries, but the cause was unknown

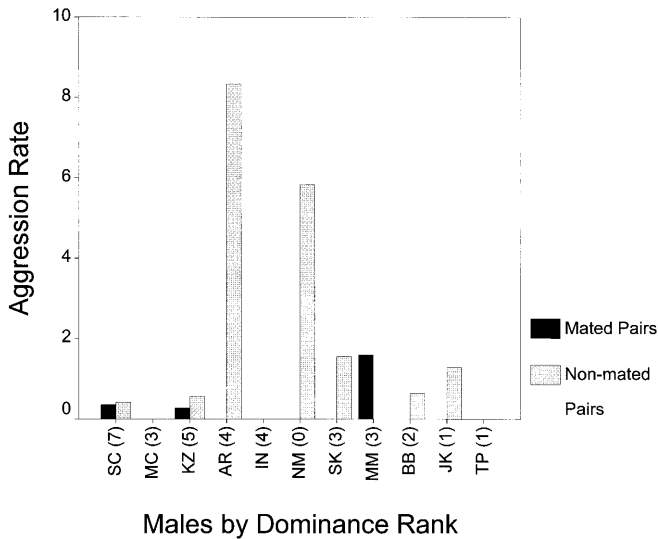


Fig. 1 Mean male contact aggression rate toward infants and mother-infant pairs, when the males have mated with the mothers (*Mated pairs*, black bars) and when they have not mated with the mothers (*Non-mated pairs*, gray bars). The aggression rate for each mother-infant pair was calculated as the number of attacks on the mother-infant pair plus the number of attacks on the infant only, divided by the number of days the male was observed to be present in the troop, multiplied by 100. Aggression during feeding is not included. Males are listed from left to right in order of dominance rank. For each male, the number of mating partners out of ten mothers is shown in parentheses (NM had no mating partners who gave birth, and he was assigned an average of zero for statistical analysis). AR left the troop early in the mating season (20 October 1998), before the infanticidal attack

Discussion

Explanations of infanticide

These cases of infant attacks are not consistent with the social-pathology hypothesis. The site is free of strong human influence, such as provisioning of animals with food, which is associated with larger group size and increased aggression in Japanese macaques (Yamagiwa and Hill 1998; Hill 1999). These observations are not likely to be a side effect of overall male aggression. First, male-to-infant aggression began in the absence of other intense male aggression, that is, several months after the changes in the dominance hierarchy, and 2 months before the mating season began. Second, male aggression was targeted specifically at unweaned infants who were most often not offspring of former mates and were never the offspring of the aggressor males (Table 2). These observations are not consistent with the cannibalism hypothesis. The male did not consume the corpse of the one victim whose killing was observed even though its motionless body lay alone for hours. Finally, these are unlikely to have been cases of resource defense. The infant victims cannot be considered substantial competitors for the males who attacked them. Moreover, because male tenure in groups is usually only several years (Sugiyama 1976; Sprague et al. 1998), attack-

ers and victims were unlikely to remain in the same group for long. Males are also unlikely to have been eliminating competitors of their own offspring. Only two of eight males who attacked infants (SC and MM) were fathers of offspring born in 1998, and three additional males who sired offspring attacked no infants at all.

These observations are generally consistent, however, with the sexual-selection hypothesis. First, most male attackers had risen in dominance rank relative to the previous year, increasing their chances of mating with the mother and siring offspring. In this group, male dominance rank and mating success are correlated ($r_s=0.7$, $n=15$, $P<0.001$; Soltis 1999). Male dominance rank and number of offspring sired are also positively correlated, and only high- and mid-ranking males (top two-thirds of 15) sired offspring ($r_s=0.587$, $n=15$, $P<0.05$; unpublished data). Second, most attackers were not observed to mate with the mother during the previous mating season, and in no case where paternity was resolved did a male attack his own offspring.

Third, the victims were unweaned infants, whose deaths could hasten their mothers' ovulation. Lactating Japanese macaques experience suppressed reproductive function (Mitsunaga et al. 1992, 1994). On Yakushima Island, the average interbirth interval when infants survive is 2.24 years (± 0.85 SD, $n=42$), but is significantly reduced when infants die within 1 year of birth (1.5 ± 0.84 years, $n=6$; Takahata et al. 1998b). Thus, infanticide can increase the probability that ovulation will occur in subsequent mating seasons. Fourth, mean male residence in troops among Yakushima macaques is short (2.8 years; Sprague et al. 1998), which increases the risk of infanticide (Borries and Koenig, in press).

Two mothers lost their infants but survived themselves, but neither female was observed to mate after infant loss. In fact, only two females who had not given birth exhibited mating behavior during all mating season observations (both early in the season). The most likely explanation for this lack of reproductive behavior was a poor fruit year. Ten years of data on Yakushima Island show that poor fruit years are associated with low birth rates in subsequent birth seasons (Suzuki et al. 1998), and the year of the infanticide was an exceptionally poor fruit year (N. Noma, unpublished data). Thus, mothers of infants who died may have failed to resume mating because of an intervening environmental variable that suppressed reproductive function.

Why is infanticide rarely observed in Japanese macaques?

Two cases of infanticide have been observed in free-ranging, provisioned groups of Japanese macaques. Yoshihiro et al. (1974) reported a case in which tourists observed an adult male kill an infant by pounding its head against a stone, cannibalizing its hand in the process. In another case (Tokida 1976), a non-group male invaded a group in which the alpha male was only 7 years old, and repeated-

ly attacked infants and their mothers. During the pre-mating and early mating season, nine babies were injured and two died. The male was seen attacking six of these infants, and repeatedly attacked one who subsequently died. The two infant deaths occurred before the onset of the mating season, so the mothers could presumably have resumed cycling and mating in the subsequent mating season, but no such data were provided. The latter case is consistent with the sexual-selection hypothesis. Both cases occurred in provisioned groups, however, so human disturbance could also be invoked as a causal factor.

The observation of infanticide reported here is the first in a wild, non-provisioned troop of Japanese macaques. If we are correct in our hypothesis that infanticide has been sexually selected in Japanese macaques, why has it been so rarely observed? We believe that the conditions for infanticide as an effective strategy are rarely met in Japanese macaques, especially in provisioned groups, where most observations have been conducted (Yamagiwa and Hill 1998).

Infanticide is most beneficial when non-fathers have an increased probability of siring offspring. This can occur when a new male enters a group at a high rank, or when a resident male rises substantially in dominance rank. Neither of these phenomena is common in large, provisioned groups of Japanese macaques where immigrant males almost invariably enter at the bottom of the dominance hierarchy and slowly rise in rank as higher-ranking males emigrate or die (Sprague et al. 1996, 1998; Manson 1998). Furthermore, the costs of attempting infanticide may be higher in provisioned groups because group spread is lower and matriline are larger (Hill 1999).

Non-provisioned troops on Yakushima Island, however, are relatively small, and males often aggressively enter troops and secure the alpha position in the dominance hierarchy (Sprague et al. 1996, 1998). Nevertheless, the present report is the first observed infanticide on Yakushima Island since habituation of macaques began in 1982 (Yamagiwa et al. 1998). Even when a male could potentially benefit from infanticide, however, other factors such as the strength of the matriline, the presence of male protectors, and female mating behavior (see below) may inhibit its initiation. Finally, short-lived, violent attacks such as infanticide are difficult to observe (e.g., one infant attack per 1,554 observation hours in Hanuman langurs, *P. entellus*; Borries 1997).

Does female multiple mating inhibit male aggression?

We have argued that infanticide may be part of the reproductive strategy of the male Japanese macaque. If so, this selective force should shape the behavior of females. Hrdy (1977, 1979) argued, for example, that if males use past mating as a cue for future interaction with infants, then it might benefit mothers to mate with many males. We found evidence in favor of the hypothesis that female mating with multiple males inhibits male-to-infant contact aggression, infanticide being the most extreme case.

Males attacked infants of non-mates eight times more often than those of former mates (Fig. 1).

This type of analysis could be improved in at least two ways, however. Most female mating behavior could not be observed, due to simultaneous mating by females and the difficulty of observation on Yakushima Island. A smaller troop in more accessible terrain may provide an opportunity for a more accurate description of female mating behavior. Second, males may use peri-ovulatory mating, rather than mating generally, as a cue to infant treatment. Without hormonal data, however, accurate estimation of ovulation is not possible in Japanese macaques (Nigi 1975, 1976).

Conclusions

Resident males were observed attacking unweaned infants in a wild Japanese macaque troop, and one infanticide was observed directly. These observations are generally consistent with the sexual-selection hypothesis, and contribute to a growing body of evidence suggesting that sexually selected infanticide can occur in seasonally breeding primates forming multi-male social groups. Female mating with multiple males may confuse paternity and reduce infant harassment and infanticide.

Acknowledgements We would like to thank Drs. Yukimaru Sugiyama and Juichi Yamagiwa for supporting the project on Yakushima Island. Dr. Naohiko Noma kindly allowed us to cite his unpublished data on fruit availability for the year of the infanticide, Sachiko Hayakawa provided valuable assistance in DNA analysis, Shunji Goto identified the two parasites found in the intestine of the baby victim, and Miki Matsubara provided support in the field. Shiho Fujita and Miki Matsubara assisted in Japanese translations. We would like to thank Carola Borries, Joseph Manson, Susan Perry, Volker Sommer, and three reviewers for very helpful discussions and critical reading of earlier versions of the manuscript. J.S. was supported by a grant from the USA National Science Foundation (NSF) and from the Japan Society for the Promotion of Science (JSPS). R.T. was supported by a grant from the German Academic Exchange Service (DAAD). This non-invasive animal research complied with the relevant laws and regulations of Japan.

References

- Bartlett TQ, Sussman RW, Cheverud JM (1993) Infant killing in primates: a review of observed cases with specific reference to the sexual selection hypothesis. *Am Anthropol* 95:958–990
- Bogges J (1984) Infant killing and male reproductive strategies in langurs (*Presbytis entellus*). In: Hausfater G, Hrdy SB (eds) *Infanticide: comparative and evolutionary perspectives*. Aldine, New York, pp 283–310
- Borries C (1997) Infanticide in seasonally breeding multi-male groups of Hanuman langurs (*Presbytis entellus*) in Ramnagar (south Nepal). *Behav Ecol Sociobiol* 41:139–150
- Borries C, Koenig A (in press) Infanticide in Hanuman langurs: social organization, male migration, and weaning age. In: Schaik CP van, Janson CH (eds) *Infanticide by males and its implications*. Cambridge University Press, Cambridge, UK
- Borries C, Launhardt K, Epplen C, Epplen JT, Winkler P (1999a) DNA analyses support the hypothesis that infanticide is adaptive in langur monkeys. *Proc R Soc Lond B* 266:901–904
- Borries C, Launhardt K, Epplen C, Epplen JT, Winkler P (1999b) Males as infant protectors in Hanuman langurs (*Presbytis ent-*

- ellus*) living in multi-male groups: defense pattern, paternity, and sexual behaviour. *Behav Ecol Sociobiol* 46:350–356
- Collins DA, Busse CD, Goodall J (1984) Infanticide in two populations of savanna baboons. In: Hausfater G, Hrdy SB (eds) *Infanticide: comparative and evolutionary perspectives*. Aldine, New York, pp 193–215
- Conover WJ (1980) *Practical nonparametric statistics*, 2nd edn. Wiley, New York
- Crockett CM, Sekulic R (1984) Infanticide in red howler monkeys (*Alouatta seniculus*). In: Hausfater G, Hrdy SB (eds) *Infanticide: comparative and evolutionary perspectives*. Aldine, New York, pp 193–215
- Daly M, Wilson M (1988) *Homicide*. de Gruyter, Hawthorne, NY
- Dolhinow P (1977) Normal monkeys? *Am Sci* 65:266
- Elgar MA, Crespi BJ (1992) *Cannibalism: ecology and evolution in diverse taxa*. Oxford Science, Oxford
- Hausfater G, Hrdy SB (1984) *Infanticide: comparative and evolutionary perspectives*. Aldine, New York
- Hayakawa S, Takenaka O (1999) Urine as another potential source for template DNA in polymerase chain reaction (PCR). *Am J Primatol* 48:299–304
- Hill DA (1999) Effects of provisioning on the social behavior of Japanese and rhesus macaques: implications for socioecology. *Primates* 40:187–198
- Hiraiwa-Hasegawa M (1988) Adaptive significance of infanticide in primates. *Trends Ecol Evol* 3:102–105
- Hood LC (1994) Infanticide among ringtailed lemurs (*Lemur catta*) at the Berenty Reserve, Madagascar. *Am J Primatol* 33:65–69
- Hrdy SB (1974) Male-male competition and infanticide among the langurs (*Presbytis entellus*) of Abu, Rajasthan. *Folia Primatol* 22:19–58
- Hrdy SB (1977) *Langurs of Abu*. Harvard University Press, Cambridge, Mass
- Hrdy SB (1979) Infanticide among animals: a review, classification, and examination of the implications for the reproductive strategies of females. *Ethol Sociobiol* 1:13–40
- Hrdy SB, Hausfater G (1984) Comparative and evolutionary perspectives on infanticide: introduction and overview. In: Hausfater G, Hrdy SB (eds) *Infanticide: comparative and evolutionary perspectives*. Aldine, New York, pp xiii–xxxv
- Hrdy SB, Janson C, Schaik C van (1995) Infanticide: let's not throw the baby with the bathwater. *Evol Anthropol* 3:151–154
- Inoue M, Takenaka O (1993) Japanese macaque microsatellite PCR primers for paternity testing. *Primates* 31:563–570
- Kimmel HD (1957) Three criteria for the use of one-tailed tests. *Psychol Bull* 54:351–353
- Manson J (1992) Measuring female mate choice in Cayo Santiago rhesus macaques. *Anim Behav* 44:405–416
- Manson J (1998) Evolved psychology in a novel environment: male macaques and the 'seniority rule'. *Hum Nat* 9:97–117
- Maruhashi T (1980) Feeding behavior and diet of the Japanese monkey (*Macaca fuscata yakui*) on Yakushima Island, Japan. *Primates* 21:141–160
- Maruhashi T (1982) An ecological study of troop fissions of Japanese monkeys (*Macaca fuscata yakui*) on Yakushima Island, Japan. *Primates* 23:317–337
- Maruhashi T, Takasaki H (1996) Socio-ecological dynamics of Japanese macaque troop ranging. In: Fa JE, Lindburg DG (eds) *Evolution and ecology of macaque societies*. Cambridge University Press, Cambridge, UK, pp 146–159
- Mitsunaga F, Nozaki M, Inoue M, Takenaka A, Takenaka O, Sakura O, Sugiyama Y, Ohsawa H (1992) Steroid hormones and sexual behavior of female Japanese monkeys in an enclosed group. In: Itoigawa N, Sugiyama Y, Sackett GP, Thompson RKR (eds) *Topics in primatology*, vol 2. University of Tokyo Press, Tokyo, pp 23–34
- Mitsunaga F, Nozaki M, Shimizu K (1994) Suppressed copulatory behavior and ovarian function in lactating Japanese macaques (*Macaca fuscata fuscata*) during the mating season. *Primates* 35:79–88
- Nigi H (1975) Menstrual cycle and some other related aspects of Japanese monkeys (*Macaca fuscata*). *Primates* 16:207–216
- Nigi H (1976) Some aspects related to conception of the Japanese monkey (*Macaca fuscata*). *Primates* 17:81–87
- Palombit RA, Seyfarth RM, Cheney DL (1997) The adaptive value of 'friendships' in female baboons: experimental and observational evidence. *Anim Behav* 54:599–614
- Parmigiani S, Saal F vom (1994) *Infanticide and parental care*. Harwood, London
- Pereira ME, Weiss ML (1991) Female mate choice, male migration, and the threat of infanticide in ringtailed lemurs. *Behav Ecol Sociobiol* 28:141–152
- Perrigo G, Saal F vom (1994) Behavioral cycles and the neural timing of infanticide and parental behavior in male house mice. In: Parmigiani S, Saal F vom (eds) *Infanticide and parental care*. Harwood, London, pp 365–396
- Pusey AE, Packer C (1987) Dispersal and philopatry. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT (eds) *Primate societies*. University of Chicago Press, Chicago, pp 250–266
- Pusey AE, Packer C (1994) Infanticide in lions: consequences and counterstrategies. In: Parmigiani S, Saal F vom (eds) *Infanticide and parental care*. Harwood, London, pp 277–300
- Ruiter JR de, Hooff JARAM van, Scheffrahn W (1994) Social and genetic aspects of paternity in wild long-tailed macaques (*Macaca fascicularis*). *Behaviour* 129:203–224
- Sherman PW (1981) Reproductive competition and infanticide in Belding's ground squirrels and other animals. In: Alexander RD, Tinkle DW (eds) *Natural selection and social behavior*. Chiron, New York, pp 311–331
- Small M (1990) Promiscuity in Barbary macaques (*Macaca sylvanus*). *Am J Primatol* 20:267–282
- Smuts BB, Smuts RW (1993) Male aggression and sexual coercion of females in nonhuman primates and other mammals: evidence and theoretical implications. *Adv Study Behav* 22:1–63
- Soltis J (1999) Measuring male-female relationships during the mating season in wild Japanese macaques (*Macaca fuscata yakui*). *Primates* 40:453–467
- Soltis J, Mitsunaga F, Shimizu K, Nozaki M, Yanagihara Y, Domingo-Roura X, Takenaka O (1997) Sexual selection in Japanese macaques. II. Female mate choice and male-male competition. *Anim Behav* 54:737–746
- Soltis J, Mitsunaga F, Shimizu K, Yanagihara Y, Nozaki M (1999) Female mating strategy in an enclosed group of Japanese macaques. *Am J Primatol* 47:263–278
- Sommer V (1987) Infanticide among free-ranging langurs (*Presbytis entellus*) at Jodhpur (Rajasthan/India): recent observations and a reconsideration of hypotheses. *Primates* 28:163–197
- Sprague DS, Suzuki S, Tsukahara T (1996) Variation in social mechanisms by which males attained the alpha rank among Japanese macaques. In: Fa JE, Lindburg DG (eds) *Evolution and ecology of macaque societies*. Cambridge University Press, Cambridge, UK, pp 444–458
- Sprague DS, Suzuki S, Takahashi H, Sato S (1998) Male life-history in natural populations of Japanese macaques: migration, dominance rank, and troop participation of males in two habitats. *Primates* 39:351–363
- Sterck EHM, Watts DP, Schaik CP van (1997) The evolution of female social relationships in nonhuman primates. *Behav Ecol Sociobiol* 41:291–309
- Struhsaker TT, Leland L (1987) Colobines: infanticide by adult males. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT (eds) *Primate societies*. University of Chicago Press, Chicago, pp 83–97
- Sugiyama Y (1976) Life history of male Japanese monkeys. *Adv Study Behav* 7:255–284
- Sussman RW, Cheverud JM, Bartlett TQ (1995) Infant killing as an evolutionary strategy: reality or myth? *Evol Anthropol* 3:149–151
- Suzuki S, Noma N, Izawa K (1998) Inter-annual variation of reproductive parameters and fruit availability in two populations of Japanese macaques. *Primates* 39:313–324
- Takahata Y, Ihobe H, Idani G (1998a) Comparing copulations of chimpanzees and bonobos: do females exhibit proceptivity or

- receptivity? In: McGrew WC, Marchant LF, Nishida T (eds) *Great ape societies*. Cambridge University Press, Cambridge, UK, pp 146–155
- Takahata Y, Suzuki S, Agetsuma N, Okayasu N, Sugiura H, Takahashi H, Yamagiwa J, Izawa K, Furuichi T, Hill DA, Maruhashi T, Saito C, Sato S, Sprague DS (1998b) Reproduction of wild Japanese macaque females of Yakushima and Kinkazan islands: a preliminary report. *Primates* 39:339–349
- Takenaka O, Takasaki H, Kawamoto S, Arakawa M, Takenaka A (1993) Polymorphic microsatellite DNA amplification customized for chimpanzee paternity testing. *Primates* 34:27–35
- Tokida E (1976) Infanticide by 'Kabo' in 1970 at the Wild Monkey Park of Hell Valley, Nagano Prefecture. *Nihonzaru* (in Japanese). *Jpn Monkey* 2:124–128
- Tokuda K (1961) A study of the sexual behavior in the Japanese monkey troop. *Primates* 3:1–40
- Watts DP (1989) Infanticide in mountain gorillas: new cases and a reconsideration of the evidence. *Ethology* 81:1–18
- Wright PC (1995) Demography and life history of free-ranging *Propithecus diadema edwardsi* in Ranomafana National Park, Madagascar. *Int J Primatol* 16:835–854
- Yamagiwa J, Hill DA (1998) Intraspecific variation in the social organization of Japanese macaques: past and present scope of field studies in natural habitats. *Primates* 39:257–273
- Yamagiwa J, Izawa K, Maruhashi T (1998) Long-term studies on wild Japanese macaques in natural habitats at Kinkazan and Yakushima: preface. *Primates* 39:255–256
- Yamashita J (1963) Ecological relationships between parasites and primates. I. Helminth parasites and primates. *Primates* 4:1–96
- Yoshihiro S, Fukuda F, Iwano T (1974) A case of cannibalism observed among wild Japanese monkeys (in Japanese). *Jpn Monkey* 1:123–129