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Infanticide by Adult and Subadult Males in Free-ranging Red Howler Monkeys, *Alouatta seniculus*, in Venezuela

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Abstract

After 15 males invaded troops of wild red howler monkeys (*Alouatta seniculus*) present in Venezuela during the period from Apr. 1989 to May 1991, five infant killings and eight infant disappearances occurred. Among the eight groups that were invaded, 10 infants of less than 3 mo old and three of over 5 mo old were killed either by the adult or subadult males, or disappeared. However, on the five occasions of invasion, none of the nine infants were killed. In two other groups, there were no infants present at the time of invasion. It was also noted that no infant of kin of the invading males was killed. At least six of the females that had lost their infant during such invasion subsequently copulated both with the invader as with the original resident male. In one case, a female copulated with the resident male of a neighbouring group. In the four cases of subadult males committing infanticide there was no immediate sexual access to the females. The data presented here are inconsistent with the reproductive sexual-advantage hypothesis, but consistent with the hypothesis concerning food competition.

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Introduction

Infanticide has been reported in a wide range of primate taxa (ANGST & THOMMEN 1977; HRDY 1979; STRUHSAKER & LELAND 1987). Thus, the extent and evolutionary significance of infanticide in animals has been the subject of considerable interest (HAUSFATER & HRDY 1984). Various explanations have been proposed for the ultimate causation and function of non-human primate infanticide. These include maladaptive social pathology (DOLHINOW 1977; CURTIN & DOLHINOW 1978), adaptive advantage of immediate reproductive access (HRDY 1974, 1977, 1979), and reduction of food-based competition (RUDRAN 1979 a, b,

1994). Much controversy exists over the evolutionary function of infanticide (HAUSFATER & HRDY 1984; BREDEN & HAUSFATER 1990; BARTLETT et al. 1993; AGORAMOORTHY 1994; RUDRAN 1994).

Among the extant six species of howler monkeys, infanticide has been documented in red howlers (*Alouatta seniculus*) in Venezuela (RUDRAN 1979 a, b, 1994; SEKULIC 1983), mantled howlers (*Alouatta palliata*) in Costa Rica (CLARKE 1983), and black howlers (*A. caraya*) in Argentina (RUMIZ 1990). This behaviour in red howler monkeys has attracted the attention of primatologists because it occurs not only following male invasion but also when there is no invasion, that is, in multi-male groups (RUDRAN 1979 a, b, 1994; CROCKETT & SEKULIC 1984). Furthermore, unlike the male invasion in uni-male groups in several Old World monkeys (ANGST & THOMMEN 1977; HRDY 1979; STRUHSAKER & LELAND 1987), red howler uni-male groups have been reported to become multi-male groups following male invasions (RUDRAN 1979 a, b, 1994; CROCKETT & SEKULIC 1984). In this paper, we present the details of acts of infanticide committed by adult and subadult males, and we describe the process and consequences of this behaviour. The results are discussed in relation to hypotheses that have been suggested as explanations for the evolutionary significance of non-human primate infanticide.

Methods

The study was conducted at the savanna woodlands of Hato Masaguaral, a wildlife refuge and a working cattle ranch located in the state of Guarico in Venezuela. The ranch is well protected, where domestic animal populations are kept under control such that they have a minimal impact on the wildlife and its habitat (CROCKETT & RUDRAN 1987). Over the past 15 y, about 350 red howler monkeys, divided into 36 groups, have been the subject of demographic and behavioural research (RUDRAN 1979b; CROCKETT & SEKULIC 1984; CROCKETT & EISENBERG 1987; CROCKETT & RUDRAN 1987; POPE 1990; AGORAMOORTHY 1992; AGORAMOORTHY & RUDRAN 1992, 1993, 1994). The red howler monkeys are not provisioned with food, hunted, or otherwise disturbed by humans. They are sympatric with one other primate species, *Cebus olivaceus*. Details of the study site and climatic conditions are described elsewhere (RUDRAN 1979b; TROTH 1979).

A total of 36 red howler groups were censused for demographic data once a mo from Apr. 1989 to May 1991. During the census, groups that underwent male invasions were selected in order to collect data on social interactions. During this study, 15 of the invaded groups were monitored with the help of field assistants and each member of the group was observed on a monthly basis for a 12-h period lasting 5 continuous d. Furthermore, these groups were followed for 6 h per d. The all-occurrences sampling method (ALTMANN 1974) was used to record aggressive, affiliative and sexual behaviour (G. AGORAMOORTHY unpubl. data). The 15-min scan sampling (ALTMANN 1974) was used to record inter-individual distances between group members. All the animals in the study groups were individually identified either by their ear tags (AGORAMOORTHY & RUDRAN 1994) or by their size, scars and facial characteristics. The kin relations and age of the study animals were verified from long-term genealogical records compiled by R. RUDRAN (unpubl. data). The date of conception was estimated by subtracting the average gestation period of 191 d from the date of birth of each infant (CROCKETT & SEKULIC 1982).

Results

Male Invasions

From Apr. 1989 to May 1991, 15 invasions were observed in 15 red howler

Table 1: Group composition and ages of infants in the invaded red howler, *Alouatta seniculus* groups of Venezuela where infanticide did not occur. Abbreviations: adult (A), subadult (SA), juvenile (J), infant (I), large (L), medium (m), small (S), male (M), female (F)

Group number and composition (n)	No. of invaders	No. and ages of infants available	Probable reason for infant survival
Group 12 1AM, 4AF, 1SAM, 1LJM, 3SJM, 1SJF, 1IM (12)	2	1 (3 mo)	?
Group 24 1AM, 4AF, 1SAM, 2LJF, 1SJM, 2SJF, 2IM (13)	1	2 (7 mo)	?
Group 29 1AM, 3AF, 1SAM, 2m JM, 1SJM, 3IM, (11)	1	3 (2 mo) (0.7 mo) (0.2 mo)	invader male (father) related to resident male (son)
Group 5 1AM, 3AF, 1mJM, 2SJF, 2IM (9)	1	2 (4.3 mo) (0.7 mo)	invader male (son) related to resident (father)
Group 14 1AM, 4AF, 2SJM, 1SJF, 1IF (9)	3	1 (8 mo)	?

groups. In seven of the invasions, a uni-male group was invaded by a solitary male. In the rest, two or more males invaded uni-male groups resulting in the eviction of the resident male. By contrast, the solitary invaders stayed with their resident counterparts in all instances, thus establishing multi-male groups after invasions. The history of invading males was known in 11 of the 15 invasions, and, in all of these cases, known males invaded their neighbours. The youngest invaders recorded in our study were two medium-sized juveniles, aged 2.0 and 2.5 yr. These juveniles were accompanied by adult, male half-brothers. In total, five cases of infanticide were observed and eight infant disappearances were documented in eight of the 15 groups invaded by males. In five other groups, infants whose age ranged from 0.2 to 8.0 mo were present at the time of invasion, but infanticide did not occur (Table 1). In two other groups (groups 1 and 36), there were no infants present at the time of invasion.

Observed Cases of Infanticide

Case 1: The first infanticide was observed in group 4. An adult male (2) invaded on May 1, 1989, and stayed with the group for 19 mo. The group's resident male (1) was wounded twice after the invasion, but maintained tenure in

Table 2: Sexual activity of the red howler females who had lost infants by infanticide

Group number/ female's number	Age of lost infant (mo)	Days after infant loss in invaded groups				
		first estrus begins (d)	last estrus ends (d)	No. of cycles		No. of copulators
4/8	9.0	13	85	5		3
31/3	1.5	9	58	3		1
31/5	1.5	11	101	6		2
31/3	0.2	5	35	2		2
31/5	0.1	3	60	4		2
31/8	0.1	5	43	3		2
32/2	0.6	4	30	2		2

his group. A 4-mo-old infant present at the time of invasion was killed when it was 9-mo old and after its mother had come into estrus. On Sep. 14, an adult female (8) was seen copulating with the invader male (2) whilst her 9-mo-old infant sat 1.5 m from the copulating pair. On Oct. 10, 1989, at 14.30 h, the invader male (2) was seen sitting 3 m from the female (8). She had her infant on her lap while two other females (4 and 6) sat 7 m away. The resident male (1), who was the probable father of the infant of the female (8) was sitting in a tree 12 m away. 7 min later, the invader male (2) moved towards the female (8). Suddenly, the female (8) produced a low-pitched scream with her mouth wide open. She then attempted to chase away the approaching male (2). However, the invader male (2) grabbed the infant from the female (8) and bit its face, then letting it drop. The mother then retrieved her screaming infant. It had an open wound 2.5-cm long, 1.5-cm broad and 2-cm deep that ran between its right eye and right nostril. The 9-mo-old wounded infant was seen with its mother during the evening, but, by the next morning, it was found dead on the ground. After having lost her infant, the female (8) came into estrus and copulated with the resident, the invader, and with a neighbouring group's resident male (Table 2).

Four infanticides described (cases 2–5) below occurred in group 31. In the morning of Apr. 14, 1990, the resident male was not seen with the group. In the afternoon, an adult male (10) from group 11 was seen with group 31. On the following day, a young adult male (14; aged 5.4 yr) and a subadult male (16; aged 3.8 yr) from group 14 invaded group 31 and evicted the adult male invader from group 11. Prior to invasion, this group consisted of 10 individuals, including two 1.5-mo-old infants (Table 3). Four males from group 14, an adult (10), a large juvenile (17), and two medium juveniles, (18 and 19) were seen joining group 31 8 d later. No apparent aggression was noted during their invasion. Juveniles 17 and 18 were related (half-brothers) to males 14 and 16.

Cases 2 and 3: On the evening of Apr. 21, an adult female (5) was feeding whilst carrying two infants, her infant (5.2) and female 3's infant (3.2). Infant 5.2 was carried ventrally while infant 3.2 was on the back of female 5. It was at this moment

Table 3: Group composition, number of invaders and ages of victims in the invaded red howler groups. For abbreviations, see Table 1

Group number and total composition (n)	Total no. of male invaders (n) and their age class	Age(s) of infant at death (mo)
Group 4 1AM, 3AF, 1mJF, 2IM, 1IF (8)	(1) 1AM	9.0
Group 31 1AM, 3AF, 2LJM, 2SJM, 1IM, 1IF (10)	(6) 2AM, 1SAM, 1LJM, 2mJM	1.5, 1.5, 0.2 0.1, 0.1
Group 32 1AM, 2AF, 1SAF, 1mJF, 1SJM, 1IF (7)	(1) 1AM	0.6
Group 11 1AM, 4AF, 1mJM, 1SJM, 4SJF, 1IM (12)	(2) 1AM, 1LJM	4.0
Group 29 1AM, 2SAM, 3AF, 3SJM, 1IF (10)	(2) 1AM, 1SAM	2.3
Group 24 1AM, 4AF, 1SAM, 2mJF, 1SJF, 1SJM, 1IF (11)	(1) 1AM	1.1
Group 3 1AM, 3AF, 2LJF, 2SJF, 1IF, 1IM (10)	(1) 1AM	8.5
Group 10 1AM, 3AF, 1SAM, 1mJM, 2mJF, 1IM, 1I? (10)	(2) 2AM	0.3, 5.9

that subadult male 16 approached female 5 and attempted to grab infant 3.2. The infant screamed and female 5 managed to chase the male away, but, during that interaction, the male slapped infant 3.2 in the face. As a result the left eyeball of infant 3.2 was torn out of its socket. The mother retrieved her wounded infant 1 h after the attack. However, 6 d later, the wounded infant (3.2) was abandoned by its mother and left on a tree branch, to be adopted 8 h later by a nulliparous female of the neighbouring group 36. As the female was unable to nurse the infant, the infant disappeared 2 d later (AGORAMOORTHY & RUDRAN 1992). The mother of the infant was sexually receptive 5 d after rejecting her infant and was observed to cycle twice. During those estrus periods, she copulated only with male 10, although the infanticidal male 16 and male 14 (who was wounded) were present in the group. In mid-Oct., male 10 disappeared. Dried skin and bones found scattered within the home range indicated the high chances of male 10 having died.

On Dec. 21, female 3 was seen with a day-old infant sired by male 10. The next day, male 14 approached female 3, sat in body contact with her and suddenly



Fig. 1: Infanticide victim, group 31 infant 3.3. Note the canine puncture wound on the head

pulled her infant. He bit it on the head dropping it on the ground. Blood oozed from an open head wound (Fig.1). After the attack (5 min later), the mother went up to the infant, touching, sniffing (Fig.2) and licking its wound. The infant was already dead so the mother moved away and rejoined her group. It had a 2-cm-long, 1-cm-broad, head wound and a cracked cranium. Female 3 was in estrus during two periods after this and copulated with males 14 and 16 on both occasions.

Cases 4 and 5: A 1.5-mo-old female infant (5.1) belonging to group 31 was attacked on three occasions by an adult male invader (10). On Apr. 25, male 10 approached female 5, pulled away her infant with his mouth and ran off. Female 5 immediately set off after him, along with two other females (3 and 8), chasing the male until he let the infant drop. Female 5 retrieved the screaming infant which had been bitten near the base of its tail. The second attack took place 2 d later whilst female 5 sat in body contact with male 10. Again male 10 took hold of infant 5.1 and ran off with it in its mouth. He was pursued until he let go of it. The third attack occurred on 29 Apr. when male 10, on grabbing infant 5.1, actually bit it in the belly region, causing instant death. During the attack, neither the mother nor any of the other females chased male 10, though they watched the infant being killed.

After losing the infant, female 5 was sexually receptive on six occasions and copulated with males 10 and 14. She subsequently gave birth on Jan. 21, 1991. Only 2 d later, subadult male 16 was seen killing the infant. At 1534 h, a loud



Fig. 2: Female 3, the mother of the infant 3.3 attempts to retrieve the dead infant unsuccessfully

scream was heard while all the individuals were resting in a palm tree. A moment later, subadult male 16 emerged from the dense canopy with infant 5.2 in his left hand and moved onto a nearby tree. Once he sat on the branch he bit the infant several times in the belly region while the mother who had followed the male out of the palm tree, sat 0.5 m away and watched. The male then dropped the infant to the ground and it died instantaneously. It had a 3-cm-long, and 4-cm-wide wound in the belly with both stomach and intestines exposed (Fig. 3). From 27 to 31 Jan. 1991, female 5 was sexually receptive and copulated with the infanticidal male 16 as well as with male 14.

Inferred Cases of Infanticide

Case 6: Infanticide was suspected in group 31 nearly 11 mo. after it was invaded in Apr. 1990. In Jun., Jul., and late Aug. 1990, female 8 came into estrus and was seen copulating with adult male 10, present at that time. Subsequently, female 8 gave birth in late Feb. 1991. On Mar. first, the group was observed from 0630 to 1330 h when female 8 carried a 6-d-old infant. Aggressive interactions were not noticed during this observation period. At 1440 h, the group was

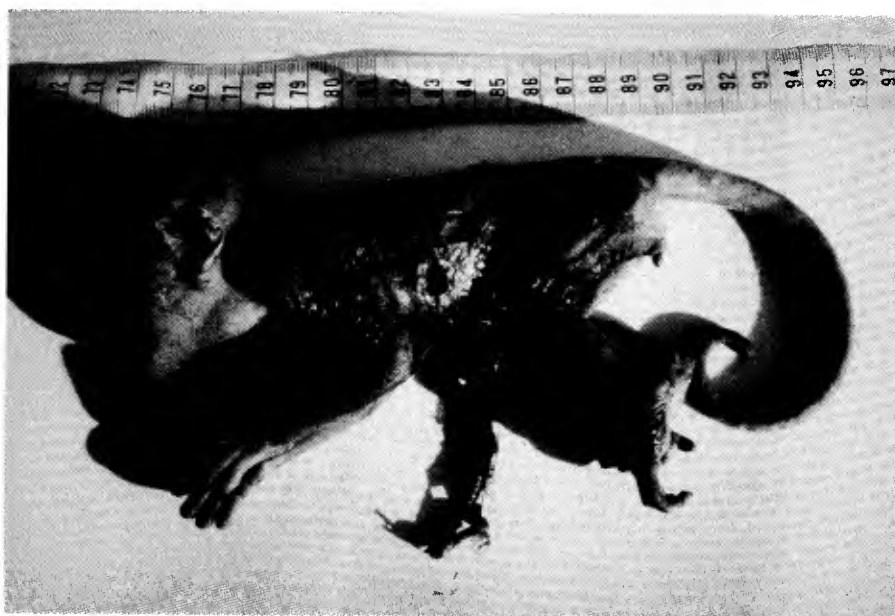


Fig. 3: Infanticide victim, group 31 infant 5.2. Note the bite wounds in the belly and exposed intestinal parts

contacted again and the infant was missing. Female 8 was seated within 1 m of subadult male 16. After a thorough search, the infant was found dead on a tree about 2 m from where female 8 and male 16 had been seated. The infant had a severe head injury with skull and ribs broken. These wounds clearly indicated that the new-born infant was a victim of infanticide, perpetrated by either male 14 or, perhaps more likely, by male 16.

Case 7: An adult male (3) from group 11 invaded a neighbouring uni-male group (32) on Jul. 8, 1989. Prior to the invasion, group 32 had seven individuals (Table 3). Female 2 of the invaded group was seen with a 1-d-old infant on Jul. 15, 1989. On Aug. first, when the observations terminated at 1230 h, the infant was with the mother. The next morning, the infant was missing. The same day, the resident male (the father of the victim) and the mother (female 2) were observed chasing invader 3. During female 2's first estrus period that followed the infanticide, she copulated only with the invader. During her second estrus period, female 2 copulated with the invader as well as the resident.

Case 8: About 8 mo after group 32 was invaded, a resident male and a large juvenile of this group successfully invaded group 11, from which the invader of this group originated (case 7). By 17 Feb. 1991, the two invaders had established themselves in group 11 evicting the single remaining adult male of this group. The evicted male was injured and later seen as a solitary animal. The 2.9-mo-old male infant of group 11 was also missing.

Case 9: In Sep. 1989, a solitary, adult male successfully invaded group 3, which had included a single adult male prior to this social change. At the time of invasion, group 3 also included an independently mobile infant (3.1). On Oct. 12, this 8.5-mo-old infant was noted with fresh wounds on his back and he was being carried by his mother. The resident male 1 (father) was observed grooming the infant and licking its wounds. On that same day, both the resident male and the mother of the infant were seen chasing away the invader. On 15 Dec., infant 3.1 sustained wounds once again, on its right arm, which it did not use during locomotion. At dusk the mother pushed the infant away from her belly and did not carry it while the group moved to settle down in a roosting tree. The infant was unable to keep up with the group and did not succeed in climbing a tree. The next morning it was missing from the group's range.

Cases 10 and 11: These two cases were documented from group 10. On Sep. first, 1989, an infant was born into this group. By Sep. 10, two adult males had evicted the resident male and subadult male. The 9-d-old infant was missing as well. A mo later, a 6-mo-old male infant also disappeared from the group.

Case 12: On 12 May 1990, adult male 1 and subadult male 9 from group 24 invaded neighbouring group 29 and evicted the resident male. A 2.3-mo-old infant disappeared 2 d later.

Case 13: On 10 Feb. 1991, an adult male in group 29 along with a subadult and a large juvenile invaded group 24 and evicted the resident male. A 1.1-mo-old infant disappeared from group 24 4 d after the invasion was documented.

Ages of Victims and Reproductive Status of Females after Infant Loss

The average age of infants that were killed or disappeared was 2.6 mo (SD = 3.2; range = 0.1–9.0; n = 13). Three of them were over 5 mo old (Table 3). The male:female sex ratio of the 12 victims was 1:2 (one unsexed excluded). Females who lost infants after male invasion became sexually receptive after, on average, 7.1 d (SD = 3.8; range 3–13; n = 7). The average number of d that elapsed between the beginning of first estrus and the end of the last estrus in these females was 58.9 d (SD = 26.2; range = 30–101; n = 7). With one exception, these females had more than one male sexual partner during their periods of sexual receptivity (Table 2). Furthermore, the female who had copulated with only one male in a multi-male group subsequently lost her offspring to infanticide (case 3).

Discussion

Social-pathology Hypothesis

According to the social-pathology hypothesis, infanticide is maladaptive, perhaps caused by unusual local circumstances such as high population densities or human intervention (DOLHINOW 1977; CURTIN & DOLHINOW 1978). This hypothesis is not applicable to the red howler data because howlers in the savanna woodlands of Hato Masaguaral live in a relatively undisturbed area (RUDRAN

1979b; CROCKETT & SEKULIC 1984; CROCKETT & RUDRAN 1987). There was no human disturbance or unusual crowding of monkeys (CROCKETT & SEKULIC 1984; RUDRAN 1994). Furthermore, these howlers are not provisioned with food, hunted or otherwise disturbed by humans. In all cases of infanticide reported here, it appears that the victims were not related to the killer males. The social-pathology hypothesis cannot, therefore, explain this non-random killing. Other reasons as to why this hypothesis may not be applicable to the red-howler population have been discussed by RUDRAN (1979a, b, 1994) and CROCKETT & SEKULIC (1984).

Reproductive Sexual-advantage Hypothesis

The reproductive sexual-advantage hypothesis proposed by HRDY (1974, 1977) is based on studies of hanuman langurs of Mount Abu, India. According to this hypothesis, infanticide induces estrus in females who have lost their offspring, it shortens their interbirth interval, and, on average, it increases the reproductive success of the killer males. But this hypothesis is not consistent with the above mentioned red-howler infanticide data for the following reasons:

1. *Older infants were victims of infanticide*: In three cases, the invading males killed older infants aged 5.9, 8.5 and 9.0 mo, respectively (Table 3). These killings had no impact on the sexual estrus of the mothers after the death of the infants. In at least one case (case 1), the mother had already resumed cycling following the social change. Thus, infanticide does not appear to be essential for the induction of sexual receptivity, in contrast to the prediction of the reproductive-advantage hypothesis (HRDY 1974, 1977).

2. *Females copulated with more than one male after infant loss*: In all cases where females lost their infants due to infanticide, the females became sexually receptive immediately and had more than one estrus cycle (Table 2), a pattern similar to that previously reported for this species (CROCKETT & SEKULIC 1984). With only one exception, all the females who lost infants then copulated with more than one adult male (Table 2). One of the females copulated with a resident male from a neighbouring group. The exception was female 3 from group 31 who only copulated with male 10 although adult male 14 and subadult male 16, who had killed her infant, were still present in the same group. However, when the infant sired by male 10 was born, it was killed by male 14. Furthermore, in the same group, female 5 copulated with male 10 and 14 after losing her infant, but not with male 16. Copulation with more than one male provides more than one opportunity for several males to sire infants and confuses the paternity among copulating males. This set of data is not consistent with the reproductive-advantage hypothesis which predicts that males kill infants in order to maximize their chances of siring their own offspring (HRDY 1974, 1977).

3. *Immature males committed infanticide*: Among red howlers, adult males were not the only ones to commit infanticide; subadult males were also observed

killing infants. In cases 2 and 5, subadult males killed infants and, in two more cases (6 and 12), subadult males were suspected of killing infants. Moreover, in case 2, the infanticidal subadult male did not copulate with the mother of the victim when she came into sexual receptivity. In similar fashion, in blue monkeys (BUTYNSKI 1982), olive baboons (COLLINS et al. 1984), chacma baboons (COLLINS et al. 1984), and red howlers (RUDRAN 1994), the infanticidal male does not always have access to the victim's mother after infanticide.

4. *Infanticide occurred when one of the males did not get sexual access:* In two cases (3 and 5), infanticide occurred after the disappearance of dominant male 10 while group 31 was stable for 7 mo after the invasion. Adult male 14 and subadult male 16 did not copulate with females 3 and 5 when they were sexually receptive. In multi-male groups, males who do not indulge in copulations with females become potential killers and the reproductive-advantage hypothesis does not make any predictions about this type of infanticide. Similar types of infanticide have also been reported in red howlers (CROCKETT & SEKULIC 1984; RUDRAN 1994), red colobus monkeys (STRUHSAKER & LELAND 1985), olive baboons (COLLINS et al. 1984), wedge-capped capuchins (VALDERRAMA et al. 1990) and chimpanzees (NORIKOSHI 1982).

Food-competition Hypothesis

The food-competition hypothesis makes some specific predictions about the killing of older infants, multiple-male copulations after infanticide, immature males' involvement in infanticide, and infanticide in a multi-male group when one of the males does not get sexual access. According to this hypothesis, infanticide of unrelated victims is considered to be an adaptive behaviour, ie. one which increases the fitness of the individuals who practice the killing and also that of their offspring (RUDRAN 1979a, b, 1994). This hypothesis in red howlers was based on the fact that howlers are a food-limited species and, for a social group, food is only available within its home range (RUDRAN 1994). By killing an unrelated infant, the infanticidal male eliminates an individual who would make increasing demands on the available food supply within the home range (RUDRAN 1994).

During invasions, some older infants over 3-mo of age were not attacked by the invading males (Table 2), probably because of reduced vulnerability. This is consistent with the high frequency of infanticidal attacks (77 %) which resulted in the death of infants who were less than 3-mo old (Table 3). There is also a wide range of variation in the ages of infanticidal victims, starting from just a few d to several mo (Table 3). The food-competition hypothesis predicts that the victims of infanticide need not necessarily be infants but can actually be of any age class. Furthermore, it specifies that killing of older infants indicates that vulnerability rather than age is the key determinant of death, and, in addition, that attacks on infants may also be situation dependent. For example, in case 1, infanticide occurred 5 mo after the invasion. In red howlers and hanuman langurs, older infants and juveniles have also been reported to be victims of infanticidal attacks

(RUDRAN 1979a, b; AGORAMOORTHY & MOHNOT 1988; AGORAMOORTHY 1994). In all cases of infanticide reported here, it is unlikely that any of the infanticidal males were related to the infants they either wounded or killed. Except for cases 3 and 5, infanticide occurred from 1 wk to a maximum of 5 mo after the invading males first joined the group. These males had probably not, therefore, sired these infants. In cases 3 and 5, the killer males did not copulate with the females when they conceived; this might have been a factor contributing to the killing after the infants were born.

When subadult males commit infanticide, they will probably sire offsprings in the group at some later stage, especially when they establish a position in the dominance hierarchy and increase the frequency of copulation (RUDRAN 1994). The food-competition hypothesis does not deny that males ultimately reproduce in order to increase their genetic fitness. It does, however, specify the importance of improved growth and survival for maintaining longer group tenure and a higher social rank, which are both necessary to maximize life time reproductive success. The effects of food-related factors on the evolution of behaviour and social organization have previously been discussed in nonhuman primates (EISENBERG et al. 1972; DITTUS 1979; WRANGHAM 1980, 1987). Thus, infanticide increases the male's reproductive success mainly through improved growth and survivorship of these males and their offspring. In red howlers, improved growth and survival is attained through food competition which is, in our opinion, the main cause of the evolution of infanticide (RUDRAN 1994). In this study, females whose infants were killed or disappeared solicited copulations within 1 wk of the death of their infants. These females had more than one sexual partner. Although the most frequent copulator probably has the greatest success in producing offspring, other males may also attain some reproductive advantage through infrequent copulations. Genetic studies of rhesus macaques who live in multi-male groups have shown that several males are responsible for siring infants within the group (SMITH 1981).

Although the majority of the invasions resulted in infant loss, some vulnerable infants survived. In two cases (Table 1; group 29 and group 5), younger infants under 3 mo of age were not harmed by invading males (AGORAMOORTHY & RUDRAN 1993). In these cases, the invader males were related to the resident males. These cases of infanticide avoidance suggest cooperation between fathers and sons, which may have increased the probability of survival and reproductive success of close kin (HAMILTON 1964).

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