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# Adult Male Replacement and Social Change in Two Troops of Hanuman Langurs (*Presbytis entellus*) at Jodhpur, India

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*I studied the process of adult male replacement and social change in two one-male troops (B20 and B21) of hanuman langurs (*Presbytis entellus*) at Jodhpur, India. Male–male competition lasted for about 6 months before the successful takeover of one troop (B20). During that period, five adult males from three neighboring bands (AMB7, AMB9, and AMB10) and a resident male of a neighboring troop (B21) were involved in taking over the troop. The latter male also copulated with six females during his interim residency, which suggests that he may have opportunistically maximized his mating chances with females of a neighboring group. During an intertroop interaction, a 14-month-old female infant of the other troop (B21) was fatally attacked by an adult female of the first troop and the infant eventually died. The attacker may have taken advantage of the disorganization created by male–male competition, perhaps to eliminate a future food competitor. In addition, the first troop gained an additional feeding area from the other troop's range; it included a sleeping site and a waterhole, indicating that territorial fights during social instability may have led to the expansion of the winner's resource area.*

**KEY WORDS:** hanuman langur; *Presbytis entellus*; social change; infanticide; food competition.

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## INTRODUCTION

The occurrence and significance of infanticide in animals have received considerable attention among biologists in recent years (Hausfater and Hrdy, 1984). Infanticide following adult male replacements and social changes has been reported frequently in the hanuman langurs, *Presbytis entellus* (Sugiyama, 1965; Mohnot, 1971; Hrdy, 1974; Makwana, 1979; Agoramoorthy, 1986; Newton, 1986; Sommer, 1987; Agoramoorthy and Mohnot, 1988). Various hypotheses have been proposed to explain the cause and function of infanticide. Initially, it was considered to be maladaptive (Dolhinow, 1977; Curtin and Dolhinow, 1978), but now it is regarded as adaptive normal behavior by several researchers (Hausfater and Hrdy, 1984). Controversy continues over the evolutionary function of infanticide in nonhuman primates (Hrdy, 1979; Rudran, 1979a, b, 1993; Hiraiwa-Hasegawa and Hasegawa, 1992). I report for the first time a fatal attack on an older infant by an adult female of a neighboring troop and provide information on the process of adult male replacement and social change in two hanuman langur troops.

## MATERIALS AND METHODS

### Study Troops

Jodhpur (26°19′N latitude, 73°8′ longitude; elevation, 241 m) lies at the eastern fringe of the Great Indian Desert and has a population of about 1300 langurs, organized in 28 one-male bisexual troops (66.7%), 1 multi-male bisexual troop (2.4%), and 13 all-male bands (30.9%) (Agoramoorthy, 1992). These troops are distributed over an area of approximately 85 $km^2$. There were no other nonhuman primates in a radius of about 100 km around Jodhpur. The entire langur population of Jodhpur lives in a semiarid habitat dominated by plant species such as *Prosopis juliflora, Euphorbia caducifolia,* and *Acacia senegal.* Mohnot (1974) provided details on the habitat and climatic condition of the study site.

I studied two one-male troops, designated B20 (Kailana II) and B21 (Bijolai), for 13 months. They lived in the Kailana-Bijolai area, about 8 km west of Jodhpur city. B21 was observed in 1969 by Mohnot (1971) and later by several other scientists (Agoramoorthy, 1992). All adult members of B21 were individually known since 1977. Before 1977, troops B19 and B20 were a single troop named B25 (Mohnot, 1971). In 1977, a fission occurred during a male-band invasion. The adult male of B25 continued his stay with 14 females, later designated troop B19 (KI), and a new adult

male along with eight females formed troop B20. The individual life histories of B19 and B21 were published by Winkler *et al.* (1984; Winkler, 1988), and Agoramoorthy (1992). I saw three all-male bands—AMB7, AMB9, and AMB10—interact with B20 and B21. During my study, the largest band was AMB10, which contained 32 males. AMB7 and AMB9 were composed of three males each.

### Study Methods

I observed B21 and B20 1026 and 824 hr, respectively, between January 1983 and January 1984. All members of troops B20 and B21, and most of the adult males of the three neighboring bands—AMB7, AMB9, and AMB10—were individually identifiable by size, facial characteristics, tail carriage pattern, and scars on the face and arms. I recorded data on the social changes and social interactions between the male bands and the study troops on an ad libitum basis (Altmann, 1974). I estimated the home range sizes by recording the location and movement of langur troops in a field map using quadrants (National Research Council, 1981).

## RESULTS

### Process of Adult Male Replacement in Troop B20

Aggressive interactions between all-male band members and the resident male of troop B20 began on the afternoon of 7 July 1983 and lasted until 25 January 1984 (Fig. 1). Five males from three all-male bands (Nos. 37 and 42 from AMB7, Nos. 52 and 70 from AMB10, and No. 72 from AMB9), and a resident male (No. 38) of a neighboring troop (B21) interacted with troop B20 and became interim residents for various periods, ranging from 3 to 86 days. Moreover, the former resident male (No. 10) regained power and stayed as an interim resident for 13 days in the troop. Important interactions between the band males and the troop members during male invasions are as follows.

On 7 July 1983 at 1235, four adult males of band AMB7 (Nos. 37, 42, 47, and 48) approached troop B20, while its members were resting near the sleeping site. An adult male (No. 37) rushed toward the resident male (No. 10) of troop B20, leading to a fight that lasted for about 5 min. Male No. 10 received a bite wound about 8 cm long on his left leg and then he left the troop. However, he stayed within the troops's home range (Fig. 2). On 11 July, when AMB10 invaded the troop, the males of AMB7 retreated.

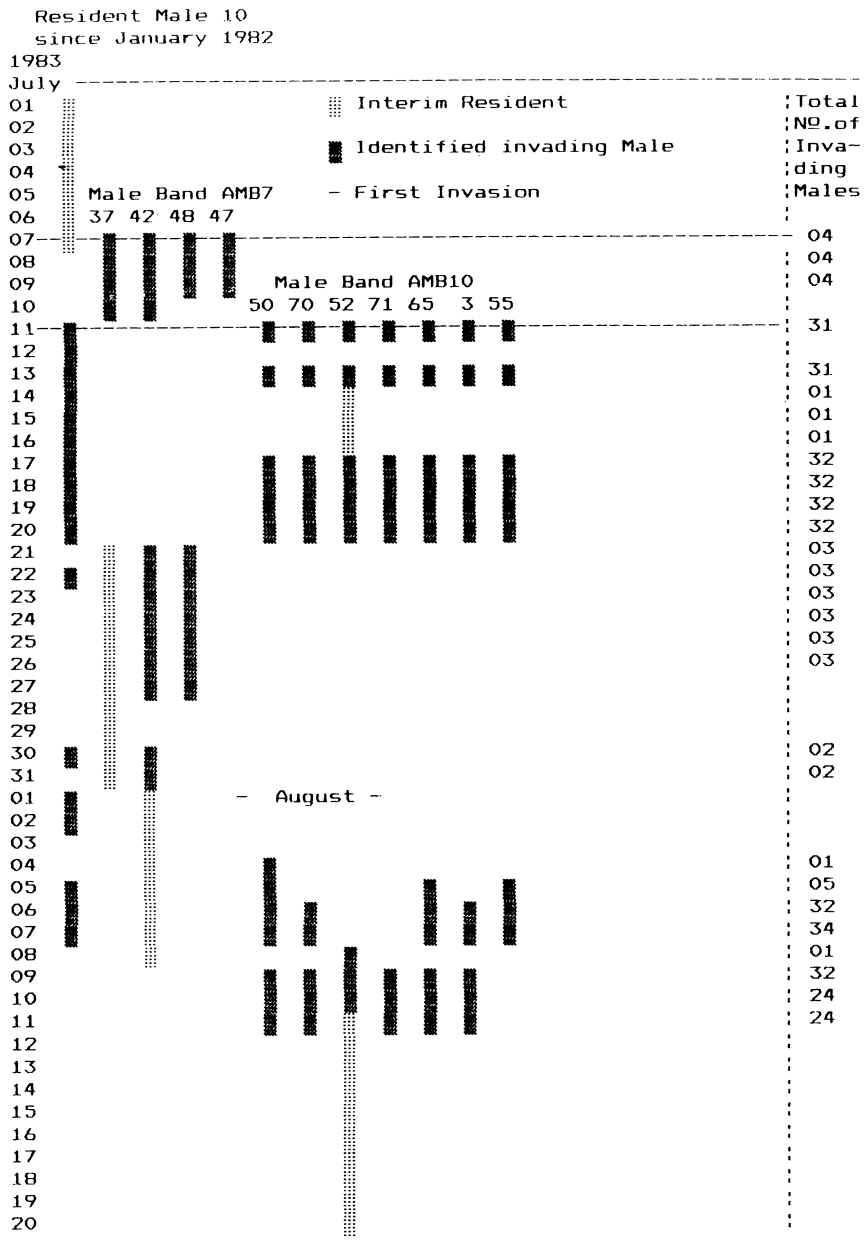
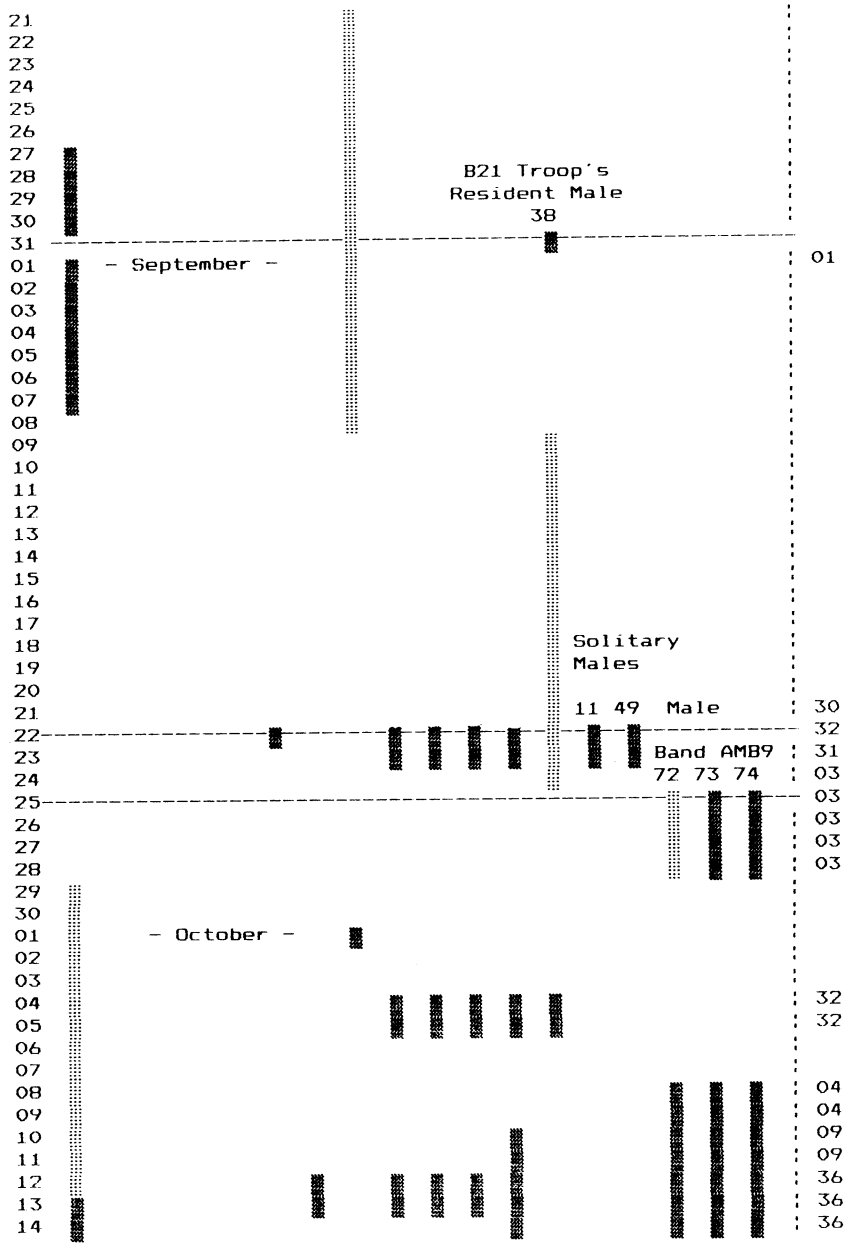



**Fig. 1.** Succession of resident male tenures, extratroop male invasion, and the presence of individually identified extratroop males in the home range of troop B20 from 1 July 1983 to 1 February 1984.

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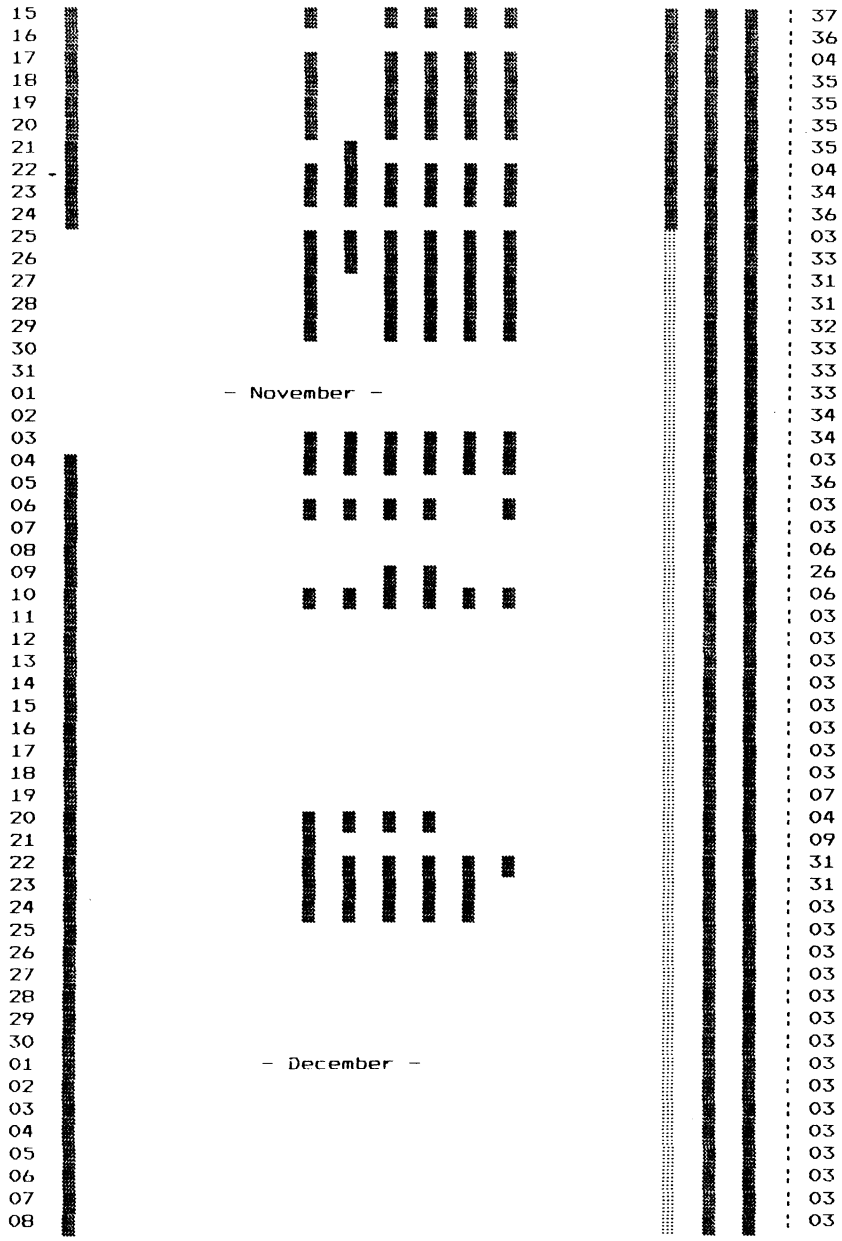


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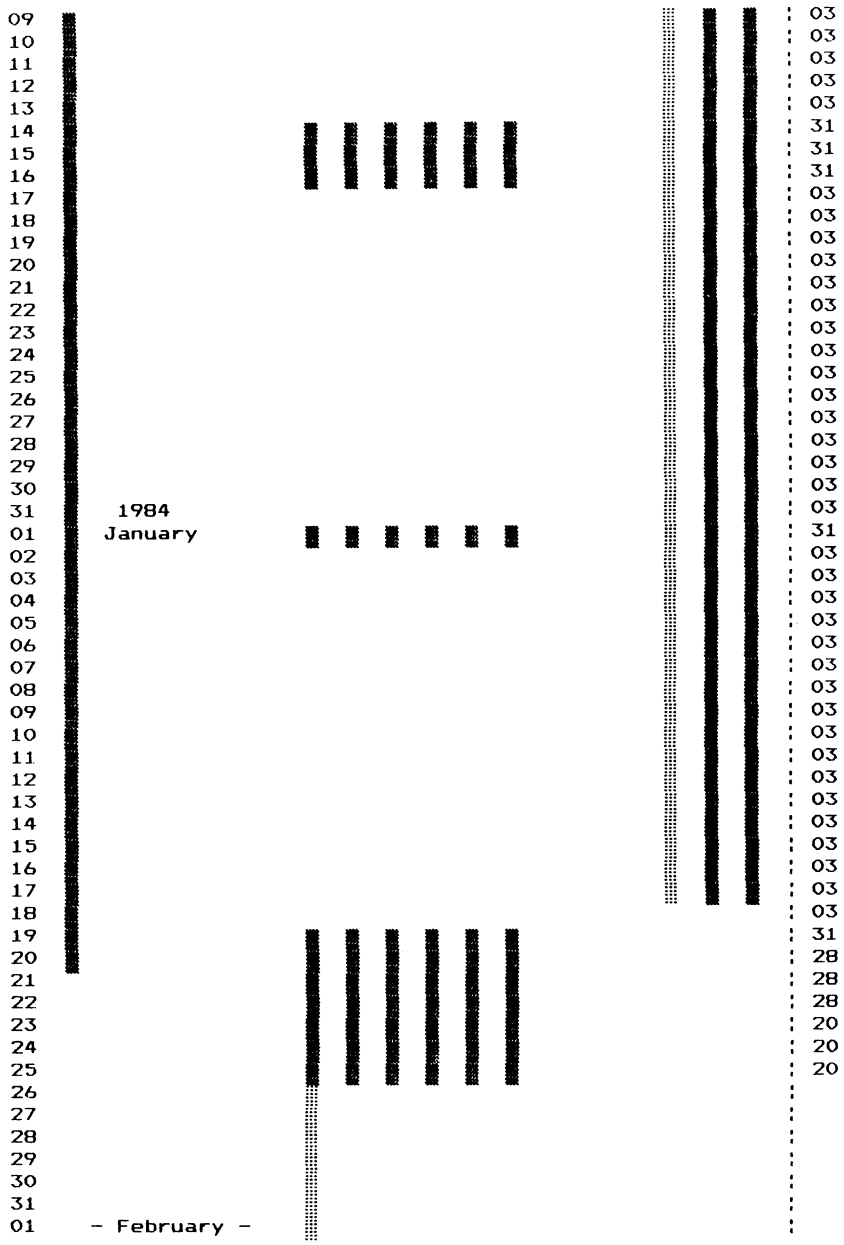


Fig. 1. Continued.

The following day, no males of AMB10 or AMB7 visited the troop. The former resident male was seen with females of the troop. On 13 July, the males of AMB10 were within the home range of B20. A low-ranking adult male (No. 52) was seen with the females of B20, and the former resident male was out of sight. Male No. 52 was with the troop only for the next 3 days. However, AMB10 did not visit the troop between 21 July and 3 August, but three males of AMB7 (Nos. 37, 42, and 48) were with the troop. On 31 July at 1515, a fight occurred between the male No. 37 and male No. 42 of AMB7; male No. 37 was wounded, which probably forced him to leave the troop.

Following the reinvasion of male No. 52 (AMB10) on 8 August, a fight occurred between male No. 42 and male No. 52. The next day, male No. 42 disappeared. From 11 August to 7 September, male No. 52 was in the troop. On 31 August at 1650, troops B20 and B21 were separated by 100 m. An adult female from B20 approached the resident male (No. 38) of B21 and performed head-shaking—sexual presentation—toward him, but sexual interaction did not occur. A few minutes later, an exchange of aggressive convulsive threats and teeth-grinding between male No. 38 and male No. 52 occurred for 25 min, without any physical contact. Then, male No. 38 and his troop returned to their sleeping site.

On 8 September at 0820, B21 was 15 m from B20. The resident male (No. 38) of troop B21 chased the interim resident male (No. 52) of the other troop and they fought for about 13 min. Male No. 52 received a bite wound near his tail base. Forty minutes later, he was 400 m away from B20, and he later disappeared. Then male No. 38 stayed with B20. However, B21 returned to their roosting site at dusk, without their resident male. The neighboring band males did not visit the home ranges of B20 and B21 for the next 12 days, during which male No. 38 was the only adult male with troop B20. He copulated with 6 of the 12 adult females. At that time, B21 had only four adult females. Although he stayed with B20, he kept visual contact with B21. On the evening of 21 September, AMB10 and two solitary males (Nos. 11 and 49) invaded B20. On 23 September, male No. 38 had wounds on his left thigh. He was probably attacked by the invading males. On the same evening, he returned to B21. Also, the males of AMB10 and the two solitary males left B20 by that evening. Two days later, two adults and a subadult male of AMB9 invaded B20 for the first time. Despite the presence of the band males, the former resident (No. 10) stayed as an interim resident of B20 from 29 September until 12 October. After the band males forced him out of his troop on 7 July 1983, he stayed within their home range and maintained intermittent visual contact with individuals of B20 and invading band males, from distances of 20 to 400 m. He was within their range for 133 days of the total period of 202 days

of male invasion. I saw him last on 20 January 1984. Seven months later, he was about 3 km away with a new male band, AMB11 (Rajpurohit and Mohnot, 1988).

The males of AMB9 were with B20 between 8 October 1983 and 18 January 1984. Despite the irregular presence of AMB10 males, the dominant male (No. 72) of AMB9 acted as an interim resident from 24 October through 18 January 1984. On the evening of 18 January, the males of AMB10 chased No. 72 and his allies. Starting 26 January, the dominant male (No. 70) of AMB10 stayed with B20. Following his establishment there, four infants were killed and one female aborted a fetus (Agoramoorthy and Mohnot, 1988; Agoramoorthy *et al.,* 1988).

## Social Change After Adult Male Replacement in B21

I found the resident male (No. 22) of B21 dead on 17 January 1983 at 1700. He had a deep bite wound and his third and fourth ribs were exposed (Agoramoorthy and Mohnot, 1988). The neighboring all-male band (AMB10), containing 28 individuals, had mixed with B21, which suggests that he had probably been attacked by males of the invading band. After his death, the following changes occurred in B21.

*A Shift in Roosting Site and a Change in Home Range Size.* Before the death of No. 22, B21 used a sleeping site at the southern end of a deserted palace (Bijolai palace), while B20 lodged at the northern end of the same palace, about 60 m away (Fig. 2). On 17 January 1983 at 1730, when 16 members of B21, without their resident male, attempted to approach this lodge site, they were chased by the females of B20. Subsequently, B20 occupied B21's sleeping site, and they were forced to shift to a new sleeping site (a cave hillock) about 600 m away. However, the resident male of B20 neither chased the females of B21 nor in any other way induced them to change their sleeping site. Before the death of male No. 22, B21 had a home range of about 40 ha, while B20 had a range of approximately 30 ha. After the change of mates, B20 acquired about 4 ha of B21's home range, which included B21's roosting site and a water hole. To my knowledge, B21 did not use the waterhole or roosting site again during my study.

*A Female Infant Attacked.* A day after the death of male No. 22, B21 contained 16 individuals without a resident male. On that day at 0730, the members of B21 were only 25 m away from Bijolai palace. Concurrently, B20, which contained 27 individuals, was resting on top of the place. Four adult females of the B20 produced aggressive low-grunts accompanied by teeth-grinding. A minute later, the adult females of B20 chased the members of B21, which retreated and ran for cover. During that time, an adult

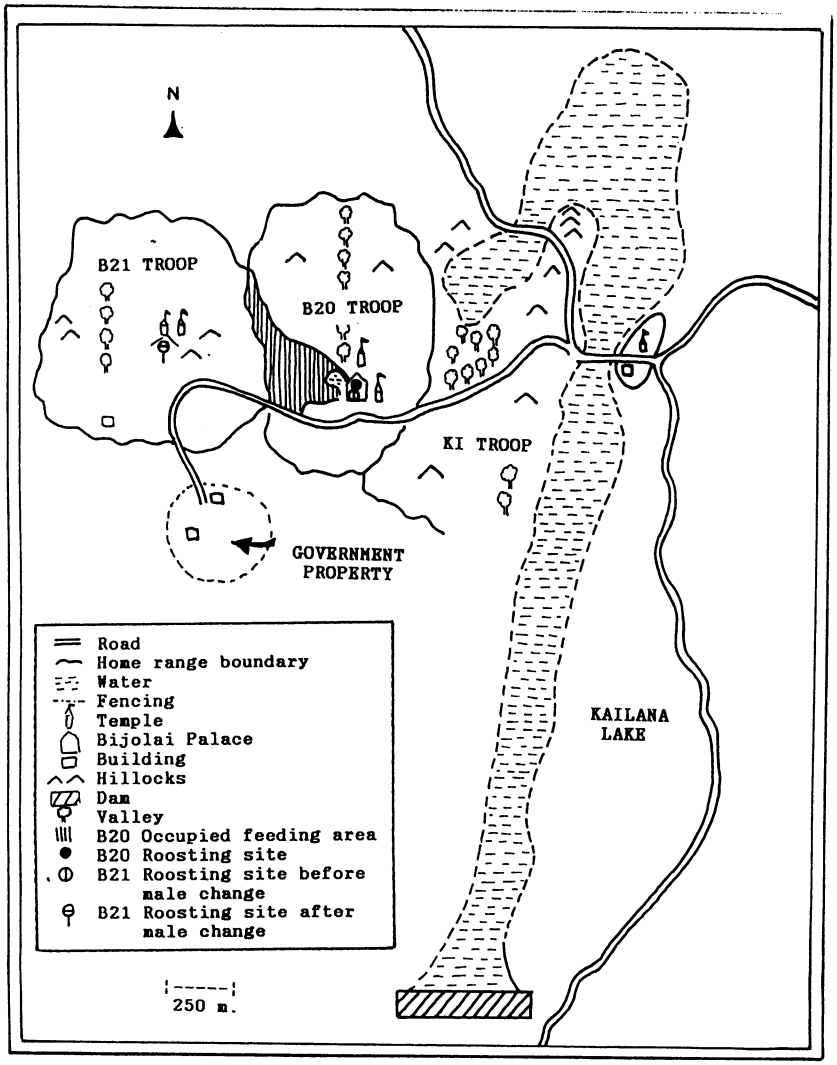


**Fig. 2.** Home ranges of troops B20 and B21 in Jodhpur, India, during January 1983—January 1984.

female (No. 8) of B20 ran behind an independently mobile (14-month-old) female infant of B21. She attempted to hide inside a thick cactus (*Euphorbia caducifolia*). But before she had reached safety, No. 8 jumped on her and bit her near the tail base, thereby inflicting a would about 1 cm long and 1 cm deep, from which blood flowed. The infant screamed and man-

aged to enter the cactus bush. A few minutes later, the attacker attempted to enter the dense, thorny cactus, but her larger body size prevented her from entering. No members of B20 were within a radius of about 25 m. The infant stayed silently inside the cactus bush for about 20 minutes. The attacking female moved about 10 m away from the cactus and sat behind an *Acacia* tree, keeping a watch on the infant's hideout.

At 0813, the infant poked her head out of the cactus bush, looked around (probably unable to see the attacker), and emerged. Suddenly the attacker ran to the infant, jumped on her, and bit her neck, leaving a wound about 1.5 cm long. The infant screamed intermittently for a few minutes and ran toward the new sleeping area of B21. Her wounds bled as she ran slowly toward the sleeping site, where the rest of the troop had moved. About 15 min after the second attack, adult female No. 6.1 of B21 approached the victim and the attacker retreated immediately. The wounded infant and female No. 6.1 later joined their troop.

Thereafter, the wounded infant frequently scratched her wounds and was unable to move with her troop members to feed. She was alone, close to the sleeping site, from 18 until 29 January 1983. The following day at 0700, she was dead under a roosting tree. On 23 January 1983, male No. 38 of AMB10 succeeded in taking over B21. Following his establishment in the troop, three infants were killed and an adult female aborted her fetus (Agoramoorthy and Mohnot, 1988; Agoramoorthy *et al.,* 1988).

## DISCUSSION

In hanuman langurs at Dharwar and Jodhpur, temporary multimale stages occur during male invasions (Sugiyama, 1964; Mohnot, 1984; Vogel and Loch, 1984). At Dharwar, Mount Abu, and Jodhpur, the resident males of one-male troops left their troops after they were defeated by band males (Sugiyama, 1965; Hrdy, 1977; Sommer, 1987). My study confirms that residents and interim residents leave their troops because of aggressive encounters with invading band males, which result in physical injury.

Interestingly, an established resident male (No. 38) of B21 invaded a neighboring troop (B20) and temporarily stayed there. During his stay in B20, he copulated with six adult females. At that time, B21 had only four adult females. In addition, the interim resident male, No. 52 of troop B20, appeared to be smaller than No. 38. It was obvious that No. 38 risked losing his resident status in B21 by temporarily taking over a neighboring troop. However, factors such as the availability of a higher number of mature females, the larger troop size, and the presence of a weaker interim resident male may have influenced him to invade troop B20. This suggests

that he may have opportunistically maximized his mating chances with females of a neighboring group (Hrdy, 1977).

Territorial fights among monkeys sometimes lead to the expansion of the winner's resource area. In green monkeys (*Cercopithecus sabaeus*) intense and mutually aggressive encounters occur among neighboring troops over important resources (Harrison, 1983). At Amboseli, Kenya, resident vervet monkeys (*Cercopithecus aethiops*) prevented neighboring female conspecifics from gaining access to a waterhole in their range via a typical pattern of range defense (Wrangham, 1981). In my present study, after the death of the B21's resident male, B20 expanded their range about 4 ha and obtained a new sleeping site and a waterhole. This suggests that B20 may have overpowered the weaker troop (B21) during their social instability.

Infanticide following male invasion occurs in several species of nonhuman primates (Hrdy, 1979; Struhsaker and Leyland, 1987). Nevertheless, serious wounding of individuals, leading to death, during intertroop encounters is uncommon among female primates. Although female participation in aggressive encounters with other troops of hanuman langurs has been witnessed (Sugiyama *et al.*, 1965; Mohnot, 1971; Hrdy, 1977), no fatal attacks had been observed before my observation. Intragroup female infanticide occurs also in chimpanzees and gorillas (Goodall, 1977; Fossey, 1984).

When B21 underwent social change, an older infant was attacked by a neighboring troop's adult female. Although she died 11 days after the attack, death was probably caused by a combination of infection of her wounds, physical stress, and starvation. It appears that the female attacker may have opportunistically used the disorganization created by male–male competition to eliminate a future food competitor. The food competition hypothesis predicts that victims can be infants, juveniles, and even adults; and the attackers can be of both sexes (Rudran, 1979a, b, 1993). Moreover, in the hanuman langurs, killing older infants and juveniles by adult males has been reported previously (Sugiyama, 1967; Agoramoorthy and Mohnot, 1988).

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