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Strategies Used by Bonnet Macaques (*Macaca radiata*) to Reduce Predation Risk While Sleeping

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ABSTRACT. Sleep results in a decrease in alertness, which increases an animal's vulnerability to predation. Therefore, choice of sleeping sites would be predicted to incorporate predator-avoidance strategies. The current study, conducted in two national parks in southern India, examined the behaviors adopted by bonnet macaques (*Macaca radiata*) to reduce the risk of being preyed upon while sleeping. Bonnet macaques from an urban setting with a low predatory risk were included for comparison. The physical characteristics of the sleeping sites in the forest corresponded with features that were most difficult for predators to access; bonnet macaques selected emergent trees with high boles near human settlements. These trees typically overhung water. Within the canopy, individuals slept in huddled subgroups near the terminal ends of branches, preferentially selecting branches over water. Subgroups were generally composed of members of the same age and sex, which likely promoted social bonding. Adult males and females with infants selected branches higher than members of other age and sex categories. The lateral distances of individuals along branches from the main trunk were similar across demographic categories. The size of a subgroup appeared to be limited by the weight a branch could support; lateral distances were maintained by regulation of mean subgroup weight, with heavier individuals forming smaller subgroups. The urban troop slept on the top of a building. Subgroup compositions at the urban site were similar to those at the forest sites. However, subgroup size, not restricted by branch fragility, resulted in larger subgroups than those found in the forest. Our results indicate that bonnet macaques adopted a suite of behaviors that reduced their risk of being preyed upon at night by selecting sleeping sites that minimized predator encounters and by selecting the safest locations within the canopy.

Key Words: Bonnet macaque; *Macaca radiata*; Sleeping trees; Predator-avoidance.

INTRODUCTION

In regions of moderate to high predation, the choice of sleeping sites selected by prey would, in part, be influenced by the security it affords from predators. Although a number of studies have reported predatory attacks on primates at sleeping sites (see ANDERSON, 1984 for review), few studies have examined the adaptive aspects of the sleeping habits of wild primates that might mitigate predation. We thus focus on recording the sleeping site choices of a diurnal primate species (*Macaca radiata*), and its potential correlation to predator-avoidance. These strategies include the location and morphological characteristics of sleeping sites as well as individual preferences within a sleeping site, all of which could be manipulated to minimize predation risks.

Choice of sleeping sites has been related to environmental influences, such as the possibility of parasitic infection (HAUSFATER & MEADE, 1982) and the activity of predators (ALTMANN & ALTMANN, 1970; HAMILTON, 1982). Many primates sleep in relatively tall trees, often at a higher level in the canopy than they are found during the day. This behavior has been interpreted as reducing risk from terrestrial predators (ANDERSON, 1984). Similarly, some species have been recorded choosing sleeping trees with few or no low branches, a strategy that restricts predator access (ANDERSON & MCGREW, 1983).

Food availability and distribution may also play a role in the selection of sleeping sites. The location of sleeping sites is dependent on the location of food sources for howler monkeys (*Alouatta palliata*) (MILTON, 1980). Chacma baboons (*Papio ursinus*) (HAMILTON, 1982) and bonnet macaques (RAHAMAN & PARTHASARATHY, 1969) have been observed shifting their sleeping sites in order to remain near food sources in times of food scarcity. Rhesus macaques (*Macaca mulatta*) choose sleeping sites near water during the dry season, probably to gain easy access to drinking water in periods of drought (LINDBURG, 1971). The selection of sleeping sites near water by Talapoin monkeys (*Miopithecus talapoin*) has been attributed to predator-avoidance (GAUTIER-HION, 1973). Stump-tailed macaques (*Macaca arctoides*) also sleep preferentially on branches that overhang water (ESTRADA & ESTRADA, 1976), and ANDERSON (1984) has argued that this sleeping site preference serves a sanitary function via the washing away of excreta.

Strategies for predator-avoidance include manipulation of group size and group composition, interspecific and intraspecific associations, and the selective use of habitat (TERBORGH & JANSON, 1986). Group-living species tend to sleep in close proximity, usually in the same sleeping tree. Some species have been observed breaking up into sleeping clusters (howler monkeys: GAULIN & GAULIN, 1982; bonnet macaques: KOYAMA, 1973; toque macaques, *Macaca sinica*: DITTUS, 1977a, b; vervet monkeys, *Cercopithecus aethiops*: BRAIN, 1965). Competition and conflict for positions at sleeping sites have been recorded in howler monkeys (GAULIN & GAULIN, 1982) and toque monkeys (DITTUS, 1977a). KOYAMA (1973) found that bonnet macaques tended to form sleeping subgroups with members of the troop that they interacted with the most, probably kin or alliance partners. BRAIN (1965) reported that three dominant vervet monkeys in a troop of seven regularly formed a single huddling subgroup at night while the four subordinate members formed another subgroup, suggesting that sleeping subgroups might be based partly on rank.

STUDY RATIONALE AND OBJECTIVES

This study on bonnet macaques in southern India was prompted by experimental evidence that bonnet macaques face threats from terrestrial predators, as revealed by their alarm vocalizations and flight behavior in response to leopards (RAMAKRISHNAN & COSS, 2000a; COSS & RAMAKRISHNAN, 2000) and the leopard-evoked alarm vocalizations of heterospecific species (RAMAKRISHNAN & COSS, 2000b). A complementary study of leopard diets at the study sites documented leopard predation on bonnet macaques (RAMAKRISHNAN et al., 1999). Our preliminary research on leopard recognition also showed that the presence of a realistic model leopard positioned at the base of a sleeping tree caused bonnet macaques to abandon that tree and select an alternative tree for nighttime refuge. This model and other leopard models occasionally elicited mobbing at our study sites.

Due to logistical constraints of obtaining detailed nighttime observations, little systematic research has been conducted on the sleeping site choice of individuals within a sleeping tree. We considered that sleeping site choice in regions with nocturnal predators could be regulated by the safety it afforded from those predators. If this assumption were true, we predicted that the locations of sleeping sites would reflect the protection they afforded from nocturnal predators, and sleeping site configuration should restrict predator accessibility and provide opportunities to escape. A second facet of this study examined if the behavior of individual bonnet macaques at sleeping sites reflected enhanced personal security against nocturnal predators.

STUDY SITE AND METHODS

The data collection was carried out between June and September 1996, and April and October 1997, at three study sites.

FOREST SITES

The Mudumalai Wildlife Sanctuary is located between 11° 32' to 11° 43' N latitude and 76° 22' to 76° 45' E longitude and covers an area of 321 km^2. The park has a variety of vegetation types, ranging from tropical semi-evergreen forests and moist deciduous forests to dry deciduous forests and dry thorn forests (SUKUMAR et al., 1992). Two troops were selected for observation at this site, the Theppakadu troop and the Kargudi troop. The Kalakad-Mundanthurai Tiger Reserve is located between 8° 25' to 8° 53' N latitude and 77° 10' to 77° 35' E longitude, and covers an area of 817 km^2. The habitat type ranges from moist evergreen rain forest to dry deciduous forests to scrub forests. Two troops were selected for observation at this site, the Mundanthurai troop and the Kariyar troop. The habitat type of the plateau where the two study troops were found was classified as mixed deciduous (ALI, 1981). The major predators at these two study sites were leopards (*Panthera pardus*), tigers (*Panthera tigris*), wild dogs (*Cuon alpinus*), domestic dogs (*Canis familiaris*), hyenas (*Hyaena hyaena*), and python (*Python molurus*).

Individuals of a troop were identified based on facial features, hair and body markings. Setting up feeding stations and recording dyadic interactions in which the more dominant individuals displaced subordinates established the dominance hierarchy of adults of each troop. All individuals were classified into one of six age and sex (demographic) categories (ALI, 1981): *infants* (unweaned animals that were less than 1 yr of age and weighing on average 0.7 kg); *juveniles* (weaned animals 1 – 2 yr of age and weighing on average 1.7 kg); *subadult females* (2 – 4 yr of age, smaller than adult females and larger than juveniles, and weighing on average 3.2 kg); *subadult males* (same size as adult females, smaller than adult males, and weighing on average 4.2 kg); *adult females* (females older than 4 yr of age with at least one offspring, and weighing on average 4.2 kg); and *adult males* (older than 5 yr of age, larger than adult females, and weighing on average 7.1 kg). These weight estimates are derived from FA (1989), ROSENBLUM and SMILEY (1980), and ROWE (1996). The group sizes and demographic classifications of the five study troops are listed in Table 1.

At each site, one field assistant recorded the location and physical characteristics of the sleeping site selected by the same troop every night (Kariyar and Kargudi troops). Measurements of overall tree height and the bole height of sleeping trees were made using a clinometer. Other information recorded was proximity of the sleeping site to a stream or river as well as its distance to the nearest human settlement. In addition to the physical characteristics of the sleeping sites, the researchers recorded the locations of individual troop members within the sleeping sites (Mundanthurai and Theppakadu troops). The Theppakadu troop was observed for 42 nights; the Mundanthurai troop was observed for 58 nights; and the Bangalore troop was observed for 54 nights. A schematic diagram of each sleeping tree was labeled with overall

Table 1. Number of individuals in each troop and demographic category.

	Adult male	Adult female	Subadult male	Subadult female	Juvenile	Infant	Total
Mundanthurai	8	8	5	3	7	3	34
Theppakadu	6	10	4	5	3	7	35
Kariyar	7	9	3	5	3	4	31
Kargudi	5	9	2	4	6	2	28
Bangalore	9	12	6	8	9	10	54

height, bole height, and height of branches using the clinometer. The location of branches overhanging water was also indicated. Branches were numbered for recording sleeping site choice selected by individual monkeys. The identity of the first animal to climb the sleeping tree was recorded.

Animals slept alone or in small subgroups, with the subgroup sizes ranging from 2 to 11 individuals. The age and sex of individuals in a sleeping tree were determined using binoculars (7X magnification) equipped with a narrow-beamed flashlight. Only one subgroup was observed during any night, permitting age and sex categorization of a large subgroup in less than 2 min. Longer illumination caused animals to wake up and change their location, precluding the sampling of more than one subgroup per night. To randomize subgroup sampling, branches were preselected on the tree diagram prior to the animals settling on the tree. We recorded the height of the branch selected by the subgroup, the horizontal distance of the subgroup from the main trunk, and the age and sex of each individual in the subgroup, starting from the member closest to the trunk and moving laterally from the trunk. The subgroup selected for observation was surveyed again after two hours to see if animals had changed positions from where they were previously recorded.

A second sampling procedure focused on determining the branch-site fidelity of individuals within the sleeping tree as a function of social dominance. This procedure, which determined

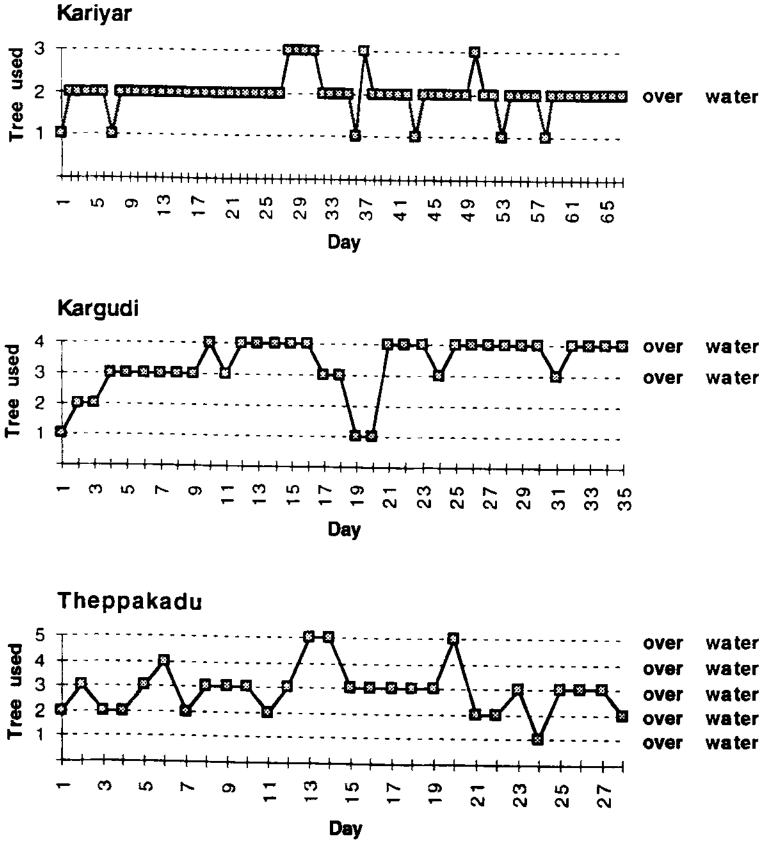


Fig. 1. Use of multiple sleeping trees by three forest troops on consecutive nights of observation. Trees overhanging water are labeled.

the frequency of specific branch choice within the same sleeping tree, was limited to observations on the Mundanthurai troop. Thirteen of a total of 16 adults were observed for 15 consecutive nights. The 13 focal animals included all adult males of the troop (intrasex dominance rank of 1 to 8) and 5 adult females (intrasex dominance rank of 1 to 5). Three low-ranked adult females were excluded from this survey because their rank order was ambiguous. As in the procedure used for determining subgroup composition, the locations selected by individuals within a sleeping tree were marked on the tree diagram every night.

URBAN SITE

Bangalore city was selected as a low-risk predator-rare setting where the only threat to bonnet macaques came from domestic dogs. The urban troop selected for study was free ranging and was located at a University campus on the periphery of the city. Habitat consisted of forest plantations interspersed with agricultural fields and buildings. The troop repeatedly selected to sleep on the roof of a 5-story building. Individuals slept exclusively on the parapet walls of the roof, forming huddled subgroups as they did on branches. A diagram of the roof floor plan was made to mark subgroup locations. One subgroup was randomly selected for observation each night by preselecting a parapet wall segment. The location of the selected roof segment was marked on the roof floor plan and the age and sex of the individuals of the subgroup that chose to sleep there were recorded sequentially from left to right. The identity of the first animal to climb to the roof of the building was also recorded. Since the researchers had access to the roof, individual monkeys could be observed at a much closer distance using a Hitek International night vision scope equipped with a Global Supply 100 infrared illuminator and Pentax 135 mm lens, making it possible to identify individuals from 3 – 5 m distance. This close proximity did not cause the animals to move from their sleeping locations. This night-vision setup was not used in the forest because of insufficient magnification.

RESULTS

SLEEPING SITE CHARACTERISTICS

At the two wildlife parks, bonnet macaques selected tall, emergent trees (mean sleeping tree height = 23.75 m, SD = 4.89, n = 13). These trees had a relatively high crown (mean bole height = 8.8 m, SD = 2.31, n = 13) with few or no low branches. Trees typically selected as sleeping sites included species of *Ficus, Mangifera, Sizizium, Dalbergia,* and occasionally *Bambusa.* Most of the trees selected were along the edge of a body of water (Fig. 1). The mean distance of sleeping trees to the edge (cleared area or fence) of a human settlement was 126.9 m (SD = 91.9, n = 13).

Analysis of the choice of sleeping over water was restricted to individuals that selected trees on the edges of streams and rivers. Such trees had some branches overhanging the ground and some overhanging water. Assuming that branches that overhung the ground and water were equally accessible, we employed a two-factor (sex and age) log-linear model with Pearson χ^2 tests, comparing the frequency of individuals (as a function of age and sex pooled from all troops) sleeping over ground with the frequency of those sleeping over water. Individuals were significantly more likely to select positions on the sleeping tree that were over water than over the ground (Table 2). This observation did not differ by the age or sex of the individual (interaction major effect; Pearson χ^2 =7.22, df=4, p =0.12).

Table 2. Comparison of age and sex categories sleeping over land and water.

Category	No. of over land	No. of over water	Pearson χ^2	p-value
Adult male	2	40	34.381	<0.001
Adult female	9	42	21.353	<0.001
Subadult male	3	28	20.161	<0.001
Subadult female	4	10	2.571	0.109
Juvenile	5	19	8.167	0.004
Infant	0	12	11.308	<0.001

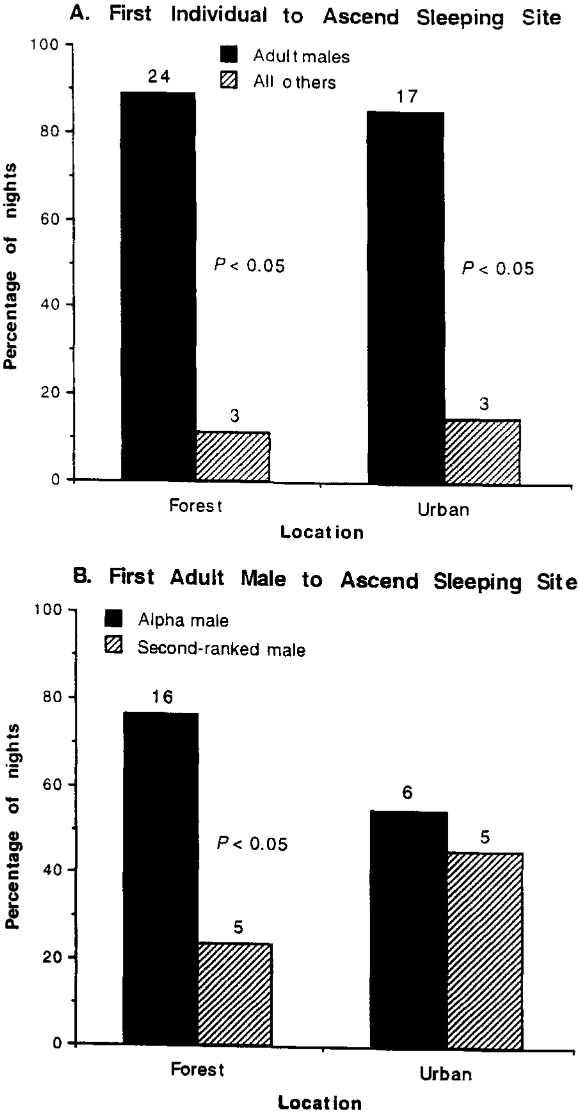
FIRST ANIMAL TO ASCEND SLEEPING SITE

We identified the first individual to ascend the sleeping site each night. This yielded frequency distributions that were examined separately for the forest sites (pooled across sites) and for the urban site using two-tailed binomial tests. At the forest sites, the first animal climbing the sleeping tree (Fig. 2A) was usually an adult male (adult males = 24 nights vs all other individuals = 3 nights; $p < 0.05$). Among adult males, the alpha male was significantly more likely to be first to climb the sleeping tree (alpha male = 16 nights vs second-ranked male = 5 nights; $p < 0.05$, Fig. 2B). This preeminent behavior was maintained even when a new alpha male replaced the previous alpha male (new alpha male = 12 nights vs replaced alpha male = 2 nights; $p < 0.025$). Although at the urban site, adult males were significantly more likely to ascend the building first (adult males = 17 nights vs all other individuals = 3 nights; $p < 0.05$), there were no appreciable differences between the number of times the alpha male and the next highest-ranking male climbed the building first ($p > 0.5$).

INDIVIDUAL BEHAVIOR WITHIN SUBGROUPS

Analyses of site fidelity for the 15-night sampling period employed a log-linear model with a Pearson χ^2 test of the frequency that each of the 13 focal animals selected its most preferred branch compared with the frequency it selected any other branch in the same tree. This procedure was complemented by regression analyses of each individual's rank as the predictor variable and the percentage of nights this individual selected its preferred branch as the response variable using Permute! version 3.4 (see LEGENDRE et al., 1994), a program which computes regression coefficients using a distribution-free, permutational approach. The proportion of times an individual used the same branch was significantly higher in six of eight males and in all five females (Pearson χ^2 range: 4.08 – 13.66, $df = 1$, $p < 0.05$). These proportions were associated significantly with intrasex rank for males and for the intrasex ranks of males and females combined (Fig. 3), with higher-ranked individuals showing greater site fidelity (males:β coefficient = −0.879, $R^2 = 0.772$, $p < 0.025$; females: β coefficient = −0.698, $R^2 = 0.487$, $p < 0.02$; males and females combined: β coefficient = −0.828, $R^2 = 0.687$, $p < 0.005$).

To compare the differences between the demographic categories in height of selected sleeping branches, we used a Kruskal-Wallis one-way analysis of variance (ANOVA) on ranks followed by pairwise comparisons between these categories. These tests thus compared the median height of branches selected by adult males ($n = 14$) with the median height of branches selected by each of the other demographic categories (adult females without infants: $n = 8$; adult females with infants: $n = 10$; subadult males: $n = 9$; subadult females: $n = 8$; juveniles: $n = 10$). These latter categories were similarly compared using pairwise tests. The same type of analysis on the same individuals was used to compare differences among demographic categories in median lateral distances along branches from the main trunks.


A. First Individual to Ascend Sleeping Site

B. First Adult Male to Ascend Sleeping Site

Fig. 2. The first animal to ascend sleeping sites in the forest and urban settings. Numbers over bars indicate the frequency of nights. **A.** Adult males compared with members of all other demographic categories. **B.** Alpha males compared with second-ranked males.

Adult males selected branches significantly higher ($\alpha = 0.05$) than those selected by adult females without infants ($Z = 2.004$), subadult females ($Z = 2.162$), and juveniles ($Z = 2.297$). However, there was no significant difference between the median height of branches selected by adult males and adult females with infants ($Z = 0.086$). The median lateral distance of individuals from the main trunk did not differ appreciably for the different demographic categories (Kruskal-Wallis one-way ANOVA on ranks: $H = 4.433$, $p = 0.3$). These results could not be compared with observations from the urban site, since the sleeping site of the urban troop was the roof of a building.

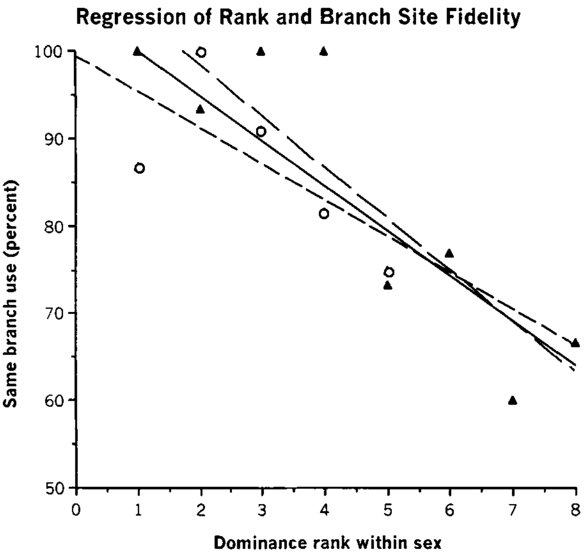


Fig. 3. Bivariate plot of intrasex dominance rank and percentage of same branch use for sleeping, with the solid line characterizing the slope for both sexes combined. Solid triangles and long-dashed slope represent males. Open circles and short-dashed slope represent females.

SUBGROUP SIZE

To compare subgroup size, as a function of sex and age, we counted the number of individuals in each subgroup and used a Kruskal-Wallis one-way ANOVA on ranks with pairwise comparisons. These tests compared the median subgroup sizes of each of the six demographic categories, yielding a total of 15 pairwise comparisons each within the forest and urban sites.

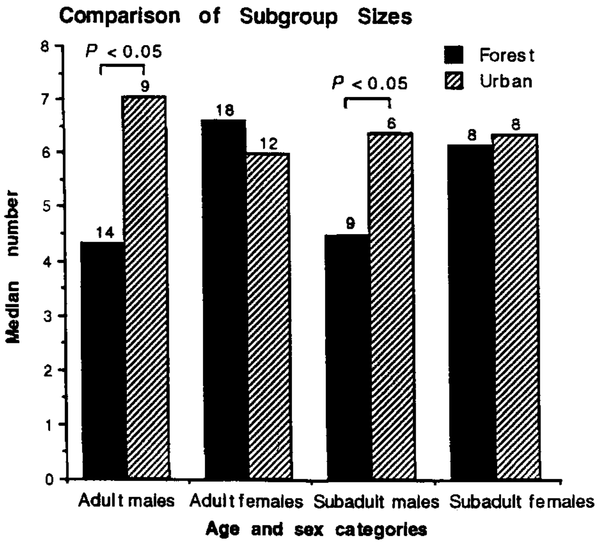


Fig. 4. A comparison of subgroup sizes between the forest and urban sites as a function of age and sex of individuals. Numbers over bars indicate sample sizes in each age class, listed separately for the urban and forest sites.

Four additional pairwise comparisons examined differences in subgroup sizes between forest and urban sites. For the forest site, the total sample sizes include all individuals in the Mundanthurai and Theppakadu troops combined. The total sample size for the urban site included all individuals in the Bangalore troop.

At the forest sites, these analyses revealed that adult males were found in subgroups with significantly smaller median sizes than those of adult females ($Z = 4.2306$), subadult females ($Z = 2.28$), juveniles ($Z = 3.016$), and infants ($Z = 3.138$). At the urban site, the median subgroup size did not differ markedly for the different demographic categories ($H = 6.164$, $df = 5$, $p = 0.29$). Comparisons of the forest and urban sites showed that adult males and subadult males formed significantly larger subgroups at the urban site (Fig. 4).

To identify a causal association between body weight and subgroup size, we conducted a regression analysis, examining individual body weight as the predictor variable and subgroup size as the response variable. At the forest site, there was a negative association between subgroup size and individual weights ($r^2 = 0.106$, $F = 20.479$, $df = 1$, $p < 0.001$), indicating that lighter individuals formed larger subgroups. These results differed from those obtained from the urban troop where there was no significant association between individual weight and subgroup size ($r^2 = 0.018$, $p = 0.11$).

DISCUSSION

The aim of this comparative study of forest and urban bonnet macaques was to examine sleeping site choice and concomitant social interactions in relation to predatory risks. In the forest, bonnet macaques appeared to be relatively successful in evading a major predator, the leopard. Analyses of leopard scat revealed that, of a total of 296 leopard scat samples collected, evidence of bonnet macaques was found only in one sample (Ramakrishnan et al., 1999). This is in contrast with Nilgiri langurs (*Trachypithecus johnii*) that appeared in eight samples and Hanuman langurs (*Semnopithecus entellus*) that appeared in six samples. Since leopards are predominantly nocturnal predators, such success might be explained by how bonnet macaques organized their behavior at night.

SLEEPING SITE CHARACTERISTICS

Bonnet macaques appeared to select sleeping sites that were difficult for predators to access. By selecting tall trees as sleeping sites, nonclimbing predators, such as tigers, dogs, and hyena are less of a threat. Emergent trees also reduce the number of access routs to the tree from surrounding vegetation. A high bole with few or no low branches could serve the same purpose, making it difficult for terrestrial predators to reach them. All sleeping trees were close to human settlements, areas that are generally avoided by all predators (with the exception of domestic dogs). Isbell and Young (1993) found a correlation between distance from human settlements and leopard predation on vervet monkeys, with predation increasing with greater distances from settlements. Hanuman langurs appear to follow a similar strategy (Hrdy, 1977). While sleeping near human settlements might serve the function of access to human food, we frequently observed bonnet macaques returning to sleeping trees near settlements after completing foraging for the day away from these settlements.

At the urban site, animals had access to tall trees as sleeping sites, but instead, they chose to sleep on the roof of a 5-story building. Other buildings of similar height were also available in the vicinity, thus the choice of using the same building every night was not because of a scarcity of available undisturbed sleeping sites. The use of rooftops as sleeping sites has been reported previously for urban bonnet and rhesus macaques (RAHAMAN & PARTHASARATHY, 1969; SINGH, 1969). However, SINGH (1969) noted that the repeated use of the same buildings by rhesus macaques was due to a scarcity of sleeping sites in the city. Bonnet macaques at the urban site never slept on the floor of the roof, but slept at the edge of the roof on the 1-m high parapet walls. This tendency to sleep off the ground continues in captivity in species that experience predation in nature, such as rhesus macaques (VESSEY, 1973), chimpanzees (RISS & GOODALL, 1976), and tamarins (CAINE et al., 1992). However, a study on wild Japanese macaques (*M. fuscata*) in a predator-free region reported that these macaques slept predominantly on the ground (TAKAHASHI, 1997).

The function of sleeping over water could be: (1) to protect individuals from injury if they fell while sleeping; (2) to gain easy access to water in times of scarcity (LINDBURG, 1971); (3) to avoid predators (GAUTIER-HION, 1973); and (4) to maintain hygiene (ANDERSON, 1984). Reports of serious injury from falling from sleeping trees have been recorded in a number of primates (ALTMANN, 1980; BUSSE, 1980; SHARMAN, 1981). Our results on sleeping site selection based on tree height showed that bonnet macaques chose trees that were over 20-m high, and slept at a minimum of 10 m from the ground. While sleeping at this height makes it difficult for predators to gain access to them, falling from this height, especially when startled by a loud noise, could cause serious injury if not death.

While sleeping near water may be important during drought, it cannot be used to explain their choice of sleeping over water. Furthermore, our observations indicated that bonnet macaques slept over water irrespective of the seasonal changes of monsoon and drought. Sleeping over water precludes adjacent trees from that side of the sleeping tree, reducing predator access. However, water cannot be used as an effective escape route from predators because most predators are excellent swimmers. Since we did not note the accumulation of excess fecal matter under sleeping trees, sleeping over water might serve the function of maintaining hygiene. Thus, it is reasonable to propose that one function of sleeping over water could be to avoid injury from falls.

FIRST ANIMALS TO ASCEND SLEEPING SITES

A dominant adult male, usually the alpha male, was the first to ascend the sleeping tree. One possible reason for this could be to survey the tree for predators before the other animals climb up. Adult male baboons have been reported as the first to leave the sleeping tree, and ANDERSON and MCGREW (1983) equate this behavior to protection of the troop in a potentially dangerous situation. Similarly, adult male patas monkeys usually survey the area before group members settle there for the night (HALL, 1967). However during our study on the effects of predator presentations (unpubl. data), bonnet macaque alpha males usually stayed in the center of the troop and did not exhibit active troop defense. A more plausible explanation is that the alpha male is exerting his choice of which tree to sleep in. In troops that use multiple sleeping sites, the selection of sleeping trees by alpha males might attract the rest of the troop. Alpha males of other species have been recorded leading troops to specific sleeping sites as is the case in which dominant male gorillas decide where the group nests (SCHALLER, 1963), and dominant stump-tailed macaques usually lead the troop to the sleeping tree (ESTRADA & ESTRADA, 1976).

USE OF MULTIPLE SLEEPING SITES

One troop in Mundanthurai selected the same sleeping tree ever night throughout the study period. Based on our survey of potential sleeping sites in the home range of this troop, we concluded that this troop chose the same site every night because there were no other trees that met the preferred height, proximity to water, and proximity to human settlements within the troop's home range. Of the other three troops observed, each troop appeared to have a preferred sleeping tree, typically overhanging water (Fig.1). However, these troops did use between 2 – 4 other sleeping trees.

Some of the functions of using multiple sleeping sites have been attributed to reduction of parasitic infection from feces (HAUSFATER & MEADE, 1982), and confusing predators (ALTMANN & ALTMANN, 1970; HAMILTON, 1982). In the current study, there did not appear to be an accumulation of fecal matter on the tree branches; animals were always observed defecating off the branch onto the water or ground below. The Mundanthurai troop that used the single sleeping tree was never observed using that tree during the day throughout the study period. This active avoidance could be to reduce parasitic infection. The unsystematic rotation of sleeping tree use in troops with multiple sleeping sites might have an antipredator function by reducing site predictability. Conversely, using the same sites might provide the advantage of having known escape routes (STRUHSAKER, 1967). In our study, the sleeping sites selected by troops that used multiple trees were few and closely distributed. Thus, it would not be difficult for predators to find the troop if they were familiar with the general location of where the troop slept.

One possible advantage of having regular sleeping sites may be that individuals that have accidentally been separated from the troop can rejoin the troop in the evening (BERT, 1973). This was observed very frequently during our study at both the forest and urban sites. Troops often split up into subgroups while foraging and returned at different times in the evening to the sleeping site. The fact that there were few regular sleeping sites might have made it easier for the members to reunite before sleeping. By selecting sleeping trees near food sources, yellow baboons, *P. cynocephalus* (RASMUSSEN, 1979) and black and white colobus monkeys, *Colobus guereza* (VON HIPPEL, 1998) reduced the time and energetic costs of travel. This argument of minimizing travel costs was not supported by our data because sleeping trees were clumped in their distribution along rivers and differences in energy expenditure between trees would have been minimal.

SLEEPING IN SUBGROUPS

Members of a troop usually split into small subgroups, with each subgroup occupying different branches of the tree. The formation of sleeping subgroups has been reported in a number of primate species (ANDERSON, 1984). One of the functions attributed to sleeping in huddled subgroups is to maintain warmth (ALTMANN, 1980; GARTLAN & BRAIN, 1968; KUMMER, 1971; TAKAHASHI, 1997). In the current study, huddling was observed even in the peak of summer, and this pattern did not differ when temperatures dropped moderately during the monsoon. Huddling behavior in Guinea baboons (*P. papio*) has been interpreted as providing additional support while sleeping (ANDERSON & MCGREW, 1983). Bonnet macaques sleeping in tall trees risk injury from falling. They did not use their hands to grasp branches, but used them instead to hold other individuals. It is possible that subgroup clinging reduces the likelihood of individuals falling.

Subgroup formation may also serve the function of strengthening social bonds. The choice of an individual as a sleeping partner was not random; individuals preferred to sleep with members of the same age and sex. Another study on bonnet macaques reported that members that formed subgroups during the day also preferred sleeping with members of the same age and sex

(KOYAMA, 1973). Subadult females often continued to sleep with their mothers, but males left their mothers' subgroups to form their own subgroups with other males of the same age. Based on our observations during the day, subadult females usually continued to maintain interactions with their mothers, often providing sibling care. Thus, sleeping with their mothers might be an extension of these supportive interactions. Our observations on adult males immigrating into a group ($n = 2$) indicated that these new males were initially prevented from sleeping with other troop members, thereby forcing them to sleep on adjacent trees. When eventually allowed to sleep with troop members, the new immigrants slept with subadult males rather than with adult males.

All subgroups slept near the terminal ends of branches, a strategy adopted by a number of primates that face predatory threats at night (reviewed by ANDERSON, 1984). Notwithstanding the increased risk of falling, sleeping near the terminal ends of branches can afford several antipredator benefits: (1) as motion detectors of predator climbing activity; (2) as possible escape routes to adjacent trees; and (3) as inaccessible refuges since thin branches cannot support the weight of a heavy arboreal predator.

INDIVIDUAL BEHAVIOR WITHIN THE SLEEPING SITE

Our results suggest that there is some competition for higher branches, with adult males and females with infants obtaining the higher branches. However, there were no significant differences in the mean distances away from the main trunk as a function of age and sex. To reduce the chance of an individual being preyed upon, bonnet macaques appear to adjust their subgroup size, as a compromise between the weight a branch can support and the lateral distance from the main trunk that could preclude predatory attacks. This, in effect, regulates the critical constraint of branch fragility impacted by subgroup weight, resulting in heavier individuals forming smaller subgroups.

Bonnet macaques in the urban setting selected a single, tall building with multiple access routes and slept in linear arrays of subgroups on elevated parapet walls. As in the forest, adult males were the first to ascend the sleeping site, which could reflect some assertion of social dominance. Subgroup compositions were similar to those of forest bonnet macaques. Such similarities in subgroup compositions in both predator-dense and predator-rare environments, suggest that these subgroup compositions serve to reinforce social bonds.

Adult and subadult male subgroup sizes were larger than those of their forest counterparts and there was no statistical association between body weight and subgroup size. Unlike trees that engender subgroup size constraints via branch fragility, the building afforded a stable platform for the formation of larger sleeping subgroups. From a comparative perspective, similarities in forest and urban subgroup compositions suggest a basic pattern of sleeping social organization, which is adjusted according to the degree of predatory risk and the constraints of the sleeping substrate.

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