

Sleeping Sites, Sleeping Places, and Presleep Behavior of Gibbons (*Hylobates lar*)

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The sleeping habits of wild white-handed gibbons (*Hylobates lar*) were investigated to assess the risk of predation and predation-avoidance behavior. Sleeping sites were distributed throughout home ranges, including areas where they overlapped with neighbors, and appeared to be selected independently of habitat characteristics. Individuals did not build night nests or otherwise manipulate the vegetation around the sleeping place but slept on open branches. Group members usually slept in separate trees, and, except for females with infants, they never shared a sleeping place. Sleeping trees were entered several hours before dusk and were used for about 14–17 h. The majority of sleeping trees were used only once, and fewer were selected repeatedly by the same or other group members. Usually females with infants went into a sleeping tree first, then juveniles, and last were mostly subadult and adult males. Intra-group competition over access to a sleeping place was observed once. Average time difference between the first and last group member to enter a sleeping tree was 13 min. The sequence of departure from sleeping trees was more variable. Gibbon sleeping habits seem to primarily reflect adaptations to minimize predation risk. The predation-risk hypothesis was indirectly supported by observations of mobbing pythons, alarm calls given in response to birds of prey flying low over the canopy, and more importantly by 1) the predominant use of large sleeping trees, which were among the tallest trees available, particularly by adult females with small infants and juveniles, 2) an unpredictable long-term pattern of reuse of sleeping places, and 3) inconspicuous presleep behavior. *Am. J. Primatol.* 46:35–62, 1998. © 1998 Wiley-Liss, Inc.

Key words: gibbons; *Hylobates lar*; sleeping sites; sleeping habits; predation risk; predation-avoidance behavior

INTRODUCTION

Avoiding predators and finding food are crucial elements of survival strategies of primates and different adaptive responses to these pressures presumably led to the large array of social grouping arrangements seen in the primate order

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[cf. Smuts et al., 1987; Dunbar, 1988]. Wrangham [1980] stressed the importance of ecological variables for the evolution of primate social systems, whereas others have emphasized the role of predation for the evolution of sociality and group living [Alexander, 1974; van Schaik, 1983]. The relative importance of resource competition and predation risk for the evolution of social groups is still controversial, and both variables are likely to be important [Pulliam & Caraco, 1984; Kummer et al., 1985].

Some studies on wild primate populations have demonstrated a critical role of predation risk for individual survival [Cheney et al., 1988; Boesch, 1991; Cowlshaw, 1997]. Adaptations reflecting predation pressures, such as specific predator alarm calls [e.g., Seyfarth et al., 1980; Zuberbühler et al., 1997], the use of different canopy heights under different levels of predation pressure [van Schaik et al., 1983a; de Ruiter, 1985], rates of vigilance [van Schaik et al., 1983b; Dehn, 1990], polyspecific associations [Gautier-Hion et al., 1983; Terborgh, 1990], and probably the number of adult males in groups [van Schaik & Hörstermann, 1994], further suggest a considerable influence of predation on primate behavior. Nonetheless, data on predation risk are still relatively sparse, and an understanding of predation-avoidance behavior is often poor [cf. Cheney & Wrangham, 1987]. This reflects the difficulties involved in studies of predator-prey interactions. Given the rarity of observed predator attacks [e.g., van Schaik et al., 1983a], the study of predation-avoidance behavior becomes more important and may be used to deduce predation pressure.

Primates are known to spend long hours at sleeping sites, and, for most diurnal species, activity during the night appears to be minimal [Anderson, 1984]. The more time spent near and at sleeping places, the higher the probability of detection by a predator. Therefore, the right choice of a place to sleep may be crucial for individual survival [cf. Cowlshaw, 1994]. Under high predation conditions, presleep behavior is expected to incorporate various efforts to minimize detection. Sleeping habits reflecting antipredator adaptations have been suggested for arboreal New World monkeys [Caine et al., 1992; Heymann, 1995] as well as terrestrial Old World species such as baboons [Byrne, 1981], macaques [Sussman & Tattersall, 1981], and vervets [Cheney et al., 1988]. However, other potential influences on the choice of sleeping places, like proximity to food and/or water resources [Chapman, 1989], ranging patterns and aspects of territoriality [Tilson & Tenaza, 1982], shelter from low temperatures and rain [Aquino & Encarnación, 1986], and comfort [Hausfater & Maede, 1982], have to be considered in the investigation of the evolutionary importance of sleeping habits.

Gibbons (*Hylobatidae*) are arboreal apes confined to the rain forests of Southeast Asia, Northwest India, and Bangladesh [cf. Preuschoft et al., 1984; Leighton, 1987]. They live in small groups of two to six individuals, which usually contain a single adult female, a single adult male, and immatures. Traditionally, gibbons have been thought to form permanent, sociosexually monogamous pairs [Carpenter, 1940; Tilson, 1979; Brockelman & Srikosamatara, 1984]. The belief that gibbons have a stereotypic nuclear family composition centering on adult pairs has recently been modified following the documentation of extrapair copulations and partner changes [Palombit, 1994a,b; Reichard, 1995]. Gibbon social monogamy is commonly understood to have evolved from strong food competition between females and a low vulnerability to predation, due to the gibbons' arboreal lifestyle, superb brachiation, and theoretical assumptions of small group size [Raemaekers & Chivers, 1980; Wittenberger & Tilson, 1980; Brockelman & Srikosamatara, 1984]. Van Schaik and Dunbar [1990] have suggested the risk of infanticide as a key factor for the evolution of the gibbons' social system and likewise assumed

predation to be of little importance. At present it is not known whether or not the threat of infanticide is or has been important in this species. Surprisingly, so far only two studies [Tenaza & Tilson, 1985; Uhde, 1997] have investigated the risk of predation in these Asian apes in any detail. Otherwise, only brief anecdotal episodes of reactions to potential predators are available [e.g., Ellefson, 1974; Kappeler, 1981] and a note by Schneider [1906], who reports a case where an adult siamang (*Hylobates syndactylus*) was found in a python. Altogether, the knowledge of predation in gibbons is poor. Hard data on the sleeping habits of hylobatids, from which it would be possible to deduce the impact of predation risk on gibbon behavior, are also largely lacking [but see Whitten, 1980]. An exception is a study of the Kloss gibbon (*Hylobates klossii*) on Siberut Island by Tenaza and Tilson [1985]; however, large cats, which are common in most gibbon habitats, are absent from this island, and in the study only humans and pythons but no birds of prey were considered potential gibbon predators.

This paper provides detailed information on sleeping habits of three well-habituated white-handed gibbon groups (*Hylobates lar*) from a long-term field study on social behavior and ecology. Many potential gibbon predators (felids, birds of prey, and pythons) are present at the site. Behavioral data prior to and while entering sleeping trees and at sleeping places were collected to assess the predation risk and antipredator behavior in gibbons. Several influences on presleep behavior and sleeping place selection were considered: 1) external factors (weather and home range), 2) comfort, 3) predawn singing, 4) resource exploitation, and 5) predation risk.

METHODS

Study Area

The Mo Singto study site is located at 730–870 m elevation in a seasonally wet evergreen tropical forest in Khao Yai National Park, Thailand (2,168 km²; 101°22' E, 14°26' N; ~130 aerial km NE of Bangkok; for a geographical map see Brockelman & Gittins [1984]). A population of white-handed gibbons (*Hylobates lar*) immediately west of park headquarters has been studied by various observers since 1978 [cf. Brockelman et al., 1998]. A few trees in the study area were illegally exploited for incense production over the last decade. Otherwise, gibbons and other wildlife are believed not to have been threatened by poaching or deforestation.

Data Collection

Gibbons were observed for more than 2,000 h over 388 days from 1989–1997 (October 1989 to January 1990, 42 days, ~150 h; January 1992 to May 1993, 259 days, ~1,600 h; October 1993, 10 days, ~17 h; October 1994, 11 days, ~20 h; May to June 1996, 23 days, ~56 h; October to December 1996, 32 days, ~170 h; October to November 1997, 11 days, ~41 h). Detailed behavioral observations focused on three adjacent groups (A, B, and C; group compositions from 1989–1997 are given in Figure 1; for the groups' social histories see Brockelman et al. [1998]). The core data set comes from a continuous 16 month period, when most dawn-to-dusk follows and focal-animal sampling [Altmann, 1974] were conducted (May 1992 to April 1993, 175 days, 1,209 h). Observations usually started shortly before or at dawn and ended about an hour after the apes had settled down. Daily foraging movements and the position of sleeping trees were recorded in relation

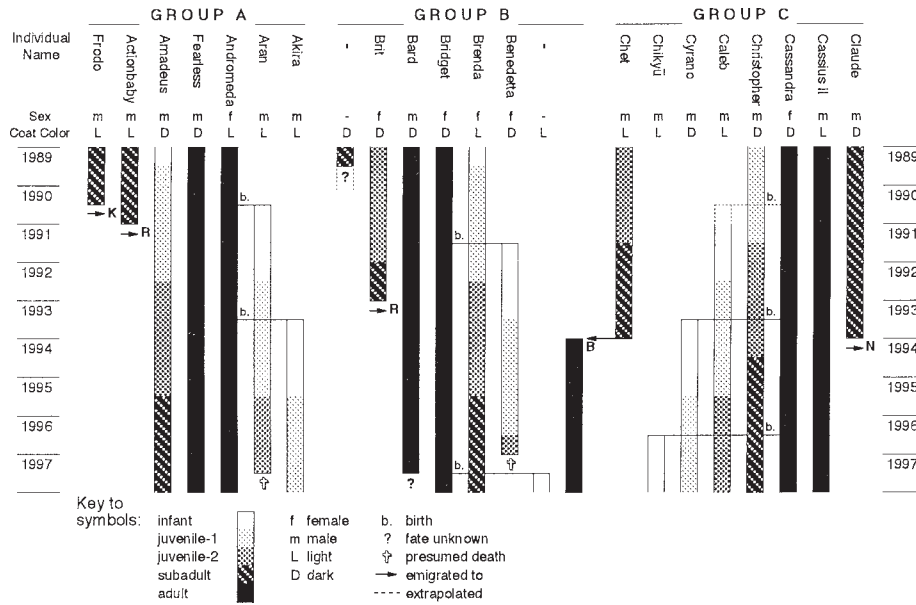


Fig. 1. Composition of main white-handed gibbon study groups, Khao Yai National Park, Thailand.

to a marked and measured trail system, which traversed the study area. Sleeping tree locations were later reconstructed on a map with grid lines spaced 10 m apart. Group members were well habituated (group A since 1981, groups B and C since early 1992 [cf. Reichard, 1996]). They were distinguished by their variable pelage color (the species is asexually dichromatic in central Thailand, with individuals being either dark brown to black or light tan to buff), facial features (particularly the white face ring), relative body size, mode of movement, and their voices. Neighboring groups (D, E, K, L, G, H, M, and N) were observed opportunistically during encounters with the main study groups [cf. Reichard & Sommer, 1997] and during surveys. Groups occupy relatively stable, partly overlapping home ranges.

Gibbon Singing Behavior

Gibbons are unique among the *Hominoidea* because they regularly sing loudly, so that they are still audible from 1–2 km away [Raemaekers et al., 1984]. Male and female white-handed gibbons sing coordinated, powerful duets, which mostly occur from about 07:00–11:00 h. Duets consist of a warm-up phase by both individuals, followed by a high-pitched female great call and a male reply. The sequence is or is not repeated several times. Adult and subadult males of this species also sing solos, mostly around dawn.

Age Classes

Age classes were based on relative size, motor skill development, and social status: 1) infancy, which is from birth to approximately 2 years (until young traveled independently of the mother, having completed their weaning period); 2) juvenile-1 or younger juvenile stage, which is from ~2–5 years; 3) juvenile-2 or

older juvenile stage, which is from ~5–8 years; 4) subadulthood, defined as the time animals reached full adult size at approximately 8 years of age; and 5) adulthood, which is >8 years (once individuals dispersed and/or paired with a member of the opposite sex [cf. Brockelman et al., 1998]).

Terminology

The following terms were used in this study.

1. *Sleeping site*: location of sleeping trees in the home range.
2. *Sleeping tree*: a tree in which gibbons stayed overnight.
3. *Sleeping place*: location of individual in a sleeping tree.
4. *Sleeping habit*: summarizing term for characteristics and activities associated with the choice of sleeping trees, sleeping places, and presleep behaviors.
5. *Sleeping position*: body orientation at the sleeping place (e.g., sitting, laying).
6. *Shared sleeping tree*: a sleeping tree simultaneously used by more than one individual. Mother–infant pairs were excluded from quantitative analyses of shared use, because gibbon infants habitually share sleeping places with their mothers until another offspring is born (about every 2–4 years [cf. Leighton, 1987]). Since the study females all carried infants during the core study period (1992/1993), they all shared their sleeping places with the infants.
7. *Reused sleeping tree*: a sleeping tree that was ever used more than once by the same or another individual during any of the observation periods.

Activity Period

Because it is impossible to determine the exact time a gibbon awakes, the interval between leaving a sleeping tree in the morning and entering a sleeping tree again in the afternoon marked the activity period. This period ignores by definition the time when a gibbon was still awake at a sleeping place before nightfall. Individual activity periods were calculated first, before group activity periods were measured. The female of group C suffered from an injury which temporarily paralyzed her right arm (January–March 1993). Because her handicap influenced the start and end of the group's daily activity, only data prior to her injury and after her complete recovery were included in calculations.

Height Measurement

Two direct-reading optical range finders were used (model 123X for heights up to 15 m and model 620 for heights above 15 m; Ranging Rangefinder, Forestry Suppliers Inc., Jackson, Mississippi). With these instruments it is not necessary to measure any angles to calculate height, which makes them near optimal reading devices in dense forests. The range finders were regularly calibrated to measured distances and adjusted. They are accurate to within about 2% at most forest heights. Readings were taken to the nearest half meter, according to scales. Corrections were added for differences in ground level and position under the tree. Sleeping place heights were taken directly beneath individuals.

Data Analysis

Analyses were with few exceptions restricted to adult, subadult, and juvenile individuals. Infants left and entered sleeping trees simultaneously with their

mothers, because they were carried, or they entered within the preceding or next minute. Their sleeping habits appeared highly related to and dependent on their mothers' sleeping habits.

RESULTS

Weather

Weather exerted little influence on gibbon sleeping habits. Even though temperatures during the main study period changed quite dramatically over the year (coldest nights were in December 1992 and January 1993, when the night temperature averaged 19.5°C, the minimum was 6.5°C, and the maximum 26.5°C (n = 33); hottest nights were in May and June 1993, when the night temperature averaged 26.0°C, the minimum was 20.5°C, and the maximum 36.0°C [n = 44]), individuals were never observed to use sleeping places communally (e.g., to keep warm during cold nights or change their solitary sleeping behavior in response to weather changes). In December 1992 and January 1993, the temperature fell to 15°C and below during 53% of nights (n = 34).

Location of Sleeping Trees in the Home Range

The majority of sleeping trees (83%, n = 178) were located in areas where only members of one group were observed foraging, and fewer (17%) were found in overlapping areas (defined by foraging activities and direct encounters) between home ranges (Fig. 2; Table I). In overlap areas, members of different groups were never ever seen to use the same sleeping trees. Food sources, in contrast, were successively and simultaneously shared in those areas, and sometimes individuals traveled along the same canopy pathways. The total number of sleeping trees found within the territory and in overlapping areas did not deviate from the expected number of trees selected for sleeping according to the relative size of the two areas (group A: $\chi^2 = 1.31$, d.f. = 1, n.s.; group B: $\chi^2 = 0.78$, d.f. = 1, n.s.; group C: $\chi^2 = 0.10$, d.f. = 1, n.s.), although settling in an overlap area was potentially riskier than sleeping deeper inside the home range, as illustrated by an encounter between groups C and L.

Groups C and L, 23 September 1992. Group C forages in an area of overlap where they had frequently met group L. At 14:26 h, the adult female enters her sleeping tree. Within 14 min the juvenile and adult male enter separate sleeping trees close (<20 m) to the female. At 14:57 h, the juvenile moves into an adjacent tree, and the male changes towards the juvenile's former sleeping place. Then, at 15:05 h, the female is suddenly attacked by the adult male of group L, who had approached her unnoticed. Screams are heard. The individuals briefly grapple and drop a few meters before the female escapes, loudly screaming and with her infant tightly pressed to her belly. At the same time, the adult male and the juvenile of group C vocalize and rush towards the female. The neighboring male pursues the female, but breaks off the chase when the female closely passes behind her mate, who emits typical encounter vocalizations. Next, the males sit opposite to each other, stare at each other, and briefly chase each other. At 15:07 h, the adult female of group L appears in a distance (>25 m). At 15:10 h, the female of group C retreats towards the inner area of their home range, and 10 min later all members of group C travel quickly and single file through their territory. They traverse the home range and pass several sleeping trees they had used at other times. They reach an area where they had slept before undisturbed—over 300 m distant to the

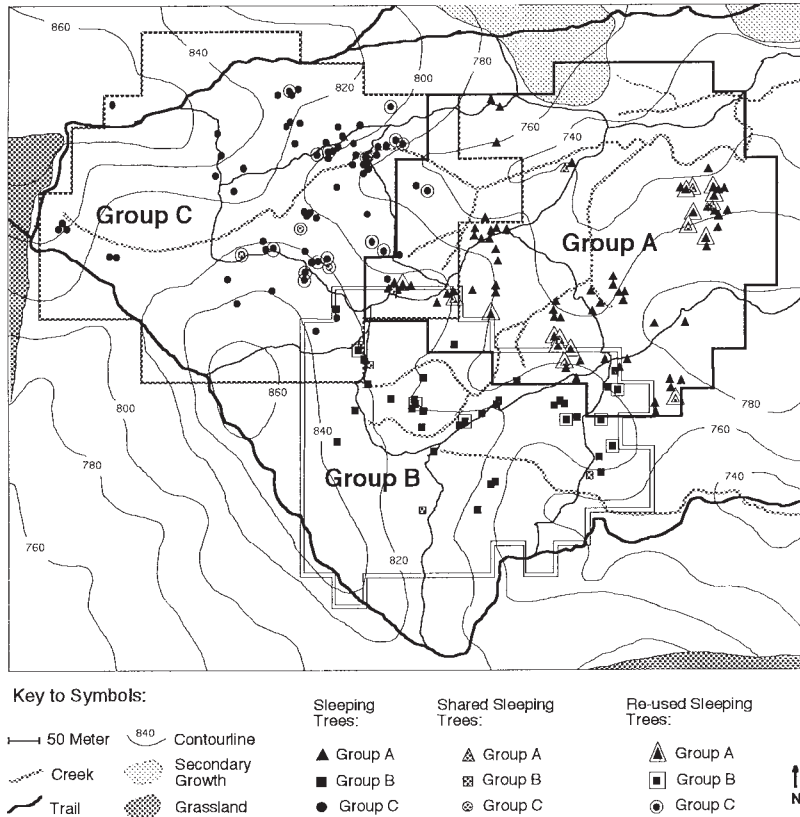


Fig. 2. Outline of home ranges and location of sleeping trees of white-handed gibbon study groups (A, B, C), Khao Yai National Park, Thailand.

encounter area with group L. At 15:30 h, the adult female again enters a sleeping tree. Soon the adult male, the juvenile, and the subadult likewise enter separate sleeping trees. All individuals quickly become quiet.

Topography

The location of sleeping trees in the groups' home ranges was apparently independent of habitat characteristics. Sites were not chosen in relation to elevation. They were located alongside ridges as well as close to creeks and at the bottom of ravines (Fig. 2). No topographic markers were detected which could provide clues for the selection of sleeping trees.

Sleeping Places and Positions

The gibbons slept in trees without exception. Places were found anywhere along a branch, and no preference was noticed for specific locations within tree crowns. In small trees, places at the trunk were commonly occupied, where individuals slept upright with bent legs leaning against the trunk. Often forks of branches functioned as basic support. When sleeping on the back or side, gib-

TABLE I. Use of Sleeping Trees and Sleeping Places by White-Handed Gibbons, Khao Yai National Park, Thailand 1989-1997.

Group	Sleeping trees used		Sleeping trees in overlapping areas between home ranges		Shared sleeping trees*		Reused sleeping trees								
	(n)	%	(n)	%	(n)	%	Same individual		Another individual		Same place†		Different place†		
							Same place	Different place	Same place	Different place	Same place	Different place			
	(n)	%	(n)	%	(n)	%	(n)	%	(n)	%	(n)	%	(n)	%	
A	75	21.3	16	14.7	11	24.0	18	92.9	26	7.1	2	6.7	1	93.3	14
B	38	21.1	8	13.2	5	18.4	7	100.0	4	0.0	0	0.0	0	100.0	4
C	65	9.2	6	7.7	5	29.2	19	90.0	18	10.0	2	44.4	8	55.6	10
Total	178	16.9	30	11.8	21	24.7	44	92.3	48	7.7	4	24.3	9	75.7	28

*Excluding mother-infant pairs

†In comparison to the individual first recorded in the tree

bons stabilized positions with one or both hands and/or feet holding onto nearby boughs or the main supporting branch. Individuals occasionally shifted their position before falling asleep but rarely used a second sleeping place during the night. The gibbons did not build night nests or otherwise manipulate the vegetation around the sleeping place, and, although vines and woody climbers sometimes effectively obscured individuals from the observer's view, plant material such as twigs, ferns, or orchids was never a component of a sleeping place. Instead, the gibbons slept exclusively on naked branches.

Interspecific Competition for Sleeping Sites

Pig-tailed macaques (*Macaca nemestrina*) frequently use dipterocarps as sleeping trees [cf. Caldecott, 1986]. They appeared the only potential sleeping site competitor for the gibbons at Khao Yai. Once a troop of 25–30 pig-tailed macaques spent the night in a *Dipterocarpus* tree in which a gibbon female slept a few weeks later, but direct competition between the two species over access to sleeping sites was never observed. The monkeys were not seen to interact with the apes around the time when the gibbons retreated to their sleeping trees. Mostly, members of the two species avoided close contact. They were only noticed interacting occasionally at fruiting trees exploited by both species [see also Whittington, 1992] and during brief play episodes. Often the gibbons ceased foraging when a pig-tailed macaque troop was heard at close range, and they rested or groomed until the monkeys left.

Intragroup Competition

Occupancy of sleeping places seemed primarily mediated through order and timing of retreat to a sleeping tree. Competition over access to a sleeping place was observed only once. This episode is described briefly in the following excerpt from field notes.

Group C, 20 February 1993. At 13:25 h, only the two subadult males (Chet and Claude) still feed in a large, fruiting tree. At 14:00 h, Chet rests, monitors the surroundings, and slowly travels 20 m, stops, and briefly self-grooms. Claude still feeds. At 14:09 h, Chet moves about 50–60 m away and reaches a sleeping tree where Claude slept twice before. At 14:10 h, Chet enters the tree and rests at the place previously used by Claude; then, at 14:11 h, he sits quietly and sometimes self-grooms. At 14:12 h, Claude appears about 20 m away, approaches further within the next minute to about 10 m, and emits low intensity hoots. This immediately alerts Chet, who appeared relaxed until now. Suddenly, at 14:13 h, Claude vigorously brachiates towards Chet, who with a great leap escapes off the tree just before Claude reaches him. Subsequently, Claude occupies the sleeping place where he will spend the night. Chet moves and rests in alternation for several minutes but does not travel far. At 14:28 h, he finally enters another sleeping tree only about 20 m distant from Claude.

Male Sleeping Habits and Singing Behavior

Subadult and/or adult males sang morning solos on 13% of mornings when the gibbons were found at dawn ($n = 114$). Most morning solos (80%; $n = 15$) were sung from the sleeping tree. When morning solos were given from a sleeping tree, these sleeping trees had an average height of 32 m (range 23–37 m, $n = 9$), not taller than sleeping trees used during other nights (Mann-Whitney U-test: $U = 221$, $n_1 = 57$, $n_2 = 9$, n.s.).

Time Spent in Sleeping Trees

The gibbons spent on average 15 h, 25 min in sleeping trees (average daily activity period 08, h 35 min; SD 54 min; range 06 h, 50 min to 10 h, 32 min; $n = 91$ follows from sleeping tree to sleeping tree; pooled data for focal individuals except infants). They entered the sleeping trees several hours before dusk, on average at 15:02 h (range 12:58–16:17 h, $n = 243$ individual entries), and left the following morning, on average at 06:14 h (range 05:27–08:29 h, $n = 156$ individual departures). Usually, little time passed after daybreak until individuals left the sleeping tree and resumed foraging or other daily activities. Differences in the start of the daily activity over the year were likely in part a consequence of the different length of the photoperiod.

The groups' activity periods differed. Group A had a significantly longer activity period on average (09 h, 02 min, range 07 h, 30 min to 10 h, 32 min, $n = 43$ follows) compared to groups B (08 h, 23 min, range 07 h, 07 min to 10 h, 15 min, $n = 17$) and C (08 h, 03 min, range 06 h, 50 min to 09 h, 40 min, $n = 31$; Mann-Whitney U-test, A/B: $U = 226$, $n_1 = 43$, $n_2 = 17$, $P < 0.05$; A/C: $U = 244$, $n_1 = 43$, $n_2 = 31$, $P < 0.01$; B/C: $U = 194.5$, $n_1 = 17$, $n_2 = 31$, n.s.). The longer activity period of group A (average departure from sleeping trees at 06:12 h, range 05:27–07:07 h, $n = 73$; average time entering sleeping trees was 15:08 h, range 13:39–16:17 h, $n = 118$) was a consequence of the later start of activity in group B (average departure from sleeping trees at 06:26 h, range 05:39–08:29 h, $n = 34$; Mann-Whitney U-test B/A: $U = 859.5$, $n_1 = 34$, $n_2 = 73$, $P < 0.05$; B/C: $U = 477$, $n_1 = 34$, $n_2 = 48$, $P < 0.01$; A/C: $U = 1527.5$, $n_1 = 73$, $n_2 = 48$, n.s.) and the earlier time of entering the sleeping trees of members of group C (average time entering sleeping trees was 14:21 h, range 13:15–15:40 h, $n = 75$; Mann-Whitney U-test A/C: $U = 1389$, $n_1 = 92$, $n_2 = 75$, $P < 0.01$; B/C: $U = 735.5$, $n_1 = 48$, $n_2 = 75$, $P < 0.01$; A/B: $U = 2009.5$, $n_1 = 92$, $n_2 = 48$, n.s.). Individuals rarely slept during the day, and no distinct daytime resting periods separated various activity bouts.

Predation Risk

Encounters of gibbons with potential predators were witnessed on several occasions. When the apes spotted a python curled up in the canopy (*Python molurus* and/or *Python reticulatus*), they became very agitated, vocalized continuously for 30 min and longer, and closely (<1 m) approached the snake. Their reactions to snakes ($n = 3$) may be summarized as mobbing behavior. The gibbons also responded repeatedly to alarm calls of squirrels and vice versa. A few times individuals emitted short alarm calls in response to large birds of prey passing low over the canopy, and group A once chased a large bird of prey.

Group A, 24 January 1993, 06:59 h. Individuals have left their sleeping trees but have not yet resumed foraging. They sit spread within ~15 m of each other when unexpectedly a large mountain hawk eagle (*Spizaetus nipalensis*) lands in a tree closest to the male (~12–15 m). Immediately the male and female gibbon start a loud Ooaa duet (for a description of these calls see Raemaekers & Raemaekers [1984a] and Raemaekers et al. [1984]), in which they are soon joined by the immatures. After about 20 s the mountain hawk eagle flies up but then lands once again even closer, about 6–7 m from the female and the 3-year-old juvenile. The gibbons become highly agitated, vocalize, and cautiously approach the raptor. At the same time, a distant neighboring gibbon group responds with its own Ooaa duet. Several variable squirrels (*Callosciurus finlaysoni*) and some small birds close to the gibbons emit sharp alarm calls. Then the gibbons give

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alarm calls but soon shift into another wave of Ooaa calls. This again elicits alarm calls and mobbing by birds and squirrels. The mountain hawk eagle flies up and lands some 25–30 m away. The gibbon female gives alarm calls, and the male cautiously brachiates towards the bird of prey while continuously emitting low key hoots. Once he approaches the eagle to within ~15 m, the raptor finally sets off and disappears in the sky. The male precedes his approach until he reaches the immediate vicinity of the raptor's last perch, where he stops and rests. Slowly and cautiously and still vocalizing, the rest of the group follows, passes the male, and resumes foraging.

Further Predation Risk

Once in the early morning a clouded leopard (*Neofelis nebulosa*) was met in a tree among a troop of pig-tailed macaques (*Macaca nemestrina*) not far from group A's home range [cf. Davies, 1990]. Other potential predators which occur at Khao Yai include tigers (*Panthera tigris*), leopards (*Panthera pardus*), and probably a few smaller cat species (marbled cat (*Felis marmorata*), Asian golden cat (*Felis temminckii*), leopard cat [*Felis bengalensis*]). In addition, gibbons at Khao Yai may be at risk from predation by birds of prey such as the mountain hawk eagle (*Spizaetus nipalensis*) or large black eagle (*Ictinaetus malayensis*).

Type and Morphology of Sleeping Trees

Sleeping trees were used specifically for overnight stay and were rarely approached for other activities, such as allogrooming, play, or calling (except for males' dawn calls). They were seldom incorporated in commonly used daily travel routes and only in exceptional circumstances provided edible foods for the gibbons.

Sleeping tree species were not investigated systematically, and only trees of the *Dipterocarpaceae* family were always noted. Dipterocarps (*Dipterocarpus* sp.) were among the tallest and most conspicuous sleeping trees of the gibbons and comprised about 13% of the sleeping trees recorded (n = 178). Of the 44 sleeping trees that were used more than once, dipterocarps comprised 16%. Mature trees of this species become very large (≥ 50 m), have straight trunks, and the first branch is usually high above the ground. The often massive branches frequently grow horizontally and rarely grow dense foliage. Therefore, the gibbons frequently slept at places surrounded only by a few small, spherically spreading, slightly foliated twigs, where they were easily visible to an observer from the ground.

Besides trees with open crowns such as dipterocarps, trees with crowns that were a dense tangle of radial branches were also chosen. Such places effectively concealed individuals. Sleeping trees were sometimes relatively isolated, fairly inaccessible with limited connections to other trees, and sometimes sleeping tree crowns were well integrated into the canopy and joined up with numerous other crowns. In addition, some sleeping trees had vines or woody climbers growing up the trunk and/or hanging down from the crown. Overall, sleeping tree morphology appeared highly variable and revealed no systematic characteristics except height.

Sleeping Height

Sleeping trees were large, mostly mature trees (average height 32 m, range 16–46 m, n = 114) (Fig. 3a). About 85% were taller than 25.5 m, and more than 50% reached higher than 31.5 m. Sleeping places were likewise located high above the ground. About 72% of places were between 21 and 30 m high, with an overall average height of 27 m (range 13–41 m; n = 109) (Fig. 3b).

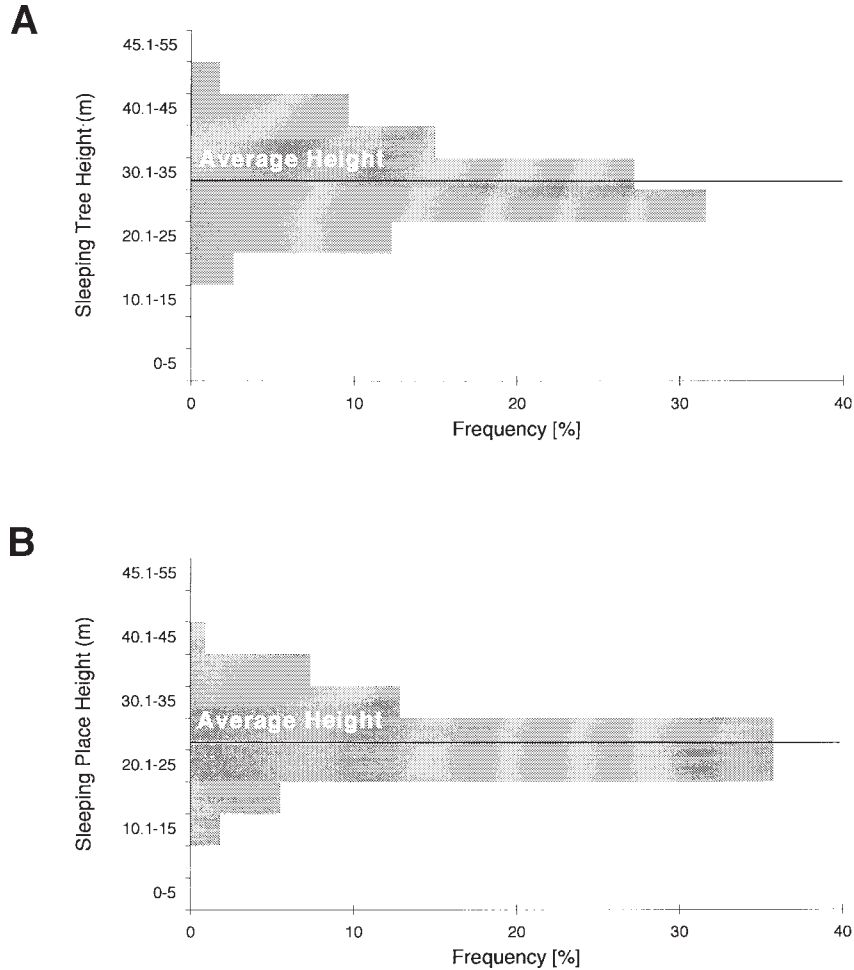


Fig. 3. Frequency distribution of sleeping tree heights (a) and sleeping place heights (b), Khao Yai National Park, Thailand.

For the following analyses, data from the three adult females, the three adult males, the three juveniles, and the two subadults of the three study groups were combined. Data were pooled, because within age–sex class comparison did not differ statistically, whereas comparison between age–sex classes revealed significant differences.

Age–sex class differences in sleeping tree height. Adult females with infants selected significantly higher sleeping trees than adult males (Mann-Whitney U-test: $U_{\text{tree}} = 611$, $n_1 = 34$, $n_2 = 41$, $P < 0.05$), and they likewise used higher sleeping trees than subadult males (Mann-Whitney U-test: $U_{\text{tree}} = 366$, $n_1 = 13$, $n_2 = 41$, $P < 0.05$). No significant differences appeared when adult males were compared to subadult males and to juveniles or when juveniles were compared to subadult males or juveniles to adult females.

Age–sex class differences in sleeping place height. Adult females with infants used significantly higher sleeping places than adult males (Mann-Whitney U-test: $U_{\text{place}} = 1015.5$, $n_1 = 33$, $n_2 = 39$, $P < 0.001$), and they also slept higher

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than subadult males (Mann-Whitney U-test: $U_{\text{place}} = 314.5$, $n_1 = 11$, $n_2 = 39$, $P < 0.05$). Likewise, juveniles selected significantly higher sleeping places than adult males (Mann-Whitney U-test: $U_{\text{place}} = 282.5$, $n_1 = 26$, $n_2 = 33$, $P < 0.05$) and subadult males (Mann-Whitney U-test: $U_{\text{place}} = 253$, $n_1 = 11$, $n_2 = 27$, $P < 0.001$). No differences in sleeping place height were detected between juveniles and adult females with infants and between adult and subadult males.

Presleep Behavior

Individuals slept in different trees during most nights. Only 12% of sleeping trees recorded ($n = 178$) were simultaneously used by several group members (Table I). Sleeping places, in contrast, were never shared (except for females with dependent infants). In shared sleeping trees, juveniles mostly stayed with adult female–infant pairs (ten episodes) or adult males (four episodes). Other combinations were rare (once or twice only) (Fig. 4). Two unusual episodes were recorded in April 1993 when all members of group A slept in one tree only 3–7 m apart during 2 nights.

Sequence and time lapse of entering and leaving sleeping trees. There was no indication that the gibbons had difficulties finding appropriate sleeping trees or sleeping places. After a last feeding bout for the day, group members usually quickly departed from the same or a nearby food source to enter a sleeping tree. Only occasionally did individuals move to a more distant food source once one member had already settled at a sleeping place. Departure for sleeping trees was usually not simultaneous, as individuals one after another dropped out from the group and separately approached their sleeping tree. Retreat to sleeping trees was not initiated or accompanied by audible or other cues detectable by a human observer. Individuals usually moved rather quietly to the sleeping tree, entered without hesitation, headed directly towards the chosen place, became silent, and seldom reemerged. Activities at sleeping places remained low key, although infants sometimes played with twigs or leaves close to the females. Self-grooming and monitoring the surroundings were the prominent activities before animals fell asleep, and females allogroomed the infants. When group members shared a sleeping tree, no vocal or physical social interactions were noticed. Around dawn, subadult and adult males occa-

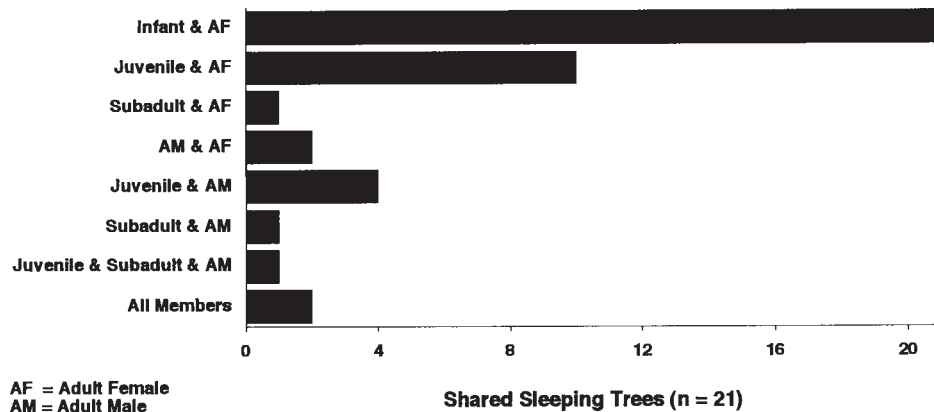


Fig. 4. Shared use of sleeping trees, Khao Yai National Park, Thailand.

sionally sang morning solos from sleeping trees, and early morning elimination sometimes occurred from the sleeping tree.

Adult females usually entered their sleeping trees first (first position: Andromeda 68%, $n = 25$ sequences; Bridget 75%, $n = 4$ sequences; Cassandra 80%, $n = 10$ sequences), closely followed by juveniles (second position: Amadeus 64%, $n = 25$ sequences; Brenda 75%, $n = 4$ sequences; Christopher 60%, $n = 10$ sequences). Finally, in groups A and B the adult males were mostly last to enter a sleeping tree (last position: Fearless 72%, $n = 25$ sequences; Bard 75%, $n = 4$ sequences). For group C, no complete sequence of retreat of all six members and only one of five could be recorded. Furthermore, the subadult Claude was not always present. Because of these difficulties, the fourth and/or fifth position was scored last for this group. In 55% ($n = 11$ sequences), one of the subadult males was last to enter a sleeping tree, and in 36% the adult male was last. In the remaining 9%, the juvenile entered a sleeping tree after the others.

On average, 13 min (range 1–97 min, $n = 39$ complete sequences; pooled data for focal animals except infants) passed between the time first and last group member entered the sleeping trees. The time lapse between adult females and adult males also averaged 13 min (range 1–65 min; $n = 57$ sequences). When females entered a sleeping tree before males, significantly more time passed than vice versa (female before male: average time lapse 15 min, range 1–65 min, $n = 49$ episodes; male before female: average time lapse 4 min, range 1–13 min, $n = 8$ episodes; Mann-Whitney U-test $U = 72.5$, $n_1 = 50$, $n_2 = 8$, $P < 0.01$). Only 6 min passed on average (range <1–27 min, $n = 52$ sequences) between juveniles and females, with negligible difference regarding the sequence (females before juveniles: average 6 min, range <1–27 min, $n = 40$ episodes; juveniles before females: average 5 min, range <1–12 min, $n = 12$ episodes). Similarly, time lapse between adult males and juveniles was short (average 9 min, range <1–34 min, $n = 41$ episodes) and did not show a significant difference (juvenile before male: average time lapse 11 min, range <1–34 min, $n = 31$ sequences; male before juvenile: average time lapse 5 min, range <1–18 min, $n = 10$ sequences; Mann-Whitney U-test $U = 94$, $n_1 = 31$, $n_2 = 10$, n.s.). During 22% of episodes, they entered simultaneously or within the following minute.

Departure from sleeping trees in the early morning was completed by the groups within 15 min on average (range 2–67 min, $n = 26$ complete sequences; pooled data for focal animals except infants). Interestingly, the sequence of departure showed more variation than the retreat to sleeping trees. During 14 sequences in Group A, the female, Andromeda, usually left first (first position adult female: 43%, last position 20%; adult male Fearless: first position 28%, last position 47%; juvenile Amadeus: first position 29%, last position 33%). The time lapse between female and juvenile was 10 min on average (range 1–38 min, $n = 20$ sequences) and between the adults 6 min (range 1–26, $n = 17$ sequences). On the other hand, in group B the adult female was mostly last and the juvenile female Brenda usually first to leave the sleeping tree (first position adult female Bridget 14%, last position 71%; first position juvenile Brenda 57%, last position 14%; first position adult male Bard 29%, last position 14%; $n = 7$ sequences). The time interval between Brenda and the female was 25 min on average (range 1–67 min, $n = 6$ sequences) and still 18 min between the adults (range 2–63 min, $n = 7$ sequences) but only 10 min (range 2–26 min, $n = 6$ sequences) between male and juvenile female. In group C, results are preliminary, given the small sample size. During the four recorded sequences, subadult male Chet left earlier than the others three times (first position: adult female Cassandra 0%, juvenile Christopher 25%, adult male Cassius II

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0%, subadult male Chet 75%, subadult male Claude 0%). Second to leave was the female or the adult male (50% each), and either the female or the juvenile Christopher was third (50% each). The time lapse between the adults, the female, and juvenile Christopher as well as between female and subadult male Chet was 10 min on average, with only slight differences in ranges (overall range 1–22 min, $n = 27$ sequences). The time lapse between juvenile Christopher and the adult male was only 5 min on average (range <1–15 min, $n = 7$ sequences) and 18 min between adult male and subadult Chet as well as between juvenile Christopher and subadult Chet (ranges 7–29 min and 2–38 min respectively, $n = 5$ sequences each).

Reuse of Sleeping Trees

The majority of sleeping trees were used only once during this study (75%, $n = 178$) (Table I), and fewer (25%) were selected repeatedly by the same or other group members (defined as reuse). The number of reused sleeping trees increased with observation time. During the last months of focal-animal observations in two groups (February–March 1993), almost half of the chosen sleeping trees were used previously (group A: 45%, $n = 11$ trees; group C: 43%, $n = 21$ trees).

Sleeping trees were rarely reused during consecutive nights (4% of reuse) or within one week (23% of reuse, $n = 75$ episodes, pooled data for three groups). Instead, they were reused over long periods. On average, 77 days (range 1–396 days, $n = 75$ episodes, pooled data for three groups) passed during consecutive use of sleeping trees. The maximum number of reuse was recorded for the adult female of group A, who over 4 years slept at the same place during 7 nights (one time in December 1989, May 1992, and April 1993 and two times in both February and March 1993). A long-term pattern of reuse was noticed for all individuals. The female of group C used a sleeping tree in May 1993 and again twice in November 1996. The adult male of group A slept in a tree in May 1992 and again in April 1993, and the subadult Chet of group C used a sleeping tree twice in May 1992 and again in February 1993. This particular tree was also reused by the adult female in December 1992, by the adult male in January 1993, and by the subadult Claude in February 1992.

Sleeping Place Fidelity

Of 89 reuse episodes, the same individuals reused sleeping trees 52 times (58%), and 37 times (42%) other group members (than the individual first recorded in the sleeping tree) reused sleeping trees. For reused sleeping trees, a comparison of four categories revealed preferences for individual sleeping places (Table I): 1) when the same individuals reused a tree they mostly slept at the same place (92%, $n = 52$ episodes), and 2) only rarely selected a new place (8%, $n = 52$ episodes); 3) when other group members reused an already recorded sleeping tree, they usually stayed at a different place than first users (24%, $n = 37$ episodes), and 4) mostly slept at a new place (76%, $n = 37$ episodes). Further analyses of repeated reuse by other group members (categories 3 and 4 again revealed a preference for individual sleeping places. When individuals were not first users but reused a sleeping tree more than once, they likewise preferred to stay at previously used places (89%, $n = 9$ episodes) and rarely chose a new place (11%, $n = 9$ episodes). This pattern was similar for the three study groups (cf. Table I).

DISCUSSION

The results of this study suggest that gibbons are vulnerable to predation. Their presleep behavior and selection of sleeping places primarily reflect adaptations to minimize the risk of being detected and attacked by predators. Gibbons retreat early to their sleeping places, often several hours before nightfall [Ellefson, 1974; Raemaekers, 1977; Srikosamatara, 1980; Kappeler, 1981; this study]. The situation at the sleeping place differs importantly from the remainder of their activity period, because individuals remain relatively stationary for many hours and do not gain safety from their high mobility, which during the day may protect them from predator attacks. During the last daylight hours, they are at risk of being detected by visual hunting predators. If a cat spots a gibbon at a sleeping place, it may at the moment or later try to stalk it, and raptors may directly attack. Furthermore, once a gibbon is in a sleeping place, predator evasion is likely more difficult, because individuals may doze or sleep and awake only upon a predator's sudden approach. The gibbons' inconspicuous behavior while retreating to their sleeping trees and the absence of vocal and physical social interactions between group members at sleeping places, even when they are staying in one tree, were interpreted as adaptive responses to avoiding detection by predators.

In addition to predation risk, weather, aspects of territoriality and ranging, comfort, male predawn singing, and resource exploitation may also influence the choice of sleeping sites of primates [cf. Anderson, 1984]. They will be briefly discussed with respect to gibbons.

Weather

Wild rhesus monkeys (*Macaca mulatta*) increase the size of their sleeping group in response to low temperature [Southwick et al., 1965], and red howlers (*Alouatta seniculus*) build sleeping clusters during cold nights [Gaulin & Gaulin, 1982], probably to reduce body heat loss. Some New World monkeys may choose to sleep in tree holes to gain protection from rain and cold temperature [Heymann, 1995]. The hylobatids, with their relatively small bodies and long limbs, are also expected to be affected by problems of heat loss during the night. Chivers [1974] noticed a juvenile siamang (*Hylobates syndactylus*) staying a meter away from the adult male at dusk, but found the two closely huddled at dawn (the coldest hour of the day). Proximity (between male and juvenile) and huddling in the sleeping tree could have been a response of the juvenile to the cold night temperature but could also have reflected prolonged intimacy resembling female-infant sleeping arrangements. Females sleep in body contact with infants or young juveniles beyond weaning and physical independence, usually until a new infant is born [Treesucon, 1984; this study]. In siamangs, some males carry infants [cf. Dielentheis et al., 1991], as was the case in Chivers' [1974] study, and, in contrast to female-juvenile sleeping habits, the pattern and termination of young juveniles sharing a sleeping place with an adult male are perhaps more flexible and may therefore only partly be a response to cold weather.

Gittins [1982] considered agile gibbons' (*Hylobates agilis*) choice of sleeping in tall trees on ridges as a response to the relatively lower night temperature in valleys. Alternatively, sleeping on ridges may coincide with a preference for tall sleeping trees which may be more abundant in well-drained soil along hill crests, as was found by Tenaza and Tilson [1985] during a study of Kloss gibbons (*H. klossii*). Whitten [1980] recognized for another Kloss gibbon group a preference

for sleeping trees located on a slope, which also seemed to be primarily caused by a preference for tall sleeping trees.

Overall, gibbon studies, including this one, have failed to document an important influence of weather on sleeping habits. At Khao Yai, night temperature sometimes dropped to 5–7°C [Treesucon, 1984; personal observation], but individuals never changed from sleeping alone to sleeping in bodily contact. Sleeping trees or places were rarely shifted during the night, and alteration of sleep-related behaviors did not coincide with weather changes. Interestingly, gibbon sleeping positions seem to reduce body surface exposure to a minimum [Ellefson, 1974; Whitten, 1980], and white-handed gibbons (*H. lar*) at Khao Yai frequently sunbathed shortly after sunrise even before their first feeding bout during the colder dry season. Both observations support the assumption that gibbons experience considerable heat loss during the night. Hylobatids have thick fur [Schultz, 1931], which is perhaps their main adaptation against weather hazards. They may not be able to afford to sleep huddled in one place, because this may increase the risk of nighttime predation by pythons. Pythons can use scent to find their prey [Bellairs, 1969], and the intensity of accumulated odors in a sleeping group may increase the likelihood of detection by pythons. The disadvantage of increased predation risk would thus outweigh any advantage of improved thermoregulation.

Topography and Home Range

Habitat landmarks were a poor predictor for the choice of gibbon sleeping sites in the present study. Ridges and gullies structured group home ranges, but the locations of sleeping trees did not show a pattern related to topography. Sites were on ridges, on almost level terrain, alongside slopes, and in ravines close to or above creeks at lower altitude.

Sleeping sites of primates are often concentrated in the area most intensively used or defended by a group [cf. Anderson, 1984], termed the core area or territory. During this study, sleeping sites were not confined to the inner boundary of the territory. Sleeping trees occurred in nearly all home range areas, including those that overlapped with neighbors. This observation corresponds with some gibbon studies (*H. syndactylus*: Chivers [1974]; *H. lar*: Raemaekers [1977]; *H. pileatus*: Srikosamatara [1980]; *H. concolor*: Chen [1995]), which have all found sleeping trees widely distributed throughout group ranges. In contrast, Kappeler [1981] recorded sleeping trees concentrated in a small portion of the home range and few in the periphery for a moloch group (*H. moloch*). Likewise, Kloss gibbons (*H. klossii*) mostly slept inside the boundary of their territory [Tilson & Tenaza, 1982]. However, disagreement about the choice of location of sleeping trees in relation to the territory and overlapping areas may result from methodological differences. Kappeler [1981] used the location of sleeping trees to define the core area, which precludes comparisons about the overnight use of the two areas. Tilson and Tenaza [1982] constructed the territory with a line of the outermost perimeter of group travel and the location of male and female song sites, which were then refined with sites of group encounters and locations from where solitary individuals were displaced by residents. In the present study, the locations of group encounters alone determined overlapping home range parts [cf. Reichard & Sommer, 1997]. Finally, Whitten [1980]—probably aware of methodological problems—found more sleeping trees in the periphery than in the center of the home range, although centrally located sleeping trees were used more frequently. Different methods of measuring home range and territory result in different boundaries and probably lead to different interpretations of locations of sleeping sites.

Additionally, the estimated range size and the number of sleeping trees ultimately depend on the length of observations. During short observation periods, only few sleeping sites can be recorded, which may then center in a relatively small part of a group's range.

In conclusion, gibbon sleeping trees can be almost anywhere in the home range, including in areas of overlap, despite the fact that settling in an area visited by neighbors is potentially dangerous, as exemplified by the reported sudden attack on one of the females in her night tree during this study. In gibbons, both sexes have large canine teeth [Plavcan & van Schaik, 1997], with which they can inflict serious wounds [e.g., Palombit, 1993].

Comfort

For humans, the most obvious increase in sleeping comfort could perhaps be the building of a nest or bed as is done by the great apes [cf. Fruth & Hohmann, 1996]. Gibbons do not build nests or otherwise manipulate the vegetation at sleeping places, they spend the night on naked branches, and so far only Whitten [1982b] has found direct evidence of a relation between the selection of sleeping trees and aspects of comfort, because the Kloss gibbons (*Hylobates klossii*) he studied avoided sleeping in trees with *Myrmecodia tuberosa* epiphytes, which host biting ants.

Accumulation of excretion at regularly used sleeping sites could result in increased odors. Primates may shift sleeping sites to avoid unpleasant smell or infestation with ectoparasites [Nagel, 1973] and intestinal parasites from their own feces [Hausfater & Maede, 1982]. In gibbons, early morning elimination often occurs from the sleeping tree [Treesucon, 1984; this study]; however, individuals usually move away from the immediate vicinity of the sleeping place to do this. They commonly eliminate while hanging by their hands with knees up over open places [Ellefson, 1974], so that most excretion falls to the ground and accumulates, if at all, only to a small degree on the sleeping place. Thus, a high parasite concentration at sleeping places seems unlikely. Nonetheless, it cannot be excluded that the large number of sleeping trees used [cf. Chivers, 1984] and patterns of reuse of places [e.g., Ellefson, 1974; Tenaza & Tilson, 1985] are related to aspects of hygiene. Moreover, feces analyses revealed light infestation with parasites, which indicates some contact with feces [Whitten, 1984].

Sound Broadcasting

Long-distance sound transmission of forest-dwelling animals increases with height above the ground, intensity (loudness), and calling at dawn or dusk [Marten et al., 1977]. Primate groups that use vocal signals as a spacing mechanism, like red howlers (*Alouatta seniculus*) [Sekulic, 1982] and Mentawai langurs (*Presbytis potenziani*) [Tilson & Tenaza, 1982], give loud morning calls before they leave the sleeping tree. Similarly, subadult and adult males of several gibbon species (*H. klossii*: Tenaza & Tilson [1985]; *H. agilis*: Gittins [1982]; *H. muelleri*: Marshall & Sugardjito [1986]; *H. lar*: Raemaekers & Raemaekers [1984b], this study) and female moloch gibbons (*H. moloch*: Kappeler [1984]) call around dawn. To avoid moving in the dark, individuals may select sleeping trees from which early morning singing is positively influenced. Agile gibbons (*H. agilis*) perhaps preferred sleeping on ridges, because in hilly terrain calling from a higher elevation is likely to increase the distance that dawn calls carry [Gittins, 1982]. Generally, gibbons prefer to sleep in tall, often emergent trees

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[Chivers, 1974; Whitten, 1982a; Srikosamatara, 1984; Kappeler, 1984; Tenaza & Tilson, 1985; this study], which may transmit early morning calls over as large an area as possible.

Nonetheless, it appears unlikely that sleeping trees are primarily selected to increase dawn song transmission. First, so far no consistent topographic effect of sleeping on relatively higher ground could be verified across gibbon study sites (see discussion above). During this study, males sang dawn solos regardless of relative elevation of the sleeping tree in the home range. Second, males sometimes left a sleeping tree before daylight to sing from another tree (20% of dawn songs) [see also Whitten, 1980]. In these cases, sleeping trees were apparently not appropriate for sound transmission, and therefore the choice of the sleeping tree was based on something else. Sleeping in taller trees when calling the next morning would be expected, because singing from tall trees enhances sound transmission and could compensate for sleeping in comparatively lower home range areas. In contrast, during this study sleeping trees from which males called at dawn were not taller than regular sleeping trees. Correspondingly, Whitten [1980] failed to discover a significant difference in heights of sleeping trees from which male Kloss gibbons (*Hylobates klossii*) called in the morning compared to the random height distribution of trees in the home range. Perhaps males did not know the previous afternoon whether or not they would call the next morning. Hence, it would be opportune to always sleep in tall trees. During this study, however, females with infants, not males, selected significantly taller sleeping trees [see also Whitten, 1982a]. In conclusion, it seems more likely that gibbons choose to sleep in tall trees for reasons of safety, which as a side effect sometimes benefits early morning song broadcasting.

Food Distribution

Hamadryas baboon bands (*Papio hamadryas*) may shift their sleeping cliffs in connection with changes in the foraging region [Sigg & Stolba, 1981], and spider monkeys (*Ateles geoffroyi*) choose the sleeping place closest to the feeding area currently being used from among several repeatedly used central ones [Chapman et al., 1989]. The above examples support the hypothesis that primates sometimes choose sleeping sites to maximize economic foraging.

For siamangs (*Hylobates syndactylus*), Chivers [1974] noticed sleeping trees usually situated around one or more of seven or eight groups of feeding trees frequently used in the late afternoon. Similarly, Raemaekers [1977] reported siamangs' sleeping trees next to big food sources currently being used. Also during this study, sleeping places were usually not far from temporarily important fruiting trees. Besides qualitative statements, however, little support exists for a close link between the location of sleeping trees and food sources in gibbons. Gibbons are known to feed on numerous sources every day [Raemaekers, 1977; Whittington & Treesucon, 1991], which in itself gives the impression that they always sleep close to a food source. An analysis of the distance traveled by Kloss gibbons (*Hylobates klossii*) between the last food source of the day and the first source the following morning revealed the opposite. The group traveled significantly further between overnight fruit sources than between daytime fruit sources, with the sleeping tree in about the middle [Whitten, 1980]. Likewise, no significant association of sleeping trees with food trees was detected in a study of agile gibbons (*Hylobates agilis*) [Gittins, 1982]. During the present study, large fruiting trees were often visited twice a day, usually once in the morning after leaving the sleeping tree and again in the afternoon shortly before the retreat to

sleeping trees. If sleeping trees were chosen to maximize the exploitation of important resources—likely those visited more than once—individuals should have spent consecutive nights in the same sleeping trees to reduce travel costs [cf. Chapman et al., 1989]. In contrast, sleeping places were reused usually only over long periods even when fruiting trees were visited daily.

Predation Pressure

Predation pressure may exert a strong influence on the sleeping habits of primates [e.g., Byrne, 1981; Caine et al., 1992; Heymann, 1995] and appears to be the central influence on the sleeping habits of gibbons. To avoid being killed, prey will generally attempt to interrupt the sequence of predation at the earliest possible stage, which is typically the detection of prey (identification against the environment) by the predator [Endler, 1991]. The risk of detection may be minimized if potential prey become as invisible to a predator as possible by means of inconspicuous behavior and concealment. In case potential prey are located, another set of predation-avoidance mechanisms are expected, because a predator may then approach and try to attack. To reduce the chance of being captured, prey should make approach and attack as difficult as possible for the predator. With this framework of risk of detection, approach, and attack by predators, the sleeping habits of gibbons are explained most comprehensively by 1) the predominant use of the tallest trees available in the home range, particularly by adult females with small infants and juveniles, 2) an unpredictable long-term pattern of reuse of sleeping places, and 3) inconspicuous presleep behavior.

Height of sleeping trees and sleeping places. During a study of wedge-capped capuchins (*Cebus olivaceus*), members of a small group were found to be higher in the trees than members of the larger group [de Ruiter, 1985]. Similarly, in yellow baboons (*Papio cynocephalus*), members of the smallest group spent more time resting in elevated locations than members of the largest group [Stacy, 1986]. By selecting higher places, members of small groups may have tried to compensate for their disadvantage in detecting terrestrial predators compared to larger groups. If this interpretation is accepted, a negative relationship between predation risk from terrestrial predators and height above the ground may exist. In other words, the higher an animal positions itself in the canopy, the less likely it is to be taken by a predator approaching from the ground [cf. van Schaik et al., 1983a]. It is assumed that this is the reason the gibbons selected tall sleeping trees. Their true preference for very large sleeping trees is illustrated by a comparison with the general canopy structure at Khao Yai [Brockelman, 1998]. The tallest tree found on a 1 ha botanical research plot in the overlapping area between groups A and C (elevation 750–790 m) measured 53 m, and average tree height was 25.5 m (SD 12.45 m; 50% canopy cover: 26 m; smallest vertical range containing 50% of height measurements: 20–34 m [values from Brockelman, 1998]). The second 1 ha plot only a few hundred meters inside the home range of neighboring group N (elevation 760–770 m) showed a similar canopy structure (maximum height: 38 m; SD 7.83 m; mean height: 22 m; 50% cover at 23 m; smallest vertical range containing 50% of height measurements: 18–27 m [values from Brockelman, 1998]). According to this canopy structure, the gibbons' preferred sleeping trees (average height 32 m; maximum height 46 m) which were among the tallest trees available in the home ranges. Furthermore, they selected sleeping places (average height 27 m) that were usually well integrated with the canopy.

Females that carry infants and small juveniles may have more difficulty es-

caping predators than subadult and adult males, because they may be slower and have more problems brachiating over gaps. The relationship of a decrease of predation risk with an increase in height above the ground could then explain why juveniles and females with infants selected significantly higher sleeping places than subadult and adult males. Alternatively, all gibbons may face the same predation risk, but subadult and adult males could employ a different strategy to minimize predation risk, perhaps involving early detection and aggression against predators [cf. van Schaik & van Noordwijk, 1989; Struhsaker & Leakey, 1990].

Even though sleeping tree and sleeping place heights were not always measured by fieldworkers, it was repeatedly noticed that gibbons selected tall [Gittins & Raemaekers, 1980; Chen, 1995], often emergent *Dipterocarpus* sleeping trees [e.g., Chivers, 1974; Srikosamatara, 1980; Whitten, 1980; Tenaza & Tilson, 1985]. Sleeping in dipterocarps perhaps maximizes safety against felids. First, their crowns are relatively open, which allows a good view over the surroundings and probably facilitates early predator detection. During the last daylight hours, early detection and escape [van Schaik et al., 1983a] are probably more effective than concealment for the highly mobile but comparatively large gibbon. Consistent with this idea, monitoring the surroundings was one of the most frequent activities before the animals fell asleep. Second, dipterocarp trunks usually reach straight up, with the first branch high above the ground. They are likely to be difficult to climb and may discourage a cat from approaching, and during the night vibrations caused by a cat's ascent could warn the gibbon and increase the chance of successful escape.

Distribution and long-term reuse of sleeping places. Reuse of sleeping places may be a strategy to reduce predation risk due to place qualities (e.g., good view, dense foliage cover, easy escape routes, difficult access for predators). Baboons are known to use few sleeping cliffs in their large home range [e.g., Sigg & Stolba, 1981] or to return to trees in the same, small strips of gallery forest for the night [Byrne, 1981], because safe sleeping sites are rare in their savanna habitat. Nonetheless, baboons suffer from nighttime predation by leopards [Cowlishaw, 1994], because local predators may frequently return to a regular sleeping site until a successful catch is made [e.g., Isbell, 1990]. When many sleeping sites are available, predation risk may be reduced, if the advantage of intentionally sleeping at places previously left undisturbed, which conveys a likelihood of safety against predators (sleeping place fidelity), is combined with the need to frequently change places. The Khao Yai gibbons used numerous sleeping trees ($n = 178$) spread over their whole range, and they reused a smaller portion on an unpredictable long-term basis (average reuse after 77 days), which is in agreement with this hypothesis. A long-time pattern of reuse of sleeping trees was also noticed for siamangs (*Hylobates syndactylus*) during a 10 year study in Malaysia [Raemaekers & Chivers, 1980]. Interestingly, Tenaza & Tilson [1985] reported only a few, regularly used sleeping trees (one to five) for Kloss gibbons (*H. klossii*), which may directly reflect the lower predation risk on the Mentawai Islands, where large felids are absent.

Presleep behavior. The way in which gibbons went to their sleeping places minimized an observer's and probably also a predator's chance of following them and discovering the sleeping place. On average, all group members disappeared within 13 min. At the sleeping place, individuals became quiet, engaged in short bouts of self-grooming, and monitored the surroundings before falling asleep, making it usually impossible to find them again had they been lost before. Their behavior contrasted sharply with the sympatric pig-tailed macaques (*Macaca*

nemestrina), which were still heard with grunts and barks an hour after they had entered their communal sleeping tree. Captive red-bellied tamarins (*Saguinus labiatus*) are less vocal prior to their retreat to the nest box than during other times of the day and become virtually silent once in the nest box [Caine, 1987]. Dawson [1979] reports rapid retreat to the sleeping site for free-ranging cotton-top tamarins (*S. oedipus*) and Heymann [1995] for wild mustached tamarins (*S. mystax*) and saddle-back tamarins (*S. fuscicollis*). In callitrichids, of which some seem to face heavy predation [Heymann, 1995], activities prior to retreat to a sleeping site probably have a main function of securing the sleeping site. The same explanation may apply to the secretive presleep behavior of gibbons. No cues signalled their departure to the sleeping trees. Individuals usually discreetly dropped out of the group one after another, approached the sleeping tree directly, and entered without hesitation. Hollihn [1984] even argues that bimanual locomotion reduces detection by predators, because short-distance movements in a horizontal or vertical direction are less conspicuous when done bimanually than when done quadrupedally. Nonetheless, the travel path of an arboreal monkey may be followed from the ground by swinging vegetation. This may increase the risk of detection for the last individual retreating to a sleeping place, because there are no movements of vegetation caused by other group members to distract a predator's attention. During this study, females with small infants were usually first to retreat to a sleeping tree, shortly followed by juveniles, whereas subadult and adult males were mostly last [see also Ellefson, 1974]. The consistent sequence of retreat to sleeping trees perhaps reflected greater risk taken by subadult and adult males than females with infants and juveniles. In contrast, early morning departure from sleeping trees was much more variable.

Another mechanism to avoid detection by predators may be the retreat to a sleeping place before potential predators become active. This function has been suggested for red-bellied tamarins [Caine, 1987] and could also explain the early retreat of gibbons for which no convincing explanation has yet been found.

Potential gibbon predators inhabiting Khao Yai. Tigers (*Panthera tigris*) are most active at twilight [Lekagul & McNeely, 1977], although at Khao Yai they were frequently seen in the afternoon by park rangers. Twice during data collection a tiger roared a few hundred meters from the still foraging gibbons, who responded with brief, soft vocalizations. Tigers may prey upon primates [Karanth & Sunquist, 1995], but, because of their large size, gibbons are assumed to be safe from attacks at sleeping places. Nonetheless, during the day gibbons occasionally come close and onto the ground to retrieve large stick insects [Ellefson, 1974], to play [Uhde, 1997], or to drink [Carpenter, 1940]; then even a tiger may have a chance to catch a gibbon.

In Africa, the leopard (*Panthera pardus*) is a chief predator of baboons [Cowlshaw, 1994] and chimpanzees at Tai, Ivory Coast [Boesch, 1991]. In Asia, leopards also hunt a variety of prey species, including primates [Karanth & Sunquist, 1995]. Wild moloch gibbons (*Hylobates moloch*) emitted loud screams mixed with bursts of agitated movement in the presence of leopards [Kappeler, 1981], and Rabinowitz [1989] identified gibbon remains in leopard feces at Huai Kha Khaeng, Thailand. The analysis of feces, however, cannot reveal if the consumed animal was hunted or found dead. Leopards are suspected to be in Khao Yai [Srikosamatara & Hansel, 1996], and, in forests where they occur, circumstantial evidence suggests that they are a threat to gibbons.

An important potential predator for forest living animals in Asia, including gibbons, seems to be the clouded leopard (*Neofelis nebulosa*). This medium-sized cat is active during day and night, can kill prey up to the size of a sambar deer

(*Cervus unicolor*), and seeks game partly in trees [Rabinowitz et al., 1987]. On Borneo they hunt the diurnal and arboreal Hose's leaf monkey (*Presbytis hosei*) [Rabinowitz et al. 1987], which is about the size of a gibbon. The report from Khao Yai [Davies, 1990], where a clouded leopard was perched 15 m up in a tree surrounded by pig-tailed macaques (*Macaca nemestrina*) departing from their sleeping site, highlights the ability of this strong cat to climb trees to reach its targets. Circumstances suggested that the cat found the troop at night, climbed the tree, and was waiting for their departure the following morning.

Smaller cats (marbled cat, *Felis marmorata*, Asian golden cat, *F. temminckii*, leopard cat, *F. bengalensis*) are perhaps a threat only to immatures. They may be at an advantage in tree hunting compared to the heavier clouded leopard, because their smaller size allows access to prey on smaller branches. However, the Asian golden cat is considered more terrestrial than arboreal, and its diet consist primarily of animals not larger than a lesser mouse deer (*Tragulus javaicus*) but may include small primates [Lekagul & McNeely, 1977; Rabinowitz, 1990].

Besides the large monkey-eating eagle (*Pithecopaga jeffereyi*) of the Philippines [cf. Mauersberger, 1995], birds of prey are usually assumed to play a trivial role as predators on Asian primates. This assumption probably results from the limited knowledge of most forest living raptors in Asia [cf. Brown, 1976]. Interestingly, the Asian black eagle (*Ictinaetus malayensis*), which hunts by slow quartering low over the canopy, is only slightly smaller (approximate body length of 69–81 cm [Lekagul & Round, 1991; Barthel & Barthel, 1995]) than the African crowned hawk eagle (*Stephanoaetus coronatus*) (approximate body length of 69–87.5 cm [Grzimek, 1968]), for whom primates make up 84% of the diet [Struhsaker & Leakey, 1990]. Crowned hawk eagles prey on six primate species, of which the largest, the black-and-white colobus (*Colobus guereza*), weighs almost twice as much as an adult gibbon (except the larger siamang *Hylobates syndactylus* [Leighton, 1987]). It appears reasonable to assume that they pose a serious threat to the lightweight gibbons. Even the smaller mountain hawk eagle (*Spizaetus nipalensis*) (approximate body length of 66–79 cm [Grzimek, 1968; Lekagul & Round, 1991]) may be capable of catching at least young gibbons. Typically hawk eagles hunt below the canopy, where they await their prey perched on a branch [Brown, 1976]. Indirect evidence of alarm calls and mobbing behavior in response to birds of prey [e.g., Ellefson, 1974; Kappeler, 1981; this study] and the reported encounter of one of the study groups with a mountain hawk eagle support the hypothesis that raptors may become dangerous for gibbons especially at the sleeping place, where they remain relatively still.

Some of the world's largest snakes (reticulated python, *Python reticulatus*, tiger python, *P. molurus*) are found in Asia [Deckert et al., 1991]. Their diet consists of fish, reptiles, birds, and small- to medium-sized mammals [Deckert et al., 1991], including monkeys [e.g., van Schaik et al., 1983a]. The observations of pythons curled up in a tree during this study confirm their use of trees. Pythons are mainly active during twilight and during the night, when they may find their prey visually or with their good sense of smell [Bellairs, 1969]. Observed encounters suggest that pythons are potentially dangerous for gibbons. When gibbons were captured in canopy cage traps for a study on malaria and traps were inspected, one to three pythons were usually found around the cages trying to get at the gibbons [van Gulik, 1967]. Schneider [1906] reports a case from Sumatra in which a reticulated python was dissected and a fully grown siamang (*Hylobates syndactylus*) found dead in the snake's stomach, but the circumstances which led to the consumption of the siamang were not known. During the day, gibbons have been repeatedly observed to give alarm calls and mob snakes in

trees or on the ground [e.g., Kappeler, 1981; this study]. Because of their comparatively slow movement, pythons are assumed to be a threat to gibbons mainly during the night, when they could glide up on an animal undetected. A dispersed sleeping pattern, as found in some gibbon species [*Hylobates lar*: Raemaekers, 1977; *H. pileatus*: Srikosamatara, 1984], may be an adaptation to reduce predation pressure from pythons, because sleeping separately probably lowers the intensity of gibbon-specific odors. The reported communal sleeping in one tree and/or a variable sleeping pattern [*Hylobates syndactylus*: Chivers, 1974; *H. moloch*: Kappeler, 1981; *H. concolor*: Chen, 1995; *H. klossii*: Tenaza & Tilson, 1985] perhaps reflects variation in predation pressure from pythons in different gibbon habitats.

CONCLUSIONS

Avoiding detection by predators and making an approach and attack of a potential predator difficult appear to be the main functions of presleep behavior and to determine the selection of sleeping places in gibbons. Adaptive behavioral responses supporting the predation-pressure hypothesis were the gibbons' inconspicuous presleep behavior and the selection of very large sleeping trees. Alternative interpretations were less convincing, although some influences could not be ruled out completely. The reuse of sleeping places on a long-term basis, for example, may have functioned to reduce predation risk or infestation by parasites or both [cf. Whitten, 1984]. The variables which potentially influence the choice of sleeping places in primates are usually not mutually exclusive. For gibbons in their forest environment, the number of safe sleeping places may not be limited, and once a spot is found to be safe, other criteria may add to the right choice. Future research is needed to quantify the magnitude of predation pressure for a better understanding of the importance of predation pressure for the evolution of social monogamy in gibbons.

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