Sleep, Sleeping Sites, and Sleep-Related Activities: Awakening to Their Significance

JAMES R. ANDERSON*
Department of Psychology, University of Stirling, Scotland
Laboratoire de Psychophysiologie (CNRS URA 1295), Université Louis Pasteur, Strasbourg, France

Since primates spend about half of their life at sleeping sites, knowledge of behavior in the vicinity of sleeping sites and analysis of factors influencing their use is important for understanding the diversity of primates' adaptations to their environment. The present paper reviews recent progress in the ethology and ecology of sleep in diurnal monkeys and apes. Emphasis is given to the following topics: safety from predators at sleeping sites, physical comfort, social behavior, and psychophysiology of sleep. In all cases, study at the group level and at the individual level can provide insights into behavioral adaptations. As well as increasing understanding of behavior in the wild, knowledge of sleep-related behavior can be applied with a view to improving the environment for captive primates. Am. J. Primatol. 46:63–75, 1998. © 1998 Wiley-Liss, Inc.

Key words: primates; sleeping sites; sleeping habits

INTRODUCTION

Sleep in primates is both universal and time-consuming. It may be preceded by some combination of unusually strenuous, dangerous, vigilant, or cryptic behaviors during progression to the sleeping site, and it may be followed by some other combination of such behaviors as the primates leave the sleeping site in order to start the day's subsistence activities. Despite the importance of sleep and sleeping habits, the primatological literature on these topics is remarkably fragmentary. Although many field studies provide basic data on some aspects of sleeping habits—for example, the location of sleeping sites and the range of times of retiring and resumption of daytime activities—for logistical and scientific reasons researchers have been more interested in daytime than nighttime behavioral profiles of monkeys and apes.

However, the ethology and ecology of sleep encompass several fundamental areas of behavioral biology [Anderson, 1984] (Table I). That sleep-related activities are being increasingly recognized as worthy of the interest of behavioral primatologists is illustrated by the recent growth in the number of publications with sleep or sleep-related behavior as the main topic. This trend contrasts with the sporadic interest in sleep-related topics shown throughout the 1950s and 1960s (Fig. 1). The present paper reviews recent developments in three broad

TABLE I. Ethology and Ecology of Sleep: Researchable Topics [after Anderson, 1984]

Site-relevant considerations
    Location, type, and number of sites
    Relation to social organization and ranging patterns
    Intra- and interspecific competition for and sharing of sites
    Physical characteristics (safety from predators, view, hygiene, comfort)
    The role of learning in site attachment, correlates of familiarity
    Behavior leading up to arrival and following evacuation of the site
Environmental considerations
    Season, weather (including cloud cover, moonlight, wind)
    Distance from food and water
    Presence of predators or other disturbances[a]
Individual and social considerations
    Information transfer at sites
    Settling down for the night
    Postural adaptations[a]
    Nocturnal activity[a]
    Group composition
    Subgrouping[a]
    Huddling, other social interactions[a]
    Postawakening, preleaving behavior

[a]Discussed in this review.

areas: factors influencing the selection of sleeping sites, social dynamics at sleeping sites, and psychophysiology of sleep, relating some recent studies to themes developed in Anderson [1984]. In order to set the recent findings in their historical context, I first summarize what is known from the most significant earlier (i.e., pre-1984) studies. Finally, some implications of findings relating to sleeping habits for improving the welfare of captive primates are discussed.

THE DATABASE

For the purpose of preparing the present review, two major sources were used to collate publications containing information on sleep, sleep-related activities, sleeping sites, nests, and nest building in nonhuman primates. First, a literature search was run by the Primate Information Center of the Washington Regional Primate Research Center, using the search terms *sleep, sleeping habits,* and *nest building,* for the years 1940–1995. This resulted in over 700 hits. Second, Anderson [1984] cites over 300 references, all of which refer to some aspect
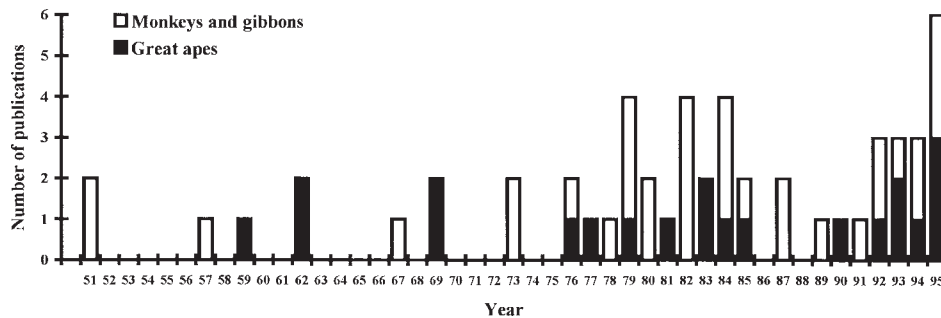

Fig. 1.   Growth of publications focusing on sleeping habits of free-moving, diurnal monkeys and apes, 1951–1995 (including nest building in great apes).

of sleeping or nesting in primates. However, the large majority of articles in these bibliographies do not address sleep-related activities as the central topic. Since the aim of the present paper was to review the most significant recent findings about sleep, articles and books in which sleep-related information is not the main focus were not considered, nor were abstracts or short commentaries. Further, focus is restricted to sleep-related events in free-moving, drug-free monkeys and apes in the wild or in captivity. This means that the following are not dealt with here: prosimians and the nocturnal monkey, *Aotus*, most physiological and all pharmacological studies of sleep, and all studies using chair restraint. Further, in the case of a series of studies by the same author or team, only one (usually the first) of the series has been taken into account. The resulting core of behavior-oriented studies of sleep in monkeys and apes (see Fig. 1) provides a solid basis for reviewing the major trends in the behavioral primatology of sleep in the second half of this century.

FACTORS INFLUENCING SELECTION OF SLEEPING SITES
Safety From Predators

Early studies. Among the factors likely to influence whether a given location may be used as a sleeping site by primates is the degree of safety it affords (e.g., reducing detectability to predators, facilitating detection of an approaching predator, or reducing accessibility for a predator). This aspect of sleeping site selection was considered in the pioneering articles by Buxton [1951] and especially Lumsden [1951] on the sleeping habits of several species of monkeys (*Colobus, Cercopithecus, Papio*) in Uganda. Although now methodologically dated, those studies obtained valuable information about the location of preferred sleeping trees, the time of settling down for the night, and the heights of sleeping positions as well as safety factors in choice of sleeping trees and positions therein. It has become standard practice to record these parameters in studies of sleep-related activities.

The importance of safety-related factors in sleeping site selection was frequently acknowledged in later studies, although it was emphasized in relatively few. Examples include a 3 week study of Guinea baboons (*Papio papio*) in eastern Senegal, in which Bert et al. [1967] recorded a preference for emergent trees at night and a tendency to take up position at some distance from the trunk, often out on terminal branches. The baboons' reluctance to flee during the night was demonstrated on one occasion when the experimenters shone lamps and created a disturbance at the base of the tree; the baboons refused to leave. Devore and Hall [1965] stated that baboons generally chose the safest places available in which to sleep. Hamilton [1982] surveyed the literature on the use of different types of sleeping site by free-ranging baboons (*Papio* sp.) and suggested that the decreasing order of preference observed (cliff faces or caves, emergent trees, closed canopy without emergent trees, open woodland) was correlated with decreasing protection against predators (especially leopards) and that this was the major determining factor in site selection. General avoidance of the trunk and major forks of an emergent kapok tree (*Ceiba pentandra*) by roosting Guinea baboons was observed by Anderson and McGrew [1984], confirming earlier observations on this species by Bert et al. [1967]. Anderson and McGrew [1984] also found that adult males were most likely to be the first members of the group to descend from the tree, an arrangement which may reduce the likelihood of a successful attack by a predator waiting around the sleeping site at dawn. For some populations, predation risk in and around sleeping sites may be considerable:

Busse [1980] described several attacks and kills by leopards at chacma baboon (*P. ursinus*) sleeping sites. Altmann and Altmann [1970] also reported finding a leopard with two dead baboons (*P. cynocephalus*) in a baboon sleeping tree. Sleeping sites may be abandoned, at least temporarily, if they have been the site of acts of predation.

The study of sleeping habits in New World monkeys gained impetus from Coimbra-Filho's [1978] description of several nest holes of *Leontopithecus rosalia*. This author suggested that the disappearance of sufficiently mature trees with appropriate cavities (i.e., big enough to permit entry of the tamarins but not predators) represented a danger to the tamarins' survival.

Some early descriptions of nests and nesting behavior by great apes also considered safety from predators as a factor influencing choice of site. Goodall [1962] reported that the Gombe chimpanzees built their night nests close to where they had been feeding in the late afternoon but that there were preferred areas, such as forest edges or trees overhanging gulleys or streams. Such locations may reduce the possibility of a successful attack by a predator. Differences in the nests of two populations of chimpanzees (Equatorial Guinea, *P. t. troglodytes,* and Senegal, *P. t. verus*) were analyzed by Baldwin et al. [1981]. The Senegalese chimpanzees' nests were higher, more open, more clumped in single trees, and more often found in larger groups. The differences were accounted for by environmental and ecological contrasts between the dense forest habitat in Equatorial Guinea and the more open woodland–savanna conditions in Senegal, with the latter site carrying a greater predation risk (i.e., a fuller complement of potential predator species).

In explaining the finding that adult female orangutans (*Pongo pygmaeus*) with dependent offspring and adolescents were more likely than adult males and non-offspring-carrying adult females to build their nests away from fruiting trees and higher in the canopy, Sugardjito [1983] considered the greater vulnerability of the first two age–sex classes to predation as the likely reason for the observed pattern.

Anderson [1984] discusses in some detail those features of sleeping sites that have been identified as influencing the likelihood of predatory attacks, including difficulty of access (e.g., height, distance from trunk, strength of supporting substrate, alternative routes), concealment (e.g., dense vegetation, other forms of cover), and degree of affordance of sensory cues (e.g., noise, vibration).

Recent studies. In the last decade or so, studies of captive and free-ranging monkeys have continued to underline the importance of predation-avoidance aspects of behavior at sleeping sites. In a study of captive groups of red-bellied tamarins (*Saguinus labiatus*), Caine [1987] found that the monkeys showed increased vigilance and made less noise in the period immediately before moving into the nest box for the night. She suggested that a combination of vigilance and cryptic behavior is advantageous for reducing the risk of predation by both diurnal and nocturnal predators. Subsequent experimental work on the same species revealed the importance of crypsis at nighttime: tamarins chose between nest boxes differing in the amount of concealment they offered [Caine et al., 1992]. More precisely, the tamarins preferred boxes that hid them from view, that were high up in the enclosure, and that provided them with overhead cover.

In a study of sleeping habits by sympatric *Saguinus mystax* and *S. fuscicollis* in northeastern Peru, Heymann [1995] also reported increased vigilance and quietness before retiring. He also confirmed the importance of concealment in the choice of sleeping sites in both species, with differences in the choice of sites between the species reflecting differences in the general ecological niche. The preference shown by tufted capuchin monkeys (*Cebus apella*) in French Guiana

for sleeping in leaves of *Jessenia* palms can also be interpreted in terms of security, as access via the trunk would be difficult for predatory cats, while leaping onto the end of a leaf would create noise and vibration [Zhang, 1995]. Choosing sleeping places that would facilitate early detection of approaching predators through noise and vibration was previously described for talapoin monkeys (*Miopithecus talapoin*) [Gautier-Hion, 1970].

The selective advantage of sleeping in trees that deny easy access routes for predators (in this case, humans) was suggested by the observations of Tenaza and Tilson [1985]. Comparing Kloss's gibbons (*Hylobates klossii*) and Mentawai langurs (*Presbytis potenziani*) on Siberut Island, these authors found that both species slept in tall emergent trees but that the gibbons used far more liana-free trees than the langurs. Langurs were killed by humans in disproportionate numbers, and hunters accessed trees via thick woody lianas. Thus, the outcome of competition for safe sleeping sites (in this case dominated by gibbons) can influence population numbers in primate communities.

Few recent studies of nesting behavior by great apes have contributed new information with regard to predation-avoidance factors, but in the first detailed account of nest building by bonobos (*Pan paniscus*) Fruth and Hohmann [1993] report that the Lomako bonobos built their nests high in the trees, presumably as an anti-predator measure [see also Goodall, 1962; Baldwin et al., 1981].

To sum up, recent observations support the established view that primates not only choose sleeping sites that are likely to afford them protection from predators but that aspects of their behavior around sleeping sites are also adapted to minimize the risk of alerting or being attacked by a predator. However, interspecies or - population comparisons of losses through predation are fraught with difficulties, including extreme variation in habitat types [Isbell, 1994], so that conclusive evidence for the preeminence of safety as a factor determining sleeping site choice for any particular group of primates will be difficult to obtain. Tenaza and Tilson's [1985] report on direct competition between two species for access to liana-free emergent trees as sleeping sites and higher mortality in the losers, through human predation, is probably the best available illustration of such a relationship.

Comfort and Hygiene

Early studies. Anderson [1984] summarized information available at the time suggesting that potential sleeping sites could be selected on the basis of physical comfort afforded (e.g., shelter from the elements, avoidance of biting insects or other disturbances). Early examples of the possible selection of sleeping sites in relation to weather conditions included groups of primates sleeping on cliff faces which are sheltered from cold winds or which retain heat absorbed during the hours of sunlight into the night (e.g., Stolz and Saayman, 1970; Boggess, 1980; Kummer et al., 1981; Anderson, 1982). Great apes may also build nests in locations likely to be sheltered from wind, to increase exposure to late evening or early morning sun, or to reduce getting soaked by rain or surface water [Goodall, 1962; Reynolds, 1965; MacKinnon, 1974]. Some authors suggested that particular sleeping sites could be chosen to avoid disturbance from other animals, such as biting insects or frugivorous bats [Rudran, 1978; Whitten, 1982]. Anderson [1984] discussed other ergonomic considerations in sleeping site selection, such as postural demands during sleep and wind sway.

Behavior patterns around sleeping sites may have significant hygienic consequences. Some primates probably reduce the chances of parasite infestation from contact with accumulated feces below their sleeping sites by, for example,

periodically shifting between sites [Hausfater and Meade, 1982] or by sleeping in locations which make contact with excreta unlikely, such as branches overhanging running water [examples in Anderson, 1984] or in emergent trees which are accessed from routes other than the base of the trunk [e.g., Anderson and McGrew, 1984]. In great apes, the possibility of infestation by ectoparasites may be reduced by the habit of constructing a new nest each night [MacKinnon, 1974].

Recent studies. Further insights into comfort- and hygiene-related factors in sleeping site selection have emerged from more recent studies of captive and free-ranging primates. For example, while favoring anti-predator factors as the major factor determining choice of sleeping boxes by captive red-bellied tamarins, Caine et al. [1992] could not rule out draft and noise reduction as potential influencing factors. Experimental confirmation of a role for these factors is awaited. Heymann [1995] pointed out that locations used most frequently for sleeping by wild *Saguinus mystax* and *S. fuscicollis*—*Jessenia* palm trees and tree hollows—provided good protection from rain and cold. The capuchin monkeys studied by Zhang [1995] also slept on *Jessenia* leaves, which the author interpreted in terms of physical comfort, the part of the leaf chosen for sleeping being flat and probably more comfortable than a rounded bough.

Interestingly, there has been a recent revival of interest in the epidemiological significance of sleeping habits [cf. Lumsden, 1951], this time with regard to malarial infection rates in New World monkeys. Davies et al. [1991] and Davies and Dye [1991] reported that infection rate correlates positively with sleeping group size when analyzed at both the species and genus levels. They suggest that potential decreases in fitness from increased pathogenic infection should be considered as a factor influencing sleeping group size. Heymann [1995] suggests that the very low infection rates in callitrichids may not be related only to these primates' small body size but also to their tendency to sleep in closed environments: sleeping in holes or dense tangles of vegetation could reduce their overall exposure to *Anopheles* mosquitoes by damping the diffusion of attractants to the insects. This hypothesis merits further attention, as does the relation between parasite risk through fecal contamination and sleep-related behavior patterns.

No new hypotheses regarding comfort or hygiene have been proposed with regard to nest building or sleeping site selection by great apes, but Tutin et al.'s [1995] suggestion that lowland gorillas (*Gorilla gorilla*) in Gabon choose nest sites to reduce the likelihood of disturbance by elephants is noteworthy. Remis [1993] raised this possibility too and considered avoidance of the damp ground in the wet season and seasonal foraging patterns as other factors likely to influence choice of nesting sites in lowland gorillas in the Central African Republic.

In summary, some recent studies have drawn attention to comfort- and hygiene-related factors associated with sleeping site selection and patterns of use in a range of primates. Perhaps more than other issues, these ones are amenable to experimental analysis in captivity through systematic variation of the physical features of potential sleeping sites [e.g., see Caine et al., 1992].

SOCIAL PROCESSES AT SLEEPING SITES
Social Dynamics and Huddles

Early studies. It was established early on that nighttime is a time of increased group cohesion for many but not all primate groups [for examples of both patterns see Anderson, 1984]. Along with predation risk and the physical structure of the site, social dynamics clearly influence the spatial relationships of group members at a sleeping site, a fact recognized early on by

Lumsden [1951]. Several social factors influence spatial arrangements at sleeping sites, including kin relations, age-related differences in sleeping partners, reproductive status, and dominance relations as well as ecological features. Increasing interest in primate social relationships during the 1970s led to several descriptions of social aspects of sleeping in free-ranging macaques: Koyama [1973] and Vessey [1973] described sleeping clusters or huddles in free-ranging bonnet (*M. radiata*) and rhesus macaques (*M. mulatta*), respectively. In both species, the most frequent huddle size was two, and huddles were composed primarily of mother–infant pairs, same-sex individuals, or male–female consortships. Even quite independent youngsters will return to sleep in contact with the mother at night [e.g., baboons: Altmann et al., 1981; gorillas: Goodall, 1979; orangutans: Horr, 1977] until independence extends to staying away from her at night and sleeping alone or with other juveniles and subadults [for examples see Anderson, 1984].

In an early study of captive, adolescent chimpanzees, Riss and Goodall [1976] reported that the group members habitually slept in close proximity or in contact with each other, with evidence of preferred sleeping partners. They suggested that cosleeping persisted due to the absence of maternal rejection, but when the chimpanzees slept indoors proximity was unavoidable due to restricted space. Some of the nighttime associations—between the older male and two females with sexual swellings—appeared to reflect temporary consortships.

The possible thermoregulatory significance of the habit of sleeping in huddles or clusters was considered by several authors, who suggested that monkeys huddled to increase warmth or to conserve body heat [e.g., Altmann, 1980; Gartlan and Brain, 1968; Suzuki, 1965; Gaulin and Gaulin, 1982]. Sleeping party size in a population of Guinea baboons varied from six to 65 (median 20–24) [Anderson and McGrew, 1984], and most of the baboons were in huddles, especially during the wet season. Also, mean huddle size was slightly greater on windy mornings than still mornings, a possible means of increasing stability on swaying boughs.

Recent studies. Sociospatial arrangements at sleeping sites continue to receive attention. Zhang [1995] noted that the broad leaves of *Jessenia* palms chosen as sleeping sites by capuchin monkeys facilitate the formation of huddles, and Chapman [1989], studying free-ranging spider monkeys (*Ateles geoffroyi*), noted that one possible consequence of having a limited number of preferred sites is that nighttime congregation of foraging subgroups was facilitated. According to Heymann [1995], nighttime huddling with other group members may improve conservation of body heat in free-ranging tamarins.

Analyses of other aspects of social processes at sleeping sites have revealed phenomena worthy of further study, such as the relationship between dominance status and the use of particular sites; this was raised by Chapman [1989], who found that dominant adult female spider monkeys were more often present at regularly used sites than subordinate females. Observations focusing on behavior around sleeping sites have been conducted on semi-free-ranging Barbary macaques (*Macaca sylvanus*) [Ansorge et al., 1992] and free-ranging olive baboons (*Papio anubis*) [Forster and Strum, 1994]. The macaques were found to change partners frequently on different nights, with juveniles especially getting involved in clusters of variable membership. Adults' preferred huddling partners were juveniles. These observations are in broad agreement with those reported for Guinea baboons [Anderson and McGrew, 1984]. In contrast, whereas in Guinea baboons nocturnal associations of adult males and females was common, adult male and female Barbary macaques did not sleep together. Anderson and McGrew [1984] suggested that Guinea baboon consortships persisted throughout the night

and that males guarded their sexual partners. A different scenario was recently depicted by Forster and Strum [1994], who considered some of the environmental and social factors that might influence a male olive baboon's decision whether to guard or relinquish a receptive female at the sleeping site. Consort turnovers at the sleeping rocks consisted of younger males taking over from older males. The authors interpreted such cases as a temporary withdrawal by the older males in order to avoid potentially dangerous fighting and maneuvering on the rocks in bad light; they sometimes resumed the consortship in the morning.

An analysis of vocalizations at sleeping sites in Barbary macaques identified increased calling rates in juveniles but not in other age–sex classes in the period between entering the sleeping tree and settling down to sleep [Hammerschmidt et al., 1994]. This dusk calling appears to be associated with juveniles' rebuffed attempts to huddle with the mother and efforts to get accepted into another sleeping cluster. Anderson and McGrew [1984] also described a tantrum by a juvenile baboon that was rejected by a pair of adults in a sleeping huddle.

There are few new accounts of social interactions in and around nests of great apes, but Fruth and Hohmann [1993] recently described social activities such as grooming and play which took place in nests of the Lomako bonobos and suggested that nest building might be an affinitive social act in this species. On the other hand, there have been some notable recent attempts to integrate knowledge about the social aspects of great ape sleeping sites into models of hominid central-place foraging and social organization. Groves and Sabater-Pi [1985] compared gorilla and chimpanzee nests from Rio Muni and included orangutan nests for a comparison of ape nests with modern hunter–gatherer campsites. Certain broad similarities emerged, such as the size and shape of the sleeping sites and the spacing of individual nests or camps. However, there were major differences in the social arrangements, with only the human camps being located around a central, communal area and only the individual human camps ("nests") being occupied by an entire nuclear family. The authors proposed that analysis of structural and functional differences in the transition from ape nest to human camps could help in the reconstruction of selective pressures acting upon hominid cognition and social organization.

Sept [1992] plotted the position of chimpanzee nests and sleeping sites around the Ishasha River, Zaire. She suggested that seasonal regularity in chimpanzees' nest sites and associated feeding remains could mean that accumulated debris as found at early archeological sites may not be indicative of hominid home bases; instead, it may reflect regular use of some sites as a result of favorable environmental or ecological conditions such as food abundance or appropriate height of canopy. This represents a challenge to archaeologists to come up with verification of the home base status of some early sites.

To sum up, it is worth restating that the analysis of social activities around sleeping sites can give additional insights into social relationships and social dynamics. Behavioral observations in association with climatic monitoring may clarify the extent to which formation of huddles is a thermoregulatory response in free-ranging primates, but this issue may be more easily addressed in captivity, where control over environmental variables is possible.

PSYCHOPHYSIOLOGY AND SLEEP AND NIGHTTIME ACTIVITY
Early Studies

There have been several studies aimed at understanding the structure or the quality of sleep of nonhuman primates on the basis of physiological mea-

sures and their ecological or social correlates. For example, electrophysiological recordings in captive Guinea baboons showed a predominance of early stage, light sleep in this species, which the authors related to the baboons' precarious nighttime positions and the need to avoid falling out of the tree during sleep. Later studies by the same authors [Bert, 1971; Bert and Pegram, 1972] described differences in the electrophysiology of sleep between closely related species of primates and between groups of the same species in different environments, in each case speculating about possible ecological correlates. Advances in biotelemetry technology allowed Reite et al. [1976] to record sleep parameters in unrestrained but captive group–living pigtail macaque (*Macaca nemestrina*) infants. In addition to obtaining normative data on the structure of infant sleep, these authors reported an interesting social influence, namely a shorter latency to sleep onset in the infants of dominant females.

Meddis [1979] drew together information on sleeping habits and physiological correlates in a range of animal species to discuss the evolution and function of sleep, including psychological theories such as memory consolidation, physiological ones such as tissue restoration and repair, and ecological ones such as the necessity of staying inconspicuous during the peak activity period of predators. In a later synthesis of information on over 150 species, electrophysiological data on the duration of sleep in 15 primate species, supplemented with sparse behavioral data (four species) were collated by Campbell and Tobler [1984]. These authors pointed out the limitations of data obtained entirely from restrained and equipment-laden subjects and called for greater use of video recording and radiotelemetry in the study of sleep.

Video recording of nighttime activity is indeed a tool of considerable potential. Todt et al. [1982] used video recording at very low light levels and found considerable nocturnal activity and locomotion in captive group–reared spot-nosed monkeys (*Cercopithecus petaurista*), including in an infant as young as 2 weeks of age. Erffmeyer [1982] studied videotapes of individually and pair-housed adult rhesus macaques (*Macaca mulatta*) and reported that nocturnal sleep occurred exclusively in a sitting position.

Recent Studies

Further advances in electrophysiological monitoring techniques have revealed that peer-reared juvenile macaques' sleep shows a number of differences to that of their mother- and group-reared counterparts, including more frequent periods of arousal and a relative predominance of slow wave, non-REM sleep. Kaemingk and Reite [1987] interpret the poorer quality of the peer-reared juveniles' sleep as being due to the absence of the stable and controlling influence of the mother. The transition from sleeping in close contact with the mother to sleeping with others is probably a period of decreased security for the juvenile primate, which may be accompanied by tantrums at the sleeping site, as observed in free-ranging primates [e.g., Anderson and McGrew, 1984].

Surprisingly, videotape as a method of observing nighttime activity has not gained much in popularity in recent years. However, Muñoz-Delgado et al. [1995] recently presented preliminary observations taken from nighttime video recordings of a captive group of *Macaca arctoides,* confirming the viability of the method for identifying individual subjects and a range of nocturnal behaviors and postures.

In an original appreciation of the ecology and ethology of sleep, McKenna et al. [1993] have looked at human parent–infant cosleeping and infant isolation sleeping from a comparative evolutionary perspective and in relation to the prob-

lem of sudden infant death syndrome. Most of the nonhuman primate evidence included comes from studies of the regulatory role of the mother in the infant's physiological adaptation (including sleep structure) and the effects of involuntary separation in macaques and squirrel monkeys (*Saimiri sciureus*). McKenna et al. [1993] did not include great ape cosleeping patterns in their review. However, for several reasons related to phylogenetic and behavioral similarities (e.g., the adoption of lying postures for sleeping), it seems reasonable to suggest that the great apes might offer a more appropriate model for human parent–infant cosleeping.

In summary, advances in telemetry are likely to lead to an increase in studies of the relationships between physiological processes and behavioral aspects of sleep. Video remains an underused tool for analyzing nocturnal behavior in diurnal primates. Detailed descriptions of behavioral adjustments by cosleeping mother–infant pairs of great apes would be particularly welcome, not least in view of the potential implications of such work for an evolutionary perspective on the development of sleep patterns in humans.

TOWARD AN APPLIED ETHOLOGY OF SLEEP

Behavioral primatologists have understandably been more interested in the daytime activities of diurnal primates than in nocturnal behavior. The same can be said of those responsible for maintaining and improving the environment of captive monkeys and apes. The literature on environmental enrichment for captive primates is replete with devices and structures aimed at reducing daytime boredom and increasing activity [Segal, 1989; Reinhardt and Roberts, 1997] and with recommendations for promoting expression of social behavioral repertoires [Visalberghi and Anderson, 1993; Reinhardt et al., 1995]. However, in view of the manifest importance of sleeping site selection processes (and, for the great apes, sleeping site preparation) in primates, it is clear that sleeping facilities have been unduly neglected in considerations of welfare [for a plea for research efforts devoted to guiding sleeping site provision see Maple and Perkins, 1996]. Typically, for most captive primates, simple perches or elevated shelves are provided, while for others a simple nest box may be fixed to one wall. The perches or shelves are usually constructed to be easily cleaned, while the nest box is usually located so that technicians can conveniently manipulate it—for example, to remove it prior to cleaning the cage.

Although the structures provided as sleeping sites may be used as such by primates, this does not mean that they are good. Yet, as illustrated by the experiment conducted by Caine et al. [1992], it should be possible, by systematically varying physical features including height, the location in the cage or enclosure, materials, the amount of concealment offered, and the degree of protection from the elements, to arrive at sleeping arrangements which seem best suited to particular groups of primates.

CONCLUSIONS

1. Sleep and sleeping habits are important aspects of the behavioral biology of primates. Their study can give insights into how individuals and species adapt to problems such as avoiding predation, staying healthy, and dealing with social relationships.

2. Information on primate sleeping habits can be usefully integrated into wider accounts of ecological adaptation and the evolution of human behavior.

3. There is a need for more information on almost all aspects of sleeping

habits in primates in natural environments. Video recording has been underused as a noninvasive method of obtaining information about the nocturnal behavior of captive and free-ranging primates.

4. Sleeping habits should be given more attention by those involved with captive primates—for example, with regard to preferences for sleeping and social arrangements. It seems clear that increased knowledge of such an important aspect of primate biology could lead to improvements in the welfare of captive primates.

ACKNOWLEDGMENTS

REFERENCES

Altmann, J. BABOON MOTHERS AND INFANTS. Cambridge, MA, Harvard University Press, 1980.

Altmann, J; Altmann, S.A.; Hansfater, G. Physical maturation and age estimates of yellow baboons, *Papio cynocephalus*, in Amboseli National Park, Kenya. AMERICAN JOURNAL OF PRIMATOLOGY 1: 389–399, 1981.

Altmann, S.A.; Altmann, J. BABOON ECOLOGY. Basel, Karger, 1970.

Anderson, C.O. Baboons below the Tropic of Capricorn. JOURNAL OF HUMAN EVOLUTION 11:205–217, 1982.

Anderson, J.R. Ethology and ecology of sleep in monkeys and apes. ADVANCES IN THE STUDY OF BEHAVIOR 14:156–229, 1984.

Anderson, J.R.; McGrew, W.C. Guinea baboons (*Papio papio*) at a sleeping site. AMERICAN JOURNAL OF PRIMATOLOGY 6:1–14, 1984.

Ansorge, V.; Hammerschmidt, K.; Todt, D. Communal roosting and formation of sleeping clusters in Barbary macaques (*Macaca sylvanus*). AMERICAN JOURNAL OF PRIMATOLOGY 28:271–280, 1992.

Baldwin, P.J.; Sabater Pi, J.; McGrew, W.C.; Tutin, C.E.G. Comparisons of nests made by different populations of chimpanzees (*Pan troglodytes*). PRIMATES 22:474–486, 1981.

Bert, J. Sleep in primates: A review of various results. Pp. 308–315 in MEDICAL PRIMATOLOGY 1970. E.I. Goldsmith; J. Moor-Jankowski, eds. Basel, Karger, 1971.

Bert, J.; Pegram, V. Sleep and environment. Pp. 244–249 in MEDICAL PRIMATOLOGY 1972, PART II. E.I. Goldsmith; J. Moor-Jankowski, eds. Basel, Karger, 1972.

Bert, J.; Ayats, H.; Martino, A.; Collomb, H. Le sommeil nocturne chez le babouin *Papio papio:* Observations en milieu naturel et données électrophysiologiques. FOLIA PRIMATOLOGICA 6:28–43, 1967.

Boggess, J. Intermale relations and troop male membership changes in langurs (*Presbytis entellus*) in Nepal. INTERNATIONAL JOURNAL OF PRIMATOLOGY 1:233–274, 1980.

Busse, C. Leopard and lion predation upon chacma baboons living in the Moremi Wildlife Reserve. BOTSAWNA NOTES AND RECORDS 12:15–21, 1980.

Buxton, A.P. Further observations of the night-resting habits of monkeys in a small area on the edge of the Semliki Forest, Uganda. JOURNAL OF ANIMAL ECOLOGY 20:31–32, 1951.

Caine, N.G. Vigilance, vocalizations, and cryptic behavior at retirement in captive groups of red-bellied tamarins (*Saguinus labiatus*). AMERICAN JOURNAL OF PRIMATOLOGY 12:241–250, 1987.

Caine, N.G.; Potter, M.P.; Mayer, K.E. Sleeping site selection by captive tamarins (*Saguinus labiatus*). ETHOLOGY 90:63–71, 1992.

Campbell, S.S.; Tobler, I. Animals sleep: A review of sleep duration across phylogeny. NEUROSCIENCE AND BIOBEHAVIORAL REVIEWS 8:269–300, 1984.

Chapman, C.A. Spider monkey sleeping sites: Use and availability. AMERICAN JOURNAL OF PRIMATOLOGY 18:53–60, 1989.

Coimbra-Filho, A.F. Natural shelters of *Leontopithecus rosalia* and some ecological implications. Pp. 79–89 in THE BIOLOGY AND CONSERVATION OF THE CALLITRICHIDAE. D.G. Kleiman, ed. Washington, DC, Smithsonian Institution Press, 1978.

Davies, C.R.; Dye, C.M. Malaria infection rate of Amazonian monkeys increases with sleeping group size. BRITISH ECOLOGICAL SOCIETY BULLETIN 22:39–44, 1991.

Davies, C.R.; Ayres, J.M.; Dye, C.; Deane, L.M. Malaria infection rate of Amazonian

primates increases with body weight and group size. FUNCTIONAL ECOLOGY 5:655–662, 1991.

DeVore, I.; Hall, K.R.L. Baboon ecology. Pp. 20–52 in PRIMATE BEHAVIOR: FIELD STUDIES OF MONKEYS AND APES. I. DeVore, ed. New York, Holt, 1965.

Erffmeyer, E.S. The nocturnal behavior of caged rhesus monkeys (*Macaca mulatta*). FOLIA PRIMATOLOGICA 38:240–249, 1982.

Forster, D.; Strum, S.C. Sleeping near the enemy: Patterns of sexual competition in baboons. Pp. 19–25 in CURRENT PRIMATOLOGY, VOL. 2: SOCIAL DEVELOPMENT, LEARNING AND BEHAVIOUR. J.J. Roeder; B. Thierry; J.R. Anderson; N. Herrenschmidt, eds. Strasbourg, Université Louis Pasteur, 1994.

Fruth, B.; Hohmann, G. Ecological and behavioral aspects of nest building in wild bonobos (*Pan paniscus*). ETHOLOGY 94: 113–126, 1993.

Ganlin, S.J.C.; Ganlin, C.K. Behavioral ecology of *Alouatta seniculus* in Andean cloud forest. INTERNATIONAL JOURNAL OF PRIMATOLOGY 3:1–32, 1982.

Gartlan, J.S.; Brain, C.K. Ecology and social variability in *Cercopithecus aethiops* and *C. mitis*. Pp. 253–292 in PRIMATES: STUDIES IN ADAPTATION AND VARIABILITY. P.C. Jay, ed. New York, Holt, 1968.

Gautier-Hion, A. L'organisation sociale d'une bande de talapoins (*Miopithecus talapoin*) dans le nord-est du Gabon. FOLIA PRIMATOLOGICA 12:116–141, 1970.

Goodall, A. THE WANDERING GORILLAS. London, Collins, 1979.

Goodall, J. Nest building behavior in the free ranging chimpanzee. ANNALS OF THE NEW YORK ACADEMY OF SCIENCES 102:455–467, 1962.

Groves, C.P.; Sabater Pi, J. From ape's nest to human fix-point. MAN (N.S.) 20:22–47, 1985.

Hamilton, W.J., III. Baboon sleeping site preferences and relationships to primate grouping patterns. AMERICAN JOURNAL OF PRIMATOLOGY 3:41–53, 1982.

Hammerschmidt, K.; Ansorge, V.; Fischer, J.; Todt, D. Dusk calling in Barbary macaques (*Macaca sylvanus*): Demand for social shelter. AMERICAN JOURNAL OF PRIMATOLOGY 32:277–289, 1994.

Hausfater, G., Meade, B.J. Alternation of sleeping groves by yellow baboons (*Papio cyncocephalus*) as a strategy for parasite avoidance. PRIMATES 23:287–297, 1982.

Heymann, E.W. Sleeping habits of tamarins, *Saguinus mystax* and *Saguinus fuscicollis* (Mammalia; Primates; Callitrichidae), in north-eastern Peru. JOURNAL OF ZOOLOGY, LONDON 237:211–226, 1995.

Horr, D.A. Orangutan maturation: Growing up in a female world. Pp. 289–321 in PRIMATE BIO-SOCIAL DEVELOPMENT. S. Chevalier-Skolnikoff and F.E. Poirier, eds. New York, Garland, 1977.

Isbell, L.A. Predation on primates: Ecological patterns and evolutionary consequences. EVOLUTIONARY ANTHROPOLOGY 61–71, 1994.

Kaemingk, C.; Reite, M. Social environment and nocturnal sleep: Studies in peer-reared monkeys. SLEEP 10:542–550, 1987.

Koyama, N. Dominance, grooming, and clasped-sleeping relationships among bonnet monkeys in India. PRIMATES 14:225–244, 1973.

Kummer, H.; Banaja, A.A.; Abo-Khatwa, A.N.; Ghandour, A.M. Mammals of Saudi Arabia: Primates: A survey of Hamadryas baboons in Saudi Arabia. FAUNA OF SAUDI ARABIA 3:441–471, 1981.

Lumsden, W.H.R. The night-resting habits of monkeys in a small area on the edge of the Semliki Forest, Uganda. A study in relation to the epidemiology of Sylvan yellow fever. JOURNAL OF ANIMAL ECOLOGY 20:11–30, 1951.

MacKinnon, J. The behaviour and ecology of wild orang-utans (*Pongo pygmaeus*). ANIMAL BEHAVIOUR 22:3–74, 1974.

Maple, T.L.; Perkins, L.A. Enclosure furnishings and structural environmental enrichment. Pp. 212–222 in WILD MAMMALS IN CAPTIVITY: PRINCIPLES AND TECHNIQUES. D.G. Kleiman et al., eds. Chicago, University of Chicago Press, 1996.

McKenna, J.J.; Thoman, E.B.; Anders, T.F.; Sadeh, A.; Schechtman, V.L.; Glotzbach, S.F. Infant-parent co-sleeping in an evolutionary perspective: Implications for understanding infant sleep development and the sudden infant death syndrome. SLEEP 16:263–282, 1993.

Meddis, R. The evolution and function of sleep. Pp. 99–25 in BRAIN, BEHAVIOUR AND EVOLUTION. D.A. Oakley; H.C. Plotkin, eds. London, Methuen, 1979.

Muñoz-Delgado, J.; Luna-Villegas, G.; Mondragón-Ceballos, R.; Fernández-Guardiola, A. Behavioral characterization of sleep in stumptail macaques (*Macaca arctoides*) in exterior captivity by means of high-sensitivity videorecording. AMERICAN JOURNAL OF PRIMATOLOGY 36:245–249, 1995.

Reinhardt, V.; Roberts, A. Effective feeding enrichment for non-human primates: A brief review. ANIMAL WELFARE 6:265–272, 1997.

Reinhardt, V.; Liss, C.; Stevens, C. Social housing of previously single-caged macaques: What are the options and the risks? ANIMAL WELFARE 4:307–328, 1995.

Reite, M.; Stynes, A.J.; Vaughn, L.; Pauley, J.D.; Short, R.A. Sleep in infant monkeys: Normal values and behavioral correlates. PHYSIOLOGY AND BEHAVIOR 16:245–251, 1976.

Remis, M.J. Nesting behavior of lowland gorillas in the Dzanga-Sangha Reserve, Central African Republic: Implications for population estimates and understandings of group dynamics. TROPICS 2:245–255, 1993.

Reynolds, V. BUDONGO: A FOREST AND ITS CHIMPANZEES. London, Methuen, 1965.

Rudran, R. Socioecology of the blue monkeys (*Cercopithecus mitis stuhlmanni*) of the Kibale Forest. SMITHSONIAN CONTRIBUTIONS TO ZOOLOGY No. 249, 1978.

Segal, E.F. HOUSING, CARE AND PSYCHOLOGICAL WELLBEING OF CAPTIVE AND LABORATORY PRIMATES. Park Ridge, NJ, Noyes Publications, 1989.

Sept, J.M. Was there no place like home? A new perspective on early hominid archaeological sites from the mapping of chimpanzee nests. CURRENT ANTHROPOLOGY 33:187–207, 1992.

Stolz, L.P.; Saayman, G.S. Ecology and behaviour of baboons in the northern Transvaal. ANNALS OF THE TRANSVAAL MUSEUM 26:99–143, 1970.

Sugardjito, J. Selecting nest-sites of Sumatran orang-utans, *Pongo pygmaeus abelii* in the Gunung Leuser National Park, Indonesia. PRIMATES 24:467–474, 1983.

Suzuki, A. An ecological study of wild Japanese monkeys in snowy areas—focused on their food habits. PRIMATES 10: 103–148, 1965.

Tenaza, R.; Tilson, R.L. Human predation and Kloss's gibbons (*Hylobates klossii*) sleeping trees in Siberut Island, Indonesia. AMERICAN JOURNAL OF PRIMATOLOGY 8:299–308, 1985.

Todt, D.; Bruser, E.; Hultsch, H.; Lange, R. Nocturnal actions and interactions of newborn monkeys. JOURNAL OF HUMAN EVOLUTION 11:383–389, 1982.

Tutin, C.E.G.; Parnell, R.J.; White, L.J.T.; Fernandez, M. Nest building by lowland gorillas in the Lopé Reserve, Gabon: Environmental influences and implications for censusing. INTERNATIONAL JOURNAL OF PRIMATOLOGY 16:53–76, 1995.

Vessey, S.H. Night observations of free-ranging rhesus monkeys. AMERICAN JOURNAL OF PHYSICAL ANTHROPOLOGY 38:613–620, 1973.

Visalberghi, E.; Anderson, J.R. Reasons and risks associated with manipulating captive primates' social environments. ANIMAL WELFARE 2:3–15, 1993.

Whitten, A.J. The role of ants in selection of night trees by gibbons. BIOTROPICA 14:237–238, 1982.

Zhang, S.-Y. Sleeping habits of brown capuchin monkeys (*Cebus apella*) in French Guiana. AMERICAN JOURNAL OF PRIMATOLOGY 36:327–335, 1995.