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Behavioral sleep in captive owl monkey (*Aotus azarae*) and squirrel monkey (*Saimiri boliviensis*)

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The objective of this study was to test the hypothesis that activity-behavioral sleep parameters differ between nocturnally-active owl monkeys and diurnally-active squirrel monkeys which are sympatric and of Bolivian origin. The total sleep time (TST) and sleep episode length (SEL) of 7 adult owl monkey siblings and 4 adult squirrel monkeys were quantitated by actigraphy for 7 days under captive conditions. The higher TST/24 h values and longer SEL/12 h quiescent phase quantitated for owl monkeys in comparison to that of squirrel monkeys clearly indicate that the behavioral sleep is markedly different between these two groups, though they are sympatric in wild. Significant differences noted in the sleep architecture between squirrel monkeys and owl monkeys can be attributed to the influences in the selected sleep niche, threat perception from predators, and disturbances from natural elements (especially rain) in the natural habitat.

Key words: actigraphy, behavioral sleep, Cebidae, Neotropical, nocturnality, vigilance

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INTRODUCTION

The cavalier and sometimes overlapping use of terms such as "sleep", "rest" and "drowsiness" in the past for reporting a continuum of sleep process prevalent among various mammals have produced confusion among sleep researchers. Thus to formulate a consensus, in a review of over 200 studies reporting the sleep or rest durations of more than 150 animal species, Campbell and Tobler (1984) had distinguished two categories of sleep. These are: (1) behavioral sleep, signifying quantitation by behavioral observations, and (2) electrographic sleep, signifying quantitation by electrographic recordings.

With the exception of a handful of studies, interspecies comparison on sleep parameters among non-human primates using the same methodological protocol have been sparse at best. Even what information available now are limited to comparison of sleep behavior and sleep quantitation among diurnally-active primates (Bert and Pegram 1969, Bert et al. 1970, 1972, Bert 1973, Ramakrishnan and Coss 2001, Zhdanova et al. 2002). This is understandable because the owl monkey (*Aotus* species) is the only nocturnally-active simian primate, and it is our view that majority of the primatology laboratories (beyond the South America) which maintain captive colonies of diurnally-active simian primates do not have either the luxury or research focus in keeping owl monkeys in their roster.

In the wild, owl monkeys preferentially sleep in the holes of tree trunks, entanglements of climbers and among dense foliage during the daytime, on average at 10-20 meters above the ground level (Moynihan 1964, Aquino and Encarnacion 1986, 1994, Garcia and Braza 1993, Puertas et al. 1995). This preferential niche also has made it difficult to quantitate owl monkey's sleep in the field. The sleeping heights of owl monkeys in their forest niches also vary between the species. While *Aotus trivirgatus* individuals slept ~28 m above ground (Wright 1989), *Aotus azarae* individuals were recorded as sleeping 9 m above ground (Garcia and Braza 1993).

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Due to its small physical frame, proportionally large brain and consolidated circadian sleep pattern similar to that of humans, diurnally-active squirrel monkeys (*Saimiri* species) have been widely popular as an experimental primate model since the 1950s for research in aerospace medicine, neurophysiology, behavioral pharmacology and sleep (Carmichael and MacLean 1961, Ploog et al. 1963, Rosenblum and Cooper 1968, Kaplan 1977, Klerman et al. 1999, Abee 2000). In some South American zones, squirrel monkeys are sympatric with owl monkeys. The similarities and differences in the colony ecology of *A. azarae* and *S. boliviensis* in the wild are summarized in Table I.

In the past decade, due to its perceived merits in comparison to polysomnography, actigraphy has gained acceptance as an alternate sleep quantitation method in human subjects (Lockley et al. 1999, Kushida et al. 2001, Ancoli-Israel et al. 2003, So et al. 2007). However, the use of actigraphy for sleep quantitation of non-human primates has been limited so far (Sri Kantha and Suzuki 2006a). Towards the objective of comparing behavioral sleep using actigraphy, we initiated behavioral sleep quantitation in captive *A. azarae* owl monkeys and three other captive Neotropical primates species including squirrel monkeys in 2002, and have reported on two sleep parameters namely, total sleep time (TST) and sleep episode length (SEL) (Sri Kantha and Suzuki 2006a,b, Suzuki and Sri Kantha 2006). Our objective in this study was to test the hypothesis that, despite a captive research setting and sympatry in nature, nocturnally-active owl monkeys and diurnally-active squirrel monkeys will exhibit differences in their TST and SEL because these primates have been exposed historically to different predation risks.

Table I

Similarities and differences in the biological characteristics of *Aotus azarae* and *Saimiri boliviensis* in the wild

Characteristics	Owl Monkey (*Aotus azarae*)	Squirrel Monkey (*Saimiri boliviensis*)
Natural range	Bolivia, Paraguay, northern zone of Argentina[1]	Bolivia and Peru[1]
Body weight range (Kg)	♂ 0.825–1.05 ♀ 0.780–1.11	♂ 0.963–1.088[1] ♀ 0.70–0.90[1]
Sexual dimorphism	absent[1]	present[1]
Activity-Habitat	nocturnal-arboreal[1]	diurnal-arboreal[1]
Family group	monogamous[1]	multi-male multi-female group[1]
Group size	2–5 (median 3)[1]	30–60[2]
Diet pattern	omnivorous[1] (fruits 65–75%, leaves 5–30%, and insects 5–20%)	omnivorous[1] (insects ~82%, and fruits and seeds ~18%)
Sleep/rest location	relatively protected within tree holes[3]	relatively unprotected; in branches suitable to hold the monkey's weight and sleep related body maneuvers[4]

[1] Rowe (1996)
[2] Terborgh (1983), Boinski et al. (2003)
[3] Garcia and Braza (1993)
[4] Du Mond (1968), Boinski et al. (2003)

METHODS

Subjects and housing

Seven adult owl monkeys (*Aotus azarae*) and four adult squirrel squirrel monkeys (*Saimiri boliviensis*), both of Bolivian origin and reared at the Kyoto University's Primate Research Institute (PRI) facility, were the subjects of this study (Table II). All seven owl monkeys were siblings born to a single mating pair, namely At 28 male and At 34 female, whose activity-sleep parameters had been quantitated by us previously (Sri Kantha and Suzuki 2006b, Suzuki and Sri Kantha 2006). These owl monkeys were housed in individual stainless steel cages (100 × 70 × 60 cm). The *Aotus* colony room was maintained on a shifted, alternating 12 h light (11:00 PM – 11:00 AM; 200 lux): 12 h dark (11:00 AM – 11:00 PM; 0.01–0.5 lux) cycle (Erkert 1989).

The squirrel monkey colony room with its group cage, which has an open access to a sun room, has been described previously by us (Sri Kantha and Suzuki 2006a). Briefly, the colony room was maintained on an alternating 12 h light (06:00 AM– 06:00 PM; 440 lux) and 12 h dark (06:00 PM – 06:00 AM; 0.01–0.5 lux) cycle. Among the four squirrel monkeys, three (Ss 114, Ss 116 and Ss 117) were kins; Ss 116 and Ss 117 were the progeny of Ss 114. The fourth monkey Ss 115 do not share a blood link with the other three monkeys. During the experimental period, the monkeys were observed to sleep in the group cage, in preference to the sun room. Sleep quantitation on two older male squirrel monkeys (Ss 114 and Ss 115) for 3 nights was reported by us (Sri Kantha and Suzuki 2006a), when the natural daylight extended to 14 h and the dark phase of the observation period was 10 h. In this study, data was collected when the natural daylight was shortened to 11 h and the dark phase of the observation period was approximately 13 h. The lighting condition of the rearing rooms was routinely checked by an illuminance meter (TopCon IM-5, Tokyo). Food and water were available to the monkeys ad libitum, and commercial pellet diet for New World Monkeys (25.1 g protein and 10.6 g lipid/100 g diet; Oriental Yeast Co., Tokyo) was supplemented daily with fresh fruits and twice-weekly with meal worms. All monkeys used in the experiments were cared for in accordance to the Guide for the Care and Use of Laboratory Animals published by the US National Academy of Press and according to the Kyoto University Primate Research Institute's (KUPRI) Guidelines for the Care and Use of Laboratory Primates. The experiments had the approval from the Research Committee of the KUPRI.

Behavioral sleep quantitation by actigraphy

The activity-sleep patterns of the monkeys were monitored *via* actigraphy (Actiwatch AW 64 model-MINIMITTER, Mini Mitter Company, Bend, Oregon, USA; containing 64KB of on-board memory) for seven consecutive days, as described previously by us (Sri Kantha and Suzuki 2006a,b, Suzuki and Sri Kantha 2006, Sri Kantha et al. 2007). Briefly, the actiwatch (weighing 17 g), pre-set to collect activity-rest data of individual monkey with a sampling rate of 32 Hz and a sampling epoch of one minute, was suspended in an elastic band, and positioned on monkey's neck following anesthesia with ketamine HCl.

For each of the owl monkey and squirrel monkey, data on daily TST, sleep episode length (SEL) and activity-rest behavior were collected for 7 days, before removal of actiwatch from monkey's neck. As per the operational definition of sleep in actigraphy, in the absence of any force made by the subject which exceed 10 mg in any direction during the measuring period (counted as epoch of 1 min duration), the animal was assumed to be at rest (equated to behavioral sleep).

The definitions for the three parameters measured, as applied according to the Actiwatch AW 64 manufacturer's instructions were:

(1) Activity Count: a mean number for 24 hours, an instrument-specific arbitrary unit (AU), quantifying primate activity computed from any omni-directional motion made by the caged monkey. Activity counts may not reflect the absolute activity of the monkey in concrete terms, but if monkeys in the same experiment wore the same brand of actiwatches from the same commercial supplier, they provide a relative measure of comparison on the activity. (2) TST: a cumulative time count (in minutes) for a continuous 24-hour circadian cycle, and equated to behavioral sleep. (3) SEL: the mean length of blocks of continuous sleep (in minutes) falling between two waking bouts. For nocturnal owl monkey, SEL was measured in a 12 h light phase of the 24 h circadian cycle. For diurnal squirrel monkey, SEL was measured in a 12 h dark phase of the 24 h circadian cycle.

Statistical analyses

Data obtained for owl monkey and squirrel monkey groups were analyzed by two tailed Student's *t*-test for independent means for any statistically significant differences. Statistical computations were performed using STATISTICA software (StatSoft.Inc., Oklahoma, USA).

RESULTS

Quantitated behavioral sleep-activity data of each of the seven owl monkeys and four squirrel monkeys for 7 consecutive days, are presented in Table II. While the daily activity levels of the owl monkeys, as indicated by the range in the mean Actiwatch (AW) activity counts, ranged between 140 ± 54 AU and 203 ± 88 AU, that of squirrel monkeys ranged between 137 ± 34 AU and 230 ± 31 AU. The quantitated daily TST of owl monkeys ranged between 529 ± 59 min and 693 ± 48 min, while the daily TST of squirrel monkeys ranged between 90 ± 88 min and 462 ± 87 min. Whereas the quantitated SEL during the 12 h light phase for owl monkeys ranged between 22 ± 5 min and 70 ± 25 min respectively, the same sleep parameter measured during the 12 h dark phase for squirrel monkeys ranged between 6 ± 2 min and 13 ± 4 min respectively.

Table III provides a statistical comparison of activity-behavioral sleep measurements between the owl monkeys and the squirrel monkeys. The two species of primates differed reliably in their mean TST/24 h [*t*(df 75)=9.564, *P*<0.01], and SEL during the pertinent 12 h quiescent phase [*t*(df 75)=6.872, *P*<0.01]. However, no statistically significant difference was noted in the daily mean activity counts between the owl monkeys and squirrel monkeys. The owl monkeys exhibited a much higher TST/24 h mean of 606 ± 93 min compared with a mean of 287 ± 200 min for the squirrel monkeys. Owl monkeys also exhibited a longer SEL/12 h quiescent phase (mean = 46 ± 28 min) compared with the squirrel monkeys (mean = 9 ± 5 min). It is reasonable to assert that these statistically significant mean differences might reflect the manner in which each species in the wild cope with daytime and nighttime predators as well as disturbances from natural elements (especially rain).

DISCUSSION

The activity-sleep profile of two of the four squirrel monkeys used in this study, namely Ss 114 and Ss 115, have been studied previously by us (Sri Kantha and Suzuki 2006a) and reported under the species name *Saimiri sciureus*. This was based on the Thorington classification, where the squirrel monkeys of Bolivian origin is assigned the status of Bolivian subtype of *Saimiri sciureus* (Thorington 1985). Subsequently, based on the prominently visible circumocular patch of Roman arch type, we have re-assigned the taxonomic status of these two squirrel monkeys (Ss 114 and Ss 115) as well their junior group mates Ss 116 and Ss 117, to *Saimiri boliviensis* species, as per Hershkovitz designation (Hershkovitz 1984).

All seven owl monkeys used in this study were siblings and three of the four squirrel monkeys (of which two were siblings) share a blood kinship. This design was specifically chosen to reduce genetic variation among experimental monkeys and is considered as a preferable protocol among nonhuman primate study design (VandeBerg and Williams-Blangero 1996). We infer that the results obtained by this protocol have comparatively less non-favorable influence on the parameters measured. Furthermore, it is also presumed that the influence of diet consumed by both owl monkeys and squirrel monkeys during the experimental session is insignificant on the measured parameters for two reasons. First, both groups are omnivorous in the wild (Table I). Secondly, both groups were fed ad libitum with commercial pellet diet supplemented daily with fresh fruits and twice-weekly with meal worms. As presented in Table III, the mean TST value of 10 h and 6 min obtained for owl monkeys was reliably higher than the mean TST value of nearly 4 h and 47 min measured for squirrel monkeys. Previous reports on the TST of adult squirrel monkeys, based on short-duration polysomnography (PSG) measurements lasting between 12–24 h recordings, provide a noticeably longer mean TST values such as 5 h 29 min (*n*=11; Breton et al. 1986), 8 h 54 min (*n*=5; Edgar et al. 1993), 9 h 36 min (*n*=4; Wexler and Moore-Ede 1985) and 9 h 53 min (*n*=3; Adams and Barratt 1974). It should be noted that, in all these previous determinations, due to restraints in PSG experimental protocol, the TST measurements were quantitated by isolating the monkey in individual cages. Compared with this restraining setup, the TST measurements obtained in the present

Table II

Total sleep time (TST), sleep episode length (SEL) and daily activity of owl monkey and squirrel monkey subjects

Monkey ID number and sex	Age (years)	Weight (kg)	Measured sleep-activity parameters		
			TST/24 h (min)	SEL/12 h (min)	Mean activity counts (Arbitrary units)
Owl Monkey					
Aa 43 ♀	9	1.135	628 ± 60	70 ± 25	157 ± 35
Aa 44 ♂	8	1.147	683 ± 47	48 ± 15	168 ± 21
Aa 46 ♀	7	1.024	551 ± 69	65 ± 54	140 ± 54
Aa 47 ♂	6	1.269	529 ± 59	22 ± 5	152 ± 15
Aa 48 ♂	5	1.061	693 ± 48	43 ± 11	178 ± 25
Aa 49 ♂	5	0.992	591 ± 51	30 ± 11	185 ± 61
Aa 52 ♂	3	1.039	570 ± 149	41 ± 10	203 ± 88
Squirrel Monkey					
Ss 114 ♂	14	1.137	331 ± 207	10 ± 4	137 ± 34
Ss 115 ♂	14	0.871	263 ± 193	7 ± 4	200 ± 33
Ss 116 ♀	7	0.889	462 ± 87	13 ± 4	230 ± 31
Ss 117 ♂	7	1.199	90 ± 88	6 ± 2	198 ± 57

study of squirrel monkeys, under the conditions of communal group cage with access to a sun-room and no restriction on movements, appear more in tune with the wild milieu. Wider variation in the TST values reported for squirrel monkeys derived from PSG measurements could also be attributed to the non-uniform selection of electroencephalographic recording sites in the brain regions and the use of different reference electrodes (Kleinlogel 1983).

The SEL/12h quiescent phase also differed significantly between owl monkeys and squirrel monkeys (46 ± 28 min vs. 9 ± 5 min $P<0.01$). The mean SEL/12 h light phase of 46 min for the seven adult owl monkeys measured in this study is consistent with the mean SEL values reported previously by us for the mother and grandmother of these monkeys (Suzuki and Sri Kantha 2006). Similarly, the mean SEL/12 h dark phase of 9 min for the four squirrel monkeys confirms our previous report (Sri Kantha and Suzuki 2006a). Because smaller groups of nocturnal owl monkeys sleep within tree holes and vine tangles during the day and are thus more protected from avian predators, such as hawks and eagles, they can likely afford a longer, less vigilant SEL.

Conversely, larger groups of diurnal squirrel monkeys would need to limit their SEL to a shorter duration because they sleep in trees at night with more open canopy in which they are more vulnerable to

Table III

Comparison of group mean variation in behavioral sleep-activity parameters between owl monkeys and squirrel monkeys

Parameter	Owl Monkey	Squirrel Monkey	*t*-test (*P*)
TST/24 h (min)	606 ± 93	287 ± 200	<0.01
SEL/12 h quiescent phase (min)	46 ± 28	9 ± 5	<0.01
Mean activity count (AU)	169 ± 51	188 ± 50	N.S.

nocturnal predators, such as felids and owls. Thus it may not be an exaggeration to infer that the shorter SEL duration in the squirrel monkeys is a premium contributed to vigilance behavior which aids in group coherence and group survival against predation risk (DuMond 1968, Caine and Marra 1988, Biben et al. 1989, Boinski et al. 2003).

Field reports on the predation risks (or mortality rate) during sleep are available for squirrel monkeys, but unavailable for owl monkeys. Isbell (1994) had summarized four adaptations as crucial for squirrel monkeys to escape from predation. These include, flight from scene of attack, vigilance, polyspecific associations and birth synchrony within groups. Among these four, flight from scene of attack was based on direct observation. While vigilance and polyspecific associations were inferred, birth synchrony within groups have been suggested (Boinski 1987). That the inferences gathered from whatever reports available on the group-size effect on vigilance shown by squirrel monkeys during their active phase are somewhat compromised by the idiosyncratic sampling rules, varying definitions of vigilance and unidentical experimental designs deserve notice as well (Treves 2000). It could be argued that to avoid predation, squirrel monkeys may select fine branch setting for sleep in the canopy, which causes the necessity for them to securely hold their body posture from falling down while they are sleeping. That the sleeping habit of squirrel monkeys is open, but that of owl monkey is closed has been attested unequivocally (Nunn and Heymann 2005). This proposition that the monkey's space preference during sleeping is influenced by the maintenance of its vigilance-linked posture and sleep parameter such as SEL also deserves additional experimental verification.

Despite its practical merits, one notable limitation in using actigraphy exclusively for sleep quantitation is that non-rapid eye movement (non-REM) and rapid eye movement (REM) sleep states were not available for species comparisons. The duration of REM sleep in owl monkey belonging to a different species (*A. trivirgatus*) has been quantitated as 108 min (Perachio 1971). The reported duration of REM sleep in squirrel monkey (*S. sciureus*) has ranged as low as 18 min from a 10 h PSG recording (Breton et al. 1986) and high as 165 min from a 12 h PSG recording (Adams and Barratt 1974) during the dark phase. Two additional studies, which have reported 24 h PSG recordings, note the REM sleep duration of squirrel monkeys as 45 min (Edgar et al. 1993) and 84 min (Wexler and Moore-Ede 1985). To reiterate, such an unusually wider variation in the duration of REM sleep reported for squirrel monkeys from four different laboratories can only be explained in terms of (1) varying experimental milieu in which the PSG recordings were made, and (2) an unusual, isolated atmosphere in which the squirrel monkeys experienced sleep, compared to how their communal sleep habits are in the wild.

A few conceptual limitations of this study deserve notice. While acknowledging that the colony ecology of *A. azarae* and *S. boliviensis* has notable differences in group size and sleeping sites (Table I), we have not specifically examined the influences of these two parameters on the activity-behavioral sleep performances of these two Cebid monkeys. Though we attribute the quantitative difference seen in the behavioral sleep of *A. azarae* and *S. boliviensis* directly to activity-habitat variation between these two species, this deserves further validation under an experimental design simulating the group sizes prevalent in the wild.

CONCLUSIONS

Three notable findings from this study are as follows: First, the quantitated values obtained for daily TST and SEL during quiescent phase in nocturnally-active owl monkeys differed reliably from the TST and SEL values recorded for diurnally-active squirrel monkeys, a result that supports our hypothesis that species differences in sleeping pattern is related to group size and daytime and nighttime predation risks.

Secondly, comparatively shorter duration of TST and SEL recorded in this study for squirrel monkeys sleeping communally is in agreement with the vigilance behavior for which these monkeys are notable (Boinski et al. 2003). Shorter duration of TST and SEL in squirrel monkeys also indicates that vigilance behavior is a circadian phenomenon, which persists even during the quiescent phase. Thirdly, the mean TST/24 h of 10 h and 6 min for seven adult *A. azarae* monkeys confirmed our previous finding obtained in the maternal grandparent, two parents and one sibling of these monkeys.

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