except two owl monkeys in our colony, that the activity routines of longevous monkey Aa 23 was neither hindered by any identifiable motor defects nor by arthritic development in the limb extremities. Veterinary care records also showed cataract formation in both eyes of this longevous monkey after it reached 20 years of captivity.

The daily mean (±SD) TST in the focal subject Aa 23 and its progeny Aa 34 are shown in Fig. 1B. The daily mean (±SD) TST for the focal subject Aa 23 in June 2003, January 2004, January 2005 and May 2005 were 887 ± 72, 790 ± 103, 1016 ± 94 and 937 ± 150 minutes respectively. In comparison, the daily mean (±SD) TST for Aa 34 in August 2003, January 2004, June 2004 and June 2005 were 643 ± 76, 612 ± 92, 614 ± 91 and 822 ± 71 minutes respectively. Again as expected, in all four data points spanning 2 years, the duration of TST of aged Aa 23 monkey was namely 4, 3, 6 and 2 hours longer to that of its progeny Aa 34. This indicated that the aged focal monkey slept more, especially in January 2005, compared with its progeny. The daily mean (±SD) TST of Aa 56 was determined to be 712 ± 55 minutes (data not included in Fig. 1B).

Figure 1C shows the daily mean (±SD) of SEL in the focal subject Aa 23 and its progeny Aa 34. The daily mean (±SD) SEL for the focal subject Aa 23 in June 2003, January 2004, January 2005 and May 2005 were 24±4, 25±8, 42 ± 19 and 28 ± 12 minutes

respectively. In comparison, the daily mean (±SD) SEL for Aa 34 in August 2003, January 2004, June 2004 and June 2005 were 32 ± 8, 22 ± 5, 24 ± 4 and 66 ± 24 minutes respectively. As opposed to the marked difference in the TST values between that of Aa 23 and Aa 34, it appears that the variation in SEL between the focal Aa 23 monkey and its progeny Aa 34 was marginal as the daily mean values varied within a narrow window of 22–32 minutes, with overlapping SD values in six of the eight data points spanning 2 years. However, the SEL of Aa 56, sharing the same cage of Aa 34, was 43 ± 13 minutes in April 2005 (data not included in Fig. 1C).

Aging-induced spinal curvature

Two types of spinal curvature, namely kyphosis (dorsally directed acute curvature of spine along the mid-sagittal plane) and scoliosis (laterally directed curvature of spine along the coronal plane) were examined. The extent of aging-induced spinal curvature of both these types in the longevous Aa 23 monkey was markedly visible in the radiographs taken. Photographs produced from the radiographs reveal the kyphosis (Fig. 2) and scoliosis (Fig. 3) of Aa 23 monkey's spine. Table 2 presents the KI values, calculated from the original radiographs, for the three studied monkeys. The KI of 2.27 for the Aa 23 monkey, compared with the values of 4.83 and 5.42, for Aa 34
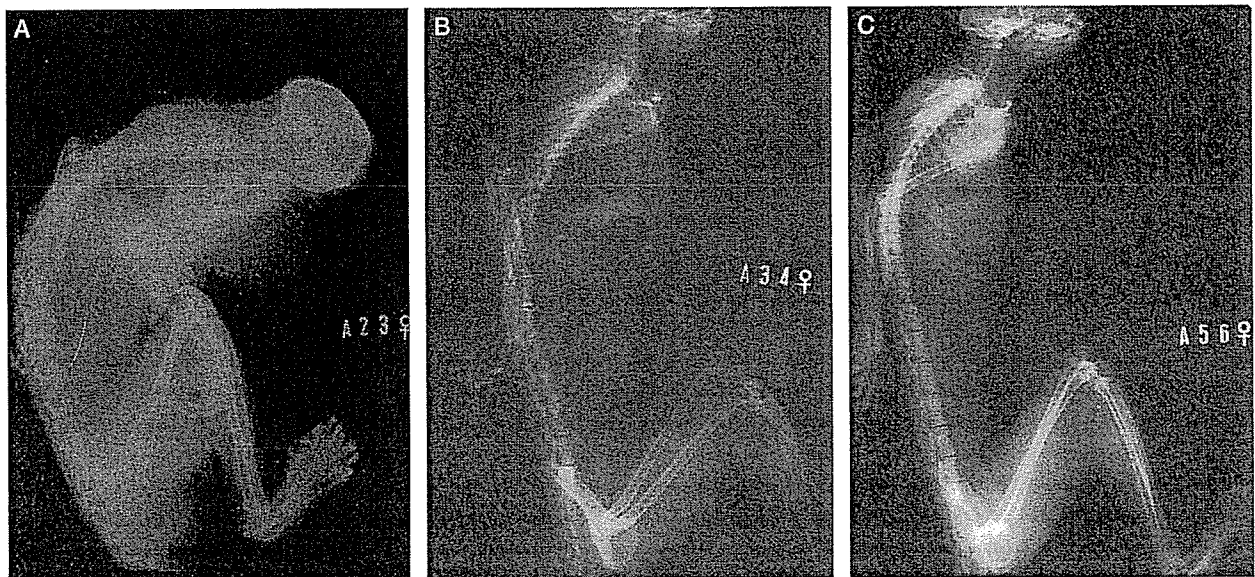

Fig. 2 Whole body radiographs (lateral positioned) of owl monkeys, for calculation of kyphotic index. (A) Aa 23, aged >26 years; (B) Aa 34, aged 16 years; (C) Aa 56, aged 1 year. The prominent vocal sac of Aa 23, bulging externally in the ventral side, is faintly visible in (A), while it is absent in (B) and (C).
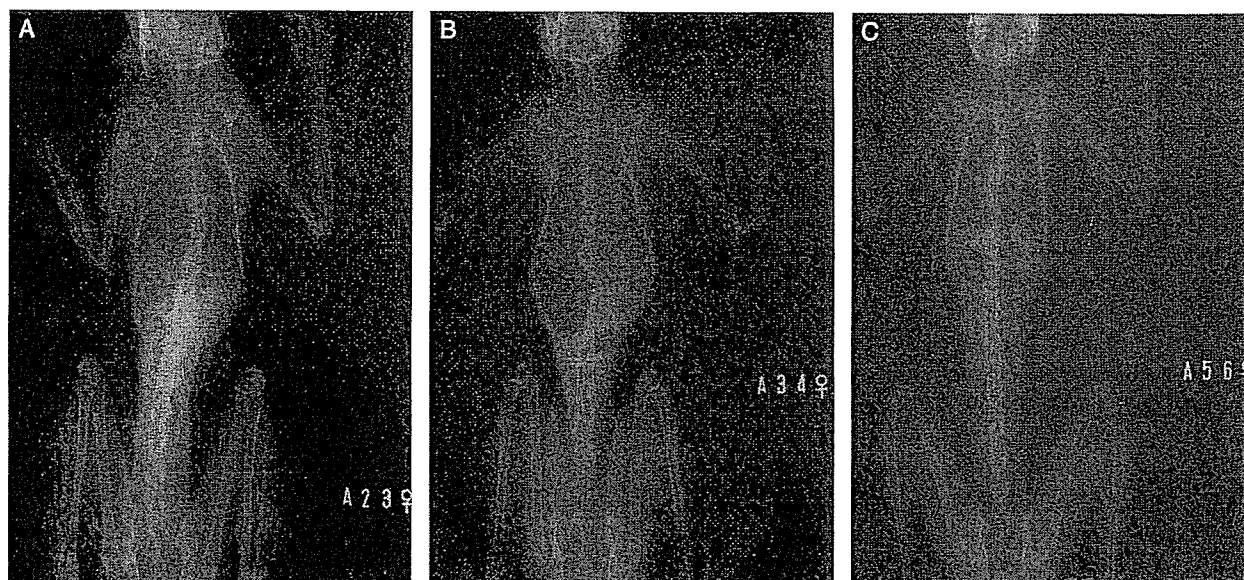
Fig. 3 Whole body radiographs (dorso-ventral positioned) of owl monkeys. (A) Aa 23, aged >26 years; (B) Aa 34, aged 16 years; (C) Aa 56, aged 1 year. Marked lateral curvature of the spine is visible in (A), compared with those in (B) and (C).

Table 2 Effect of age on spinal curvature in owl monkey indicated by radiography

Owl Monkey	Age (years)	AB[1] (mm)	CD[2] (mm)	KI[3]
Aa 23	>26	166	73	2.27
Aa 34	16	198	41	4.83
Aa 56	1	206	38	5.42

KI, kyphotic index.
[1]Length of the line marking the distance from seventh cervical vertebra to the sacral promontory. Measurement was made directly from the radiograph.
[2]The distance from AB to anterior border of the vertebral body that is furthest from AB. Measurement was made directly from the radiograph.
[3]The ratio of AB/CD.

and Aa 56 (aged 1 year) respectively, confirmed the prominent spinal curvature. Whereas the vertebral bodies of Aa 34 and Aa 56 have distinct square or rectangular shapes (Fig. 2B,C), the borders of the vertebral bodies of Aa 23 monkey appear thickened because of high degree of ossification (Fig. 2A). In addition, the intervertebral spaces of thoracic vertebrae have disappeared and those of lumbar vertebrae have diminished in Aa 23 monkey (Fig. 2A). Degeneration in the spinal vertebrae, with aging, probably have contributed to the development of marked kyphosis in Aa 23 monkey. In addition to scoliosis, disc bulge in the lumbar vertebral region of Aa 23 monkey (Fig. 3A) can also be seen, compared with those of control subjects Aa 34 and Aa 56 (Fig. 3B,C).

Discussion

Reports on longevous non-human primates

One stimulus for us to compile Table 1 was to update and summarize the available longevity records of captive non-human primates, strictly from the published primary literature which have reported on certain aspects of aging at organ, tissue or cellular level. This was considered of some merit, as the rigor of previous compilations and analyses on longevity [3, 41] appears diluted due to mixing of primary literature with that of standard secondary reference sources, unpublished personal communications and oral records. Table 1 presents an updated longevity record for 19 species of non-human primates. With the inclusion of the longevity information presented in this report for the owl monkey, the longevity records of 20 species of non-human primates now become updated.

What became revealed in the compilation of Table 1 was the fact that even among the few prospective studies on longevous primates, attention to the sleep behavior of senile subjects have been overlooked, because of oversight or lack of interest. At least in this report on a longevous female owl monkey, we have attempted to rectify this oversight. Now aged >30 years, this owl monkey appears to be an outlier to the 'Caretakers live longer' hypothesis among anthropoid primates [1], which postulated that past sexual maturity, captive owl monkey males have a strong survival advantage over females.

Activity–sleep quantitation

As indicated in past reviews [8, 60], sleep quantitation of agile and dexterous non-human primates has remained a challenging task for decades mainly due to inherent technical limitations involved in the highly invasive polysomnographic protocols. As a consequence, non-invasive actigraphy has gained acceptance recently as a viable and alternative sleep measurement method for non-human primates [36, 61]. Recently, in a cross-sectional study we [48] have established that the daily mean TST of four owl monkeys ranged between 9 hours 30 minutes and 12 hours 30 minutes.

The current longitudinal study extending for a 2-year period, incorporated four data points and included two (Aa 23 and its progeny Aa 34) of the four monkeys used in our previous study [48]. In the current study, the daily mean TST of the longevous Aa 23 monkey fluctuated between 13 hours 10 minutes and 16 hours 56 minutes, while that of its progeny Aa 34 monkey (aged 16 years and used as a suitable control) fluctuated between 10 hours 12 minutes and 13 hours 42 minutes. However, it should be noted that the fluctuation of daily mean TST in Aa 34 monkey during first three data points – 10 hours 43 minutes, 10 hours 12 minutes and 10 hours 14 minutes (between 2003 August, 2004 January and 2004 June) was marginal, the variation being only 31 minutes. During this period, Aa 34 monkey shared the same cage with its breeding mate. It conceived in 2004 January and gave birth to Aa 56 in 2004 April and continued to nurse its offspring in 2004 June. After Aa 56 monkey reached 1 year in 2005 April, Aa 34 monkey was separated from its breeding mate and housed with its progeny Aa 56 in a separate cage. Thus, the increase in mean daily TST of Aa 34 monkey to 13 hours 42 minutes in 2005 June may be attributed to this change in housing condition. Concurrently, the mean SEL of Aa 34 monkey also reflected this change in housing condition, where the mean SEL was 32, 22 and 24 minutes respectively in 2003 August, 2004 January and 2004 June, but increased drastically to 66 minutes in 2005 June. However, during the 2-year study period, the variation in the mean SEL among the four data points (24, 25, 42 and 28 minutes respectively) for the longevous Aa 23 monkey was not drastic. As five of the eight mean SEL data points for both Aa 23 and Aa 34 monkeys during the span of 2 years, cluster between a narrow window of 22 and 28 minutes, it could be inferred that the longevous Aa 23 monkey (a) has reduced activity and increased daily sleep time, in comparison with its progeny, but (b) retains similar SEL to that of its progeny.

We are aware of the fact that legitimate concerns do exist on using progeny and grandprogeny as controls for longevous subjects in primate studies [55, 58]. However we are of the opinion that sleep data on three generations of a family sharing the same genetic makeup and bred under identical captive conditions distinctly illuminate the effect of aging on sleep on subjects which are genetically related, and not inbred; and thus providing effective genetic control, which otherwise would be a compounding influence on the obtained data [54]. Furthermore, reports on the sleep data on three generations of primates including humans like the present study have been unusually rare in past somnology literature.

Cataract formation and its influence on activity

Although the owl monkey has served as a popular primate model in ophthalmologic research for nearly four decades from 1941 to 1985 [42], cataract formation because of senility failed to attract the attention of researchers. Even when numerous (n > 50) owl monkeys were used in a couple of ophthalmologic studies [46], age details of the experimental subjects have been missing. As such, information on cataract development in aging owl monkeys is scarce at best. However, senile cataracts have not been observed in rhesus monkeys which were < 20 years old [28]. This finding is somewhat in agreement with the veterinary care records of the longevous Aa 23 monkey, when early signs of cataract formation in both eyes were detected after this monkey reached 20 years of captivity. Nevertheless, we doubt that impaired vision because of developed cataract could have strongly impeded the locomotory movements of this longevous monkey within its cage, to the limit of reducing its activity profile. While it may be true in wild conditions where the visually impaired monkey may hesitate to venture into unexplored space because of poor eyesight, we infer that after 20 years of captivity, omni-directional movements within its own cage would hardly be a challenging task for this longevous monkey – even with failing eye sight. Thus, the low intensity of activity (Fig. 1A) shown by the longevous monkey could more or less be directly correlated to its old age.

Aging-induced spinal curvature

The only previous report [9] on the whole body radiography of owl monkeys featured four males aged 1, 5.5, 12 and 46 months. As the present report features three owl monkey females aged 1, 16 and > 26 years, direct comparisons with the previous report [9] seems less

appropriate, because of gender and age variations between the examined monkeys. However, the almost resembling patterns of the radiographic frames of Aa 56 (Fig. 3C) and its same aged male counterpart at 1 year, presented in the previous report [9], are in agreement.

Previously, an aged (> 20 years) female rhesus monkey with a pronounced kyphosis and degeneration of spine has also been reported [14]. Degeneration of vertebral joints resulting in kyphosis, scoliosis, and lumbar vertebral disc bulge of the longevous owl monkey in the current study (Figs 2 and 3), in comparison with the vertebral frames of its progeny Aa 34 and grand-progeny Aa 56, appear identical with the age-related degeneration of skeletal system occurring in senile rhesus macaque [14]. The probability for spinal curvature increases with advancing age as a combined effect of decrease in bone mass, reduced spinal mineral bone density, intervertebral disk thinning and reduced muscular tone, among other factors. As revealed from the radiographic evidence, it is inevitable that the spine of Aa 23 monkey has become considerably weakened because of 28 years of captive life. However, this weakened condition of spine has not led to compression fracture of spine, as repetitively demonstrated by the (a) presence of active reflexes by the monkey, to the level that anesthesia was needed for routine non-invasive experimental procedures such as tagging and removing the AW, and (b) absence of chronic pain indication. In addition, its stable weight (1.3 kg), good appetite and lack of any detectable malady other than cataracts, also reflect a good degree of health for this longevous owl monkey's advanced age.

As owl monkeys are extremely agile and naturally have a hunched back adapted for powerful leaps among the tree branches [39], it may not be inappropriate to raise a general issue on the terminology used in spinal curvature (kyphosis, lordosis and scoliosis) with relevance to the life of non-human primates in natural habitats. Medical terms relating to spinal curvature were introduced with human frame as reference. As humans are bipedal by natural evolution, terms such as kyphosis, lordosis and scoliosis have gained negative connotation in general context. Associated with this, we agree with a previous view [20] in the context of motion economy of non-human primates within the forest canopy that primate studies are greatly distorted by questions of human evolution. Therefore, how valid is the negative connotation relating to kyphosis, lordosis and scoliosis (in medical context) for obligatory quadrupedal owl monkeys, spending their whole lives in an arboreal habitat? Nevertheless, we infer that aged owl monkeys in captivity [like the longevous Aa 23 monkey presented in this report] are susceptible to a marked degree of spinal curvature because of advanced age.

To sum up, we have prospectively quantitated the sleep time and SEL of an owl monkey which have lived in captivity for 28 years, and also have radiographically assessed its age-related change in spinal integrity, in comparison with its progeny and grand-progeny.

Acknowledgments

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Sleep Profile and Longevity in Three Generations of a Family of Captive Bolivian *Aotus*

Sachi Sri Kantha[1] and Juri Suzuki[1,2]

The daily total sleep time (TST) of the only nocturnal simian primate, Aotus spp., remains little studied under controlled conditions. We conducted 3 experiments in 4 owl monkeys (Aotus sp.), aged 1–27+ yr, to determine the daily TST. We housed 3 their—a nuclear family—in 1 cage and the remaining senescent female in an adjacent separate cage. We monitored their activity-sleep pattern longitudinally for 15–20 d via actigraphy: by tagging an acclerometer-type miniature transmitter (Actiwatch-MINIMITTER) sensitive to omnidirectional movement, to the owl monkey's neck. The TST (9.5–12.5 h) was ca. 4.5–7 h less than the 17 h Perachio reported for owl monkeys in 1971 by polysomnography, under similar 12-h-light; 12-h dark conditions. Our finding corroborates well with the TST for other nonhuman primates. Four members of the Aotus colony at our facility reached 20 yr in captivity; the oldest (wild-born female) is still living at >27 yr, and the second oldest (captive-born male), is 23 years now.

INTRODUCTION

Primatologists have shown considerable interest in the uniqueness of owl monkeys (*Aotus* spp.) as nocturnal simians (Baer *et al.*, 1994; Martin, 1987; Wright, 1989). Because of their special status among extant primates, field primatologists from Perú, Paraguay, Argentina, and

[1] Center for Human Evolution Modeling Research, Kyoto University-Primate Research Institute, Inuyama City 484-8506, Japan.
[2] To whom correspondence should be addressed; e-mail: suzuki@pri.kyoto-u.ac.jp.

Bolivia have described its sleeping sites such as tree holes and platforms in lodge trees (Aquino and Encarnacion, 1986; Garcia and Braza, 1993; Hershkovitz, 1983; Rathbun and Gache, 1980; Wright, 1978, 1983;). Wright (1983, 1994) observed that owl monkeys in the wild Chaco environment of Paraguay, rather than strictly adhering to their nocturnal routine, also stay active in diurnal hours including noon and opt for random sleep tree choice instead of habitual sleep trees. Fernandez-Duque and Rotundo (2003) confirmed similar diurnal behavior in *Aotus azarai* inhabiting Eastern Formosa, Argentina. However, quantitating the daily total sleep time (TST) of owl monkeys showing such cathemeral activity (Tattersall, 1987) in their natural habitats had remained a challenge.

The purpose and need for sleep in primates, including humans, remain unsolved (Dement and Vaughan, 1999; Hairston and Knight, 2004). To comprehend the primary function of sleep in humans, quantitating the daily TST of primate species is a vital first step. Despite input from many laboratories, researchers have achieved sleep quantitation in only <10% of extant primate species (Campbell and Tobler, 1984; Zepelin, 1989) under captive conditions, and peers still need to experimentally check and confirm previous reports via identical or less invasive, alternative methods. A stimulus for our study was that researchers have not quantitated sleep in owl monkeys, with the exception of 2 brief reports of Perachio (1971, 1977) via polysomnography under heavily restrained conditions. The Primate Research Institute, Inuyama, Japan established an *Aotus* colony of Bolivian origin in the mid-1970s. Three founding members (At 23 female, At 24 male, and At 25 female; Fig. 1), have lived >20 yr in captivity. Kawamura *et al.* (2002) previously reported the Y-chromosomal red-green opsin genes of 9 members of the breeding colony (including At 23 and At 24). We had 2 specific objectives: to quantify the sleep parameters in owl monkeys by actigraphy and to report on the longevity record of captive owl monkeys at our facility, where At 23 (Fig. 2) has exceeded the currently available record on captive longevity for *Aotus*.

MATERIALS AND METHODS

While noting that the specific taxonomy of *Aotus* is still in a state of fluidity since the 1980s (De Boer, 1982; Ford, 1994; Groves, 2001; Hershkovitz, 1983), we presume that, based on their Bolivian origin, the owl monkeys at our facility are *Aotus azarae*, though karyotype analysis is needed to confirm this. Because the arrival of the owl monkeys in our colony predated the revision of *Aotus* from a single species *A. trivirgatus* into 7–9 species (Ford, 1994; Groves, 2001; Hershkovitz, 1983), for continuity and convenience only, we denote the owl monkeys at our facility with
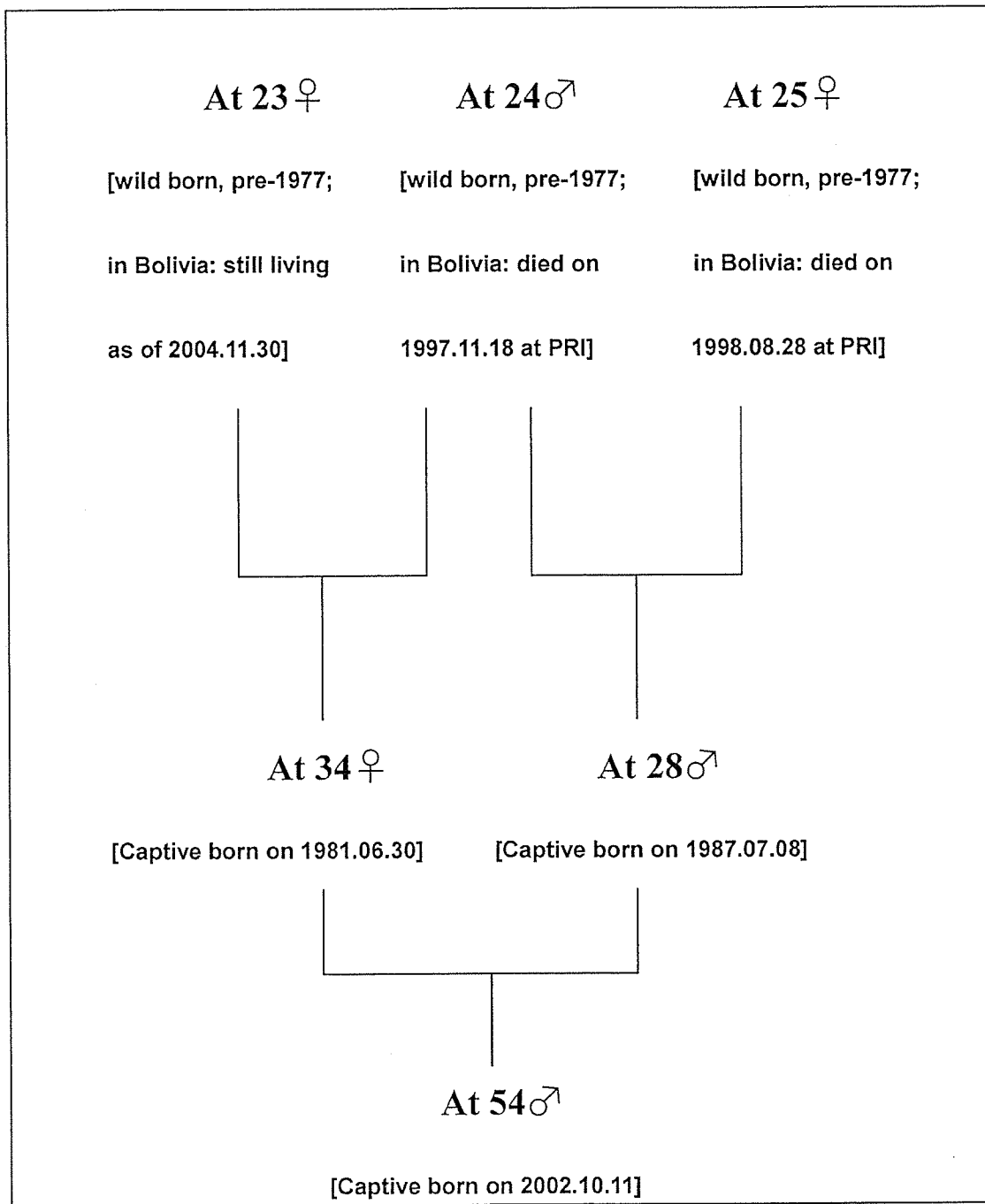
At 23 ♀   At 24 ♂   At 25 ♀

[wild born, pre-1977;   [wild born, pre-1977;   [wild born, pre-1977;

in Bolivia: still living   in Bolivia: died on   in Bolivia: died on

as of 2004.11.30]   1997.11.18 at PRI]   1998.08.28 at PRI]

At 34 ♀   At 28 ♂

[Captive born on 1981.06.30]   [Captive born on 1987.07.08]

At 54 ♂

[Captive born on 2002.10.11]

Fig. 1. Genealogy of a 3-generational owl monkey family at the Primate Research In-
stitute (PRI), Inuyama, facility. [At 28 and At 34 are step-siblings, sharing the same
male parent. At 54, the only progeny of At 28 and At 34 used for total sleep time (TST)
determination is indicated, while its elder and younger siblings are excluded.]

the marker prefix At. We used 4 owl monkeys comprising a 3-generational
family (Fig. 1, excluding At 24 and At 25, which died in 1997 and 1998,
respectively) in the determination of TST. We housed 3 (a breeding pair
comprising At 28 male, At 34 female, and the male offspring At 54) in
1 stainless steel cage (100 × 70 × 60 cm), and the remaining senescent At 23
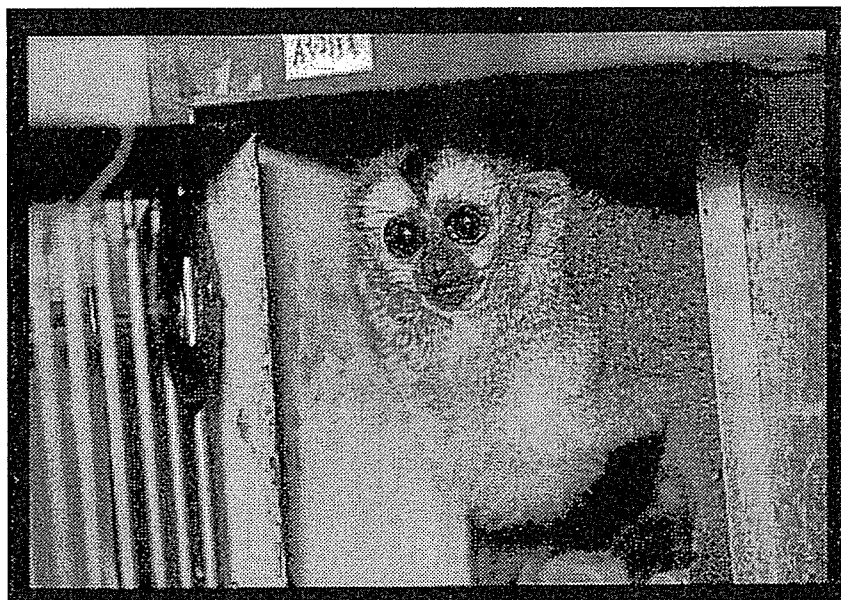female in an adjacent separate cage. The body masses of At 23, At 28, At 34,

Fig. 2. At 23♀ (wild-born), aged >27 yr, in September 2004. Note the marked ventrally drooping vocal sac. (Photograph by Minoru Kinoshita.)

and At 54 during the experimental period (July 2003–June 2004) were 1490, 1116, 1270, and 883 g, respectively. We maintained the *Aotus* colony room on a shifted, alternating 12-h light (2300–1100 h; 200 lux) –12-h dark (11:00–23:00 h; 0.01–0.5 lux) cycle (Erkert, 1989). We routinely checked lighting of the room via an illuminance meter (TopCon IM-5, Tokyo). The owl monkeys had food and water *ad libitum*, and we supplemented the pellet diet daily with fresh fruits and twice weekly with meal worms.

We monitored activity-sleep patterns of the owl monkeys via actigraphy, by tagging an acclerometer-type miniature transmitter (Actiwatch AW 64 model-MINIMITTER, Mini Mitter, Bend, OR, containing 64 KB of onboard memory) sensitive to omnidirectional movement to the individual's neck. The actiwatch is capable of sensing any omnidirectional movement with a minimal resultant force of 10 mg. We preset each actiwatch (weighing 17 g) to collect activity-rest data of individual owl monkeys with a sampling rate of 32 Hz and a sampling epoch of 1 min, suspended in an elastic band, and positioned it on the individual's neck after anesthesia with ketamine-HCl (10 mg/kg body wt; Sankyo, Tokyo). We accumulated longitudinal data on daily TST for up to 20 d before removal of actiwatch from the individual's neck. We retrieved accumulated data into the computer, via Mini Mitter Actiwatch Reader through an RS-232 Serial Port and Activity Sleep® Activity Monitoring, version 3.3 (Mini Mitter). The communication link between the actiwatch and the actiwatch reader is short-range telemetric.

We conducted 3 experiments between August 2003 and June 2004, and studied 2 (mating pairs At 28 and At 34) of the 4 owl monkeys, repetitively.

Experiment 1

From August 6 to 27, 2003, we tagged actiwatches to At 28 and At 34 (mating pair) sharing the same cage with their offspring, At 54.

Experiment 2

From January 9 to 28, 2004, we tagged actiwatches to At 28, At 34, and At 54, sharing the same cage, and At 23 in the adjacent cage. Our goals were to confirm the findings of Expt. 1 and to evaluate whether the offspring (At 54) of the mating pair exhibits a varying sleep profile compared to that of its parents (At 28 and At 34).

Experiment 3

The mating pair (At 28 and At 34) gave birth to an offspring (At 56) on April 15, 2004. Subsequently, from June 7 to 22, 2004, we tagged actiwatches individually to At 28, At 34, and their elder offspring At 54 sharing the same cage. For most of the experiment, the male parent At 28 carried the 7–8-wk-old baby dorsally (Dixson, 1982, 1983). We aimed to assess whether baby carriage influenced the sleep profile of the male parent.

In the first 2 experiments, At 28 rejected the actiwatch placed on his neck, after the first 2 d. However, when we tagged it again, he did not reject it. In Expt. 3, such a rejection did not recur. Thus, sleep profile data were missing for At 28 between d 3 and 5 in the first 2 experiments.

The Primate Research Institute's ethics committee on experiments approved our experiments, which complied with ethical standards in the treatment of primates.

RESULTS

A distinguishing physical feature in At 23 is the prominently visible, drooping vocal sac (Fig. 2), which Hill (1964, p. 160) described as "extending caudally behind clavicles and laterally deep to sternomastoids; partially subdivided in median line by septum formed by projection of infrahyoid

muscles dorsal to sac; sac communicating with interior of larynx by paired openings in thyrohyoid membrane." Also, because of advancing senescence, both eyes have well-developed cataracts, which mildly hampered At 23's movements within the cage.

Experiment 1

The fluctuations in daily TST for 20 d of continuous monitoring for At 28 and At 34 sharing the same cage are in Fig. 3A. The mean (+SD) values of daily TST for At 28 and At 34 are 658 (+64) and 665 (+92) min, respectively. Thus, on average the TST is *ca.* 11 h in the mating pair of owl monkeys. The abrupt interruption in sleep record in the actogram of At 28 (Fig. 3A) between d 4 and 6 was caused by his rejection of the actiwatch during the first weekend of the experiment.
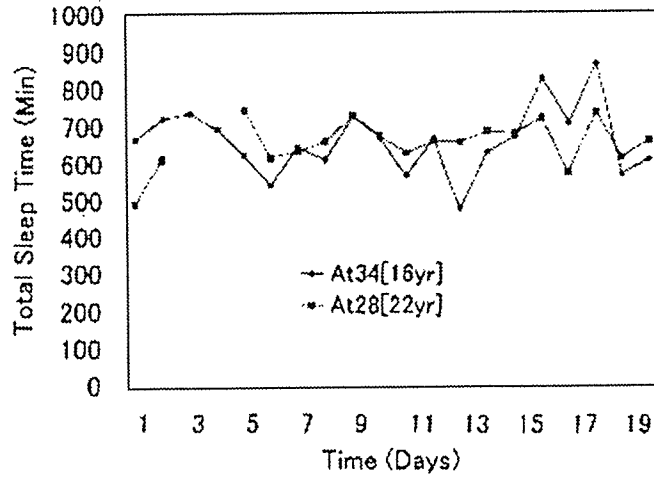
Experiment 2

The fluctuations in daily TST recorded for 19 d of continuous monitoring in 4 owl monkeys are in Fig. 3B. The mean (+SD) value of daily TST, 747 (+138) min is maximum for At 23. The TST for the other 3 owl monkeys, sharing same cage, are 711 (+85) min for At 28, 588 (+91) min for At 34, and 598 (+44) min for At 54. The daily TST of the youngest owl monkey, aged 1 yr and 3 mo, did not differ markedly from that of its parents (At 28 and At 34). However, the daily TST of the oldest, At 23, appeared longest (almost 12.5 h), though without markedly differing from that of the other 3 owl monkeys.
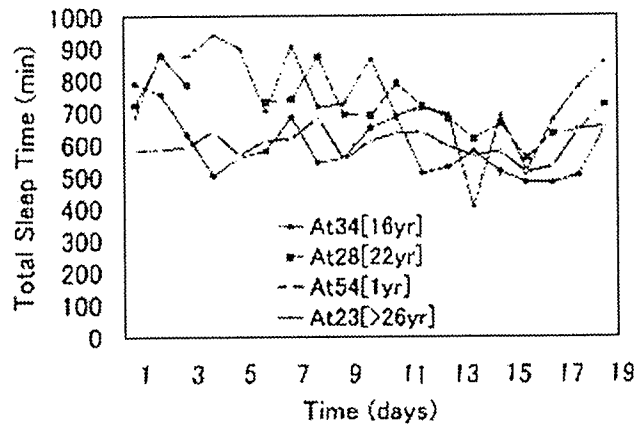
Experiment 3

The fluctuations in daily TST, recorded for 15 d of continuous monitoring, in 3 owl monkeys are in Fig. 3C. At the start of the experiment, the mating pair's new offspring was 7 wk old and the male parent (At 28) carried him on his back most of the time. Presumably because of the physiological burden, the mean (±SD) value of daily TST, 820 (±71) min, is markedly higher than the corresponding values for At 28 in Expt. 1 and 2 (Table I). Conversely, the mean (±SD) value of daily TST, 612 (±85) min for At 34, is in a similar range of the corresponding values for the subject in Expt. 1 and 2 (Table I). The daily TST values for progeny At 54 resembled the pattern of the female parent At 34.

(A) Experiment 1: Aug.06-27, 2003

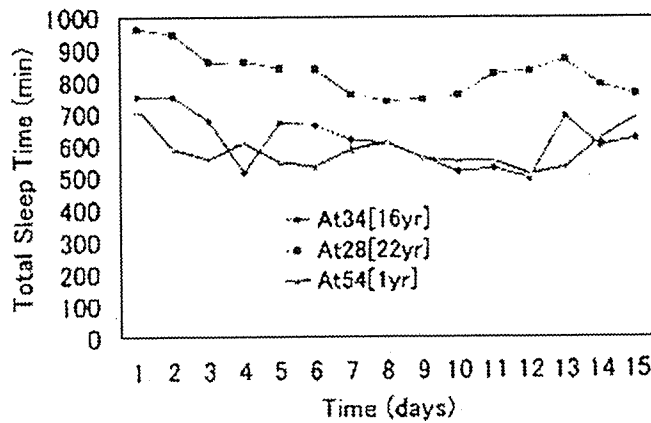(B) Experiment 2: Jan.09-28, 2004

(C) Experiment 3: Jun.07-22, 2004

Fig. 3. Daily total sleep time (TST) determinations in owl monkeys. (A) Expt. 1 (August 6–27, 2003)—At 28♂ and At 34♀; Expt. 2 (January 9–28, 2004)—At 23♀, At 28♂, At 34♀, and At 54♂; Expt. 3 (June 7–22, 2004)—At 28♂, At 34♀, and At 54♂. In all 3 experiments, mating pairs At 28♂, At 34♀, and their 1-yr-old offspring At 54♂ shared the same cage. During Expt. 3, At 28♂ also carried a new offspring, born on April 4, 2004.

Table I. Summary of 3 experiments on the quantitation of daily total sleep time (TST) in 3 generations of a family of owl monkeys

Owl monkeys[a]	Daily mean TST (min)[b]		
	Expt. 1	Expt. 2	Expt. 3[c]
At 23♀		747 ± 138	
At 28♂	658 ± 64	711 ± 85	820 ± 71
At 34♀	665 ± 92	588 ± 91	612 ± 85
At 54♂		598 ± 44	578 ± 59

[a]At 28, At 34 and At 54 occupied the same cage during the period covered in 3 experiments.

[b]Expressed as mean ± SD.

[c]An infant (At 56) born to the mating pair (At 28 and At 34) on April 15, 2004, also occupied the same cage during the experimental period.

DISCUSSION

The only other sleep-related data on owl monkeys are those of Perachio (1971, 1977), who used polysomnography to quantitate sleep in 3 adults, exact ages not reported. Perachio (1971) reported a mean total of 16 h and 56 min sleep for 24 h, under 12-h light (108 lux) and 12 dark (6.5 lux). Our data from Expt. 2 show that the TST for 2 senile monkeys (At 23 and At 28) average 12 h and 9 min for 24 h. The TST for adult At 34 and prepubescent At 54 average 9 h 48 min and 9 h 58 min, respectively, which are within the range (8–12 h) for other nonhuman primates (Campbell and Tobler, 1984; Zepelin, 1989) and also nearly 4–6 hours less than those that Perachio (1971) reported. A caveat by Perachio (1971, P.58), stating that "Since there was some difficulty in developing a reliable scoring procedure for quantification, no analysis of the data will be presented," suggests that the nearly 17-h TST for owl monkey he reported may be an overestimate, owing to excessive restraint and resulting tiredness of the monkeys. Thus, it is reasonable to infer that the daily TST range for owl monkey is 9.5–12.5 h, as in Fig. 3 and Table I.

The highest mean TST of 13 h and 40 min Expt. 3 for At 28, in comparison to TST durations in Expt. 1 and 2 for the same individual, could be caused by the parental burden of dorsal carriage of the 7–8-wk-old offspring (weighing ca. 250 g) most of the time. Though sharing the same cage with its mating partner (At 34) and an older progeny (At 54), the taxing performance of carrying an infant on its back by a male parent (At 28) results in a marked increase of nearly 2 h of daily sleep (Fig. 3C Vs. Fig. 3A and B). In place of polysomnography to quantitate total sleep time, we used actigraphy, which is a reliable, noninvasive, convenient,

Table II. Longevity records for owl monkeys in captivity

Location	Maximum longevity in captivity (yr)	Reference
London Zoo	12.0–12.7	Jones (1962); Hill (1964)
San Diego Zoo	~15	Bowden and Jones (1979)
San Diego Zoo	18.5	Jones (1982)
London[a]	12–20?	Hearn and Dixson (1984)
(unidentified)[b]	18	Scott (1992)
California Institute of Technology[c]	>20	Baer (1994)
University of Tubingen	>20	Rappold and Erkert (1994)
Lincoln Park Zoo, Chicago[c]	~25	Margulis (2004)[d]
(unidentified)[b]	~26—27	Allman et al. (1998)
University of Tubingen	>25	Erkert (1999)
(unidentified)[b]	25.3	Carey and Judge (2000)
Kyoto University, Inuyama[e]	>27	Present study (2004)

[a]Location not specifically indicated; appears to be composite information. The question mark following the numbers is as in the original.
[b]Cites the source as M. L. Jones (1980).
[c]Unpublished data.
[d]Personal correspondence from Sue Margulis (Primates Curator, Lincoln Park Zoo, e-mail, November 18, 2004).
[e]At the Primate Research Institute colony; refers to At 23, oldest owl monkey (wild born), and introduced in 1977 as an adult. That a second owl monkey, At 28 (captive born), had reached 23 yr is also of interest.

objective, and longitudinal method to quantitate sleep in primates, including humans (Ancoli-Israel et al., 2003; Kushida et al., 2001; Sadeh et al., 1995; Zhdanova et al., 2002). The underlying premise of actigraphy measurement is that, in the absence of any detected activity, i.e., below the measurement threshold set for the instrument, the subject is in complete rest, which equates to sleep.

The relevance of quantitating sleep in owl monkeys can be explained in terms of its special evolutionary adaptation as the only nocturnally active simian primate. In evolutionary terms, the intrusion of humans into primarily nocturnal frontier (as shift workers in production, health, entertainment, and service industries) opened up only from the 1880s when mass production of light bulbs and electrical accessories became a reality (Melbin, 1978). Thus, owl monkeys—as the nearest evolutionary kin of humans and a predecessor of nocturnal living—provide a unique model to comprehend the sleep behavior and its accompanying health problems of nocturnally active humans.

Table II is a literature summary of owl monkey longevity records in captivity, since 1962. At 23, >27 yr of age, has become one of the longest living captive *Aotus*. Captive born At 28 also has completed 23 yr in June 2004. Schultz (1969) and Bowden and Jones (1979), among others, have

anticipated increasing longevity of captive primates in general. Easily available balanced diet, veterinary care, absence of predators in the milieu, and reduction in physiological overexertion are leading factors that contribute to increasing longevity among captive primates. Two of our *Aotus* subjects exceeded 23 yr in captivity. The presence of a prominently visible vocal sac of long-lived At 23 (Fig. 2) is of some degree of curiosity, though reported previously (Giles *et al.*, 1974; Hayama, 1970; Hewitt *et al.*, 2002). According to Hill (1972), a vocal sac reinforces vocalization, in addition to serving a respiratory function. However, among the 15-member owl monkey colony in the room, At 23 now appears to be the least vocalizing member because of senescence. The current chronological age of At 23 can only be speculated to *ca.* 30 yr because subadults disperse in the wild at *ca.* 3 yr and At 23 became a captive member of our facility in 1977. Despite her old age, she still retains vigor, possesses good reflexes, and is healthy.

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ELSEVIER

Sleep quantitation in common marmoset, cotton top tamarin and squirrel monkey by non-invasive actigraphy

Sachi Sri Kantha, Juri Suzuki *

Center for Human Evolution Modeling Research, Kyoto University–Primate Research Institute, Inuyama City 484-8506, Japan

Abstract

Sleep quantitation data on the Neotropical primate species, apart from the squirrel monkey, are still sparse. As such, we have quantitated sleep in the common marmosets (*Callithrix jacchus*), cotton top tamarins (*Saguinus oedipus*) and squirrel monkeys (*Saimiri sciureus*) reared in one primate facility simultaneously, by non-invasive actigraphy. The range in total sleep time/24 h measured for male adult common marmosets, cotton top tamarins and squirrel monkeys were 713–793 min ($n=4$), 707–889 min ($n=4$) and 459–475 min ($n=2$) respectively. The range in sleep episode length /12 h dark phase for marmosets, tamarins and squirrel monkeys were 21–52 min ($n=3$), 10–28 min ($n=4$) and 9–15 min ($n=2$) respectively. Since vigilance is a critical evolutionary adaptive feature of predator avoidance among Callitrichid monkeys and squirrel monkeys, the shorter ranges in sleep episode length recorded, even under captivity, in this study could be interpreted as probable indicators of such vigilance behavior during the rest phase. We hypothesize that the vigilance behavior when it exists during a primate's active phase should also prevail when it is at rest (sleep). This hypothesis deserves additional testing in female Callitrichid monkeys.
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Keywords: Actigraphy; Callitrichidae; *Callithrix jacchus*; Cebidae; *Saguinus oedipus*; *Saimiri sciureus*; Sleep episode length; Vigilance

1. Introduction

It is hardly debatable that simultaneously conducted comparative biochemical studies in multiple non-human primate species provide dividends in characterizing the phylogenetic links among evolutionary kins (Welsh and Walker, 1972, 1973; McGeachin and Akin, 1982; Roger et al., 1993; Croll et al., 1993; Fukuhara and Kageyama, 2005). However, due to restraints in space, time, funds and biased concerns of activists espousing animal rights, conducting comparative, prospective physiological studies simultaneously in more than one species of primates is becoming less feasible to plan and execute. Despite such a bottleneck, curiosity and need to quantitate the yet unknown details on the sleep behavior of three prominently used laboratory primates belonging to Cebidae family prompted us to initiate this study at our primate facility in Inuyama, Japan.

Sleep behavior in mammals, according to Zepelin (1989), can be defined by two criteria: (1) sustained quiescence in a species-specific posture accompanied by reduced responsiveness to external stimuli, and (2) quick reversibility to the wakeful condition, which distinguishes sleep from coma and hypothermic states such as hibernation and torpor. In addition, a third criterion representing characteristic changes in the electroencephalogram (EEG) is also considered as a useful validatory component of sleep. Of all the behaviors exhibited by the non-human primates (hereafter, referred to as primates), sleep behavior is rather difficult to quantitate (Siegel, 2005), especially the validation by EEG under acceptable standards of scientific rigor.

As of now, sleep behavior has been quantitated in only around 5% of the 234 extant primate species (Campbell and Tobler, 1984; Zepelin, 1989). Paucity of sleep quantitation data in the primate field studies is understandable. Absence of natural light during the sleep phase of primates is a prime hindrance for observation. To further compound the issue, artificial light disturbs the sleep behavior of the focal animals. The fatigue factor of the human observer in nights which leads

* Corresponding author. Tel.: +81 568 63 0586; fax: +81 568 62 9559.
  E-mail address: suzuki@pri.kyoto-u.ac.jp (J. Suzuki).

to sub-par and erroneous data collection cannot be overlooked. One should also not underestimate the inherent danger from other poisonous and predatory animals in the milieu which may affect the concentration of the researcher. Thus, sleep behavior studies have to depend more on primates reared in captivity.

Common marmosets (*Callithrix jacchus*) and cotton top tamarins (*Saguinus oedipus*), among the New World monkeys belonging to Callitrichidae, have gained prominence as cost-effective and lab-worthy primates for experimental use in captivity (Stellar, 1960; Poole et al., 1999). While common marmosets are endemic to Brazil, the cotton top tamarins are endemic to Colombia. Though still widespread in the Pernambuco region of Brazil, the wild *C. jacchus* populations have been suffering from severe depletion and decline due to habitat destruction (Rylands, 1993; Norconk et al., 1996). As a cumulated consequence of habitat loss, hunting and illegal capture for pet trade, a harsher vulnerable-threatened fate is now faced by wild *S. oedipus* populations in its native north western Colombian habitat, bordering the Caribbean Sea — between the eastern bank of Atrato river and western banks of Cauca and lower Magdalena rivers (Mast et al., 1993; Defler, 2004). The extent of the spread of *S. oedipus* to the south is believed to be 1500 m altitudinal limit into the Andean foothills (Mast et al., 1993).

Past field studies on *C. jacchus* and *S. oedipus* monkeys and their rather unique ecological role among the anthropoid primates have been reviewed (Sussman and Kinzey, 1984; Rylands, 1993; Defler, 2004). However, there is paucity of information on the sleep behavior of *Callithrix* and *Saguinus* genera living in the wild, and what is available were based on quasi-quantitative, opportunistic and/or naturalistic observations (Hershkovitz, 1977; Dawson, 1979; Heymann, 1995; Day and Elwood, 1999). The squirrel monkey (*Saimiri sciureus*), a New World monkey belonging to Cebidae, also continues to be one of the popular primate species for studies in neuroscience and pharmacology, since its introduction into aerospace medical research and animal space flight in 1958 (Beischer, 1968). As such polysomnography-derived data on sleep–wake cycles and biorhythm of squirrel monkeys have been published from a few laboratories (Adams and Barratt, 1974; Wexler and Moore-Ede, 1984, 1985, 1986; Erny et al., 1985; Breton et al., 1986; Edgar et al., 1993; Klerman et al., 1999, 2000). A couple of the early studies on sleep quantitation using polysomnography in squirrel monkeys (Adams and Barratt, 1974; Breton et al., 1986) were limited to 10–12 h.

Though polysomnography still remains as the 'gold standard' for sleep quantitation measurements, it is a highly invasive technique. Using brain and muscle electrodes in primates, seated in a restraint chair, has come under serious criticism as well since 1980s. The inability to sustain the recording for days is another demerit for polysomnography. Thus, quantitative sleep data recorded by non-invasive methods such as actigraphy have gained acceptance lately in understanding the sleep architecture of different primate species, including humans (Zhdanova et al., 2002; Ancoli-Israel et al., 2003; Sri Kantha and Suzuki, in press). As such, our objectives were two fold: (1) to quantitate sleep in the common marmosets

and cotton top tamarins reared in our primate facility simultaneously, by non-invasive actigraphy, to fill the currently existing void on sleep literature of *C. jacchus* and *S. oedipus* populations, and (2) to calibrate the actigraphy sleep measurement in *S. sciureus* monkey with the previously reported polysomnographic sleep measurement for this species.

2. Materials and methods

2.1. Animals and housing

The age composition and masses of study subjects reared at the Primate Research Institute facility and used in the experiments are provided in Table 1. Male members of common marmosets (*C. jacchus*, $n = 5$), cotton top tamarins (*S. oedipus*, $n = 4$) and squirrel monkeys (*S. sciureus*, $n = 2$) were used in this study. As indicated in Table 1, excluding one tamarin (So 105), all five marmosets and three tamarins were pair-housed with either a female mating partner or sibling/half-sibling or parent/offspring, in metal cages of dimension, 70 cm × 70 cm × 150 cm. The two squirrel monkeys shared a stainless group cage (1.2 m × 1.2 m × 2.1 m) with two adult females and a young male. This group cage had access to a sun-room with adequate vertical space (24 m × 28.5 m × 77.5 m) incorporated with diverse small vegetation including vines, small water facility and enrichment accessories like ropes and wood planks as multiple level perches. Mention should be made that when squirrel monkeys were studied in May 2005, the natural daylight extended to 14 h, and as such, the

Table 1
Basic details of the male study subjects and the duration of sleep quantitation

Monkey ID	Age at experiment[a] (years)	Weight (g)	Duration of sleep quantitation (days)
Common marmoset[b]			
Cj 62	10	412	7
Cj 98	8	440	7
Cj 123	6	363	7
Cj 133	6	277	7
Cj 174	0.8	266	7
Cotton top tamarin[c]			
So 105	14	425	8
So 133	11	500	8
So 165	7	473	8
So 173	6	533	8
Squirrel monkey[d]			
Ss 114	13	927	3
Ss 115	13	954	3

[a] All monkeys were born in captivity.
[b] Cj 62 and Cj 98 are half-siblings sharing the same cage. Cj 123 was pair-housed with a mating partner. Cj 133 and Cj 174 are parent and male offspring, sharing the same cage.
[c] So 105, being senile, was housed in a single cage. So 133 was pair-housed with a mating partner and their baby offspring. So 165 and So 173 are siblings sharing the same cage.
[d] Ss 114 and Ss115 shared a group cage with two females and another male, age ranging from 5 to 10 years.