

activity rhythm [51] data collected from few selected members of this colony.

To remedy the then prevailing situation, we initiated our behavioral research program on this owl monkey colony in 2002. Recently, we [48] have compared the total sleep time (TST) of four members of this owl monkey colony, including the wild born oldest member Aa 23. Since in the wild, the young individuals of owl monkey disperse from the family group at the age of 3 years [59], we deduced that the oldest individual Aa 23 in our colony has already reached 30 years. According to the available published reports, and to our knowledge, this monkey thus appears to be the longest-lived owl monkey in captivity. As published data on longevous owl monkeys are scarce, our objectives for this study were (1) to prospectively quantitate the sleep of a longevous owl monkey longitudinally for 2 years, and (2) to evaluate the aging-induced change in spinal curvature.

## Materials and methods

### Animals

Three healthy female owl monkeys (*A. azarae*), sharing kinship, were used. The wild-born Aa 23 was identified as a longevous individual. Its offspring Aa 34 was used as the first control subject. At the commencement of the study in June 2003, the ages of Aa 23 and Aa 34 were > 26 and 15 years respectively. In April 2004, Aa 34 gave birth to its ninth progeny Aa 56. Thus Aa 56 (grandprogeny of Aa 23) was also included as the second control subject, for the radiographic measurements in July 2005 towards the completion of the study. When radiographic measurements were taken, Aa 23, Aa 34 and Aa 56 weighed 1.30, 1.08 and 0.78 kg respectively. During the experimental period, while Aa 23 was housed in an individual stainless steel cage (100 × 70 × 60 cm), Aa 34 and its new-born progeny Aa 56 shared an adjacent cage of equal dimensions, since June 2005. Prior to that, Aa 34 was pair housed with its male partner and the newborn offspring, to accommodate the paternal care needs of the baby [59]. The cage dimensions in our facility for individuals and family group of four are in compliance with the required minimum space for this primate (of 1 kg mean weight) as defined by the US Animal Welfare Act 1992 [15, 16].

The colony room was maintained on a reverse, alternating 12 hours light (23:00–11:00 hours; 200 lx): 12 hours dark (11:00–23:00 hours; 0.01–0.5 lx) cycle. Lighting condition of the room was routinely checked by an illuminance meter (TopCon IM-5; Irie

Seisakusho Ltd., Tokyo, Japan). 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) was supplemented daily with fresh fruits and twice-weekly with meal worms. Prior approval from the Research Committee of the Primate Research Institute for the reported experiments was obtained.

### Actigraphy

The sleep quantitation was carried out by an actiwatch (AW 64 model-MINIMITTER; Mini Mitter Company, Bend, OR, USA; containing 64 KB of on-board memory). Following anesthesia with ketamine HCl (10 mg/kg body wt; Sankyo, Tokyo, Japan), the AW (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 1 minute, was suspended in an elastic band, and positioned on monkey's neck. For each subject, longitudinal data on activity pattern, TST and sleep episode length (SEL) were collected for 13 consecutive days, before removal of AW from monkey's neck. The accumulated data were retrieved into the computer, via Mini Mitter Actiwatch Reader through an RS-232 Serial Port and Activity Sleep Activity Monitoring Software, version 3.3 [37]. The definitions of the three activity–rest (sleep) parameters, as per manufacturer's instructions [37], are as follows:

1 Activity count: an arbitrary unit quantitating primate activity, computed from any omni-directional motion made by the caged monkey with a minimal resultant force of 10 mg. The instrument tallied the activity movements with reference to degree and speed of motion and converted these parameters to produce an electrical current that varied in magnitude. This derived algorithm is referred to as AW activity count, which is instrument specific; as of now, activity counts are incompatible for comparison with AWs from different commercial suppliers [36, 37]. Though AW activity count is thus an arbitrary unit and not suitable for determining the absolute activity of the animal in concrete terms, it can be usefully employed for evaluating comparative activity patterns among the monkeys wearing the AWs from the same commercial supplier.

2 TST: The cumulative amount of time measured in minutes in a continuous 24 hours circadian cycle (12 hours light phase:12 hours dark phase), that was scored as sleep. According to the Actiware–Sleep algorithm, based on 1 minute sampling epoch, activity counts of 40 or above were recorded as a wake epoch, and activity counts below this threshold value were recorded as a sleep epoch.

3 SEL: The mean length of blocks of continuous sleep, measured in minutes, falling between two wake bouts, in a 12 hours light phase of the 24 hours circadian cycle. The 12 hours light phase was preferred to measure this parameter, as owl monkeys predominantly rest during the light phase and not in the dark phase.

### Radiography

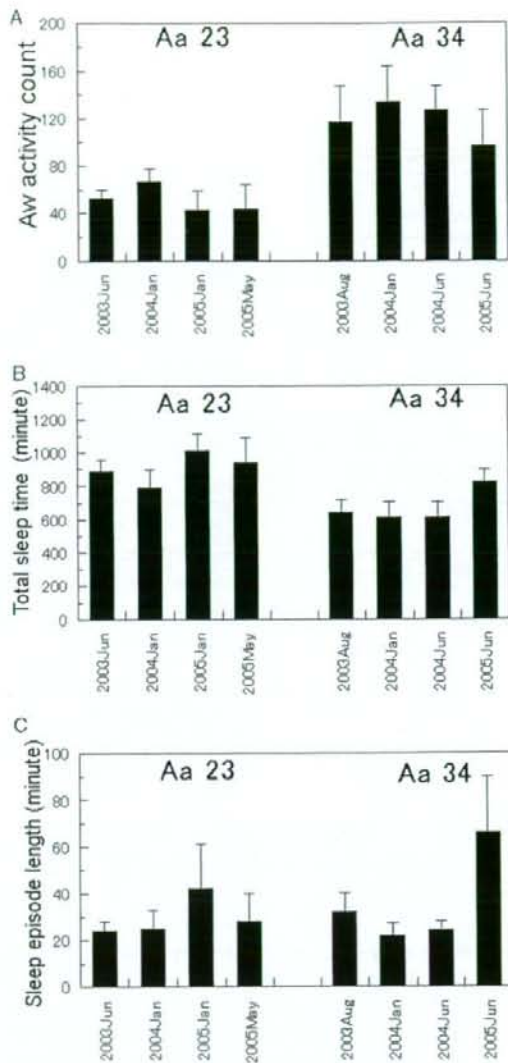
Radiographs of the whole body of the monkeys were taken to evaluate the alteration in spinal curvature as a consequence of aging. After anesthesia with ketamine HCl, as noted above, each subject was positioned (a) left lateral recumbently, and (b) dorso-ventrally, above the film cassette containing Fuji medical x-ray film 'RX-U' (Fujifilm Medical Co., Ltd. Tokyo, Japan). Care was taken to avoid overextension or flexion of limbs while the animals were positioned on radiographic cassette. The optimum X-ray exposure (Hitachi Medico portable X-ray machine) was 60 kV (20 mA) with exposure time set between 0.1 and 0.2 s. The distance between the film and X-ray beam source was 1 m. The films were wet processed at 20°C.

Spinal curvature of the monkeys was determined from the whole body radiographs, using kyphotic index (KI) as the criterion [34]. KI, calculated directly from the radiographs, is the ratio of AB/CD, where AB = length of the line marking the distance from seventh cervical vertebra to the sacral promontory and CD = the distance from AB to anterior border of the vertebral body that is furthest from AB [34].

## Results

### Activity-sleep quantitation

The daily activity levels, measured as mean AW activity counts, of the focal subject Aa 23 and its female offspring Aa 34 are shown in Fig. 1A. The daily mean ( $\pm$ SD) AW activity counts for the focal subject Aa 23 in June 2003, January 2004, January 2005 and May 2005 were  $53 \pm 7$ ,  $67 \pm 10$ ,  $43 \pm 16$  and  $44 \pm 20$  respectively. In comparison, the daily mean ( $\pm$ SD) AW activity counts for Aa 34 in August 2003, January 2004, June 2004 and June 2005 were  $117 \pm 30$ ,  $134 \pm 30$ ,  $127 \pm 20$  and  $97 \pm 30$  respectively. As expected, in all four data points spanning 2 years, the intensity of daily activity of aged Aa 23 monkey was almost one half or less to that of its progeny Aa 34. The AW activity count of Aa 56, the grandprogeny of Aa 23, was also determined in April 2005, when it reached 1 year. The daily mean ( $\pm$ SD) AW activity



**Fig. 1** Comparison of measured activity and sleep parameters of longevous owl monkey (Aa23, aged >26 years) and its progeny (Aa 34, aged 16 years). (A) Activity counts, (B) total sleep time, and (C) sleep episode length. Each histogram represents the activity-sleep quantitation of consecutive 13 days. Results are expressed as daily mean  $\pm$  SD.

count of  $323 \pm 104$  for Aa 56 (data not included in Fig. 1A) was nearly threefold higher to that of its female parent Aa 34, though it shared the same age. We also positively ascertained from comparative individual videotape records of 24 hours duration of all

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.

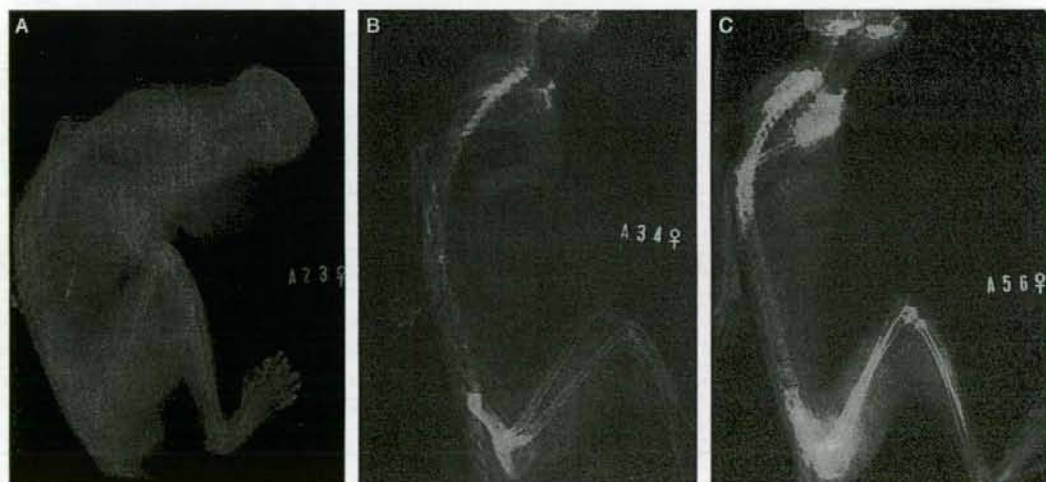
The daily mean ( $\pm$ SD) TST in the focal subject Aa 23 and its progeny Aa 34 are shown in Fig. 1B. The daily mean ( $\pm$ SD) TST for the focal subject Aa 23 in June 2003, January 2004, January 2005 and May 2005 were  $887 \pm 72$ ,  $790 \pm 103$ ,  $1016 \pm 94$  and  $937 \pm 150$  minutes respectively. In comparison, the daily mean ( $\pm$ SD) TST for Aa 34 in August 2003, January 2004, June 2004 and June 2005 were  $643 \pm 76$ ,  $612 \pm 92$ ,  $614 \pm 91$  and  $822 \pm 71$  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 ( $\pm$ SD) TST of Aa 56 was determined to be  $712 \pm 55$  minutes (data not included in Fig. 1B).

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

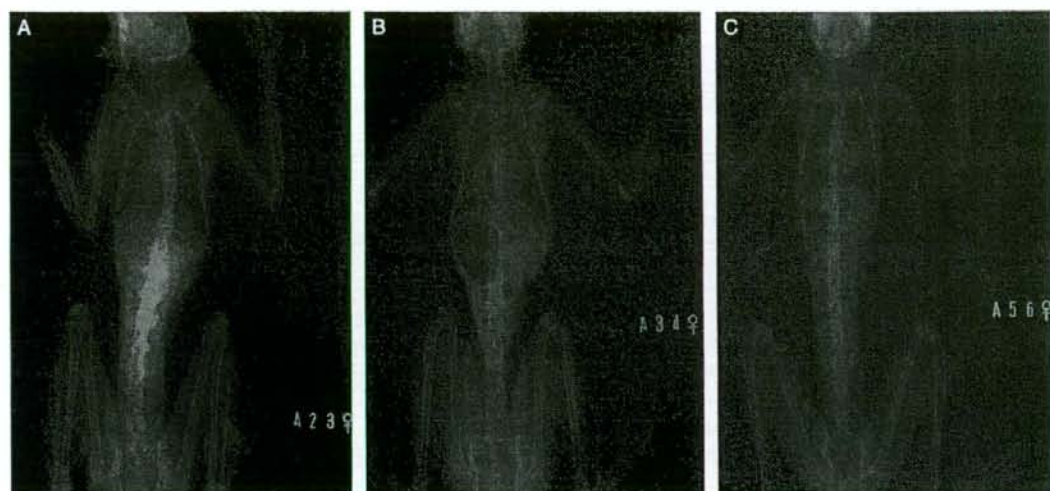
respectively. In comparison, the daily mean ( $\pm$ SD) SEL for Aa 34 in August 2003, January 2004, June 2004 and June 2005 were  $32 \pm 8$ ,  $22 \pm 5$ ,  $24 \pm 4$  and  $66 \pm 24$  minutes respectively. As opposed to the marked difference in the TST values between that of Aa 23 and Aa 34, it appears 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  $43 \pm 13$  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 <sup>1</sup> (mm)	CD <sup>2</sup> (mm)	KI <sup>3</sup>
Aa 23	>26	166	73	2.27
Aa 34	16	198	41	4.83
Aa 56	1	206	38	5.42

KI, kyphotic index.

<sup>1</sup>Length of the line marking the distance from seventh cervical vertebra to the sacral promontory. Measurement was made directly from the radiograph.

<sup>2</sup>The distance from AB to anterior border of the vertebral body that is furthest from AB. Measurement was made directly from the radiograph.

<sup>3</sup>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.

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

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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 accelerometer-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.

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**KEY WORDS:** actigraphy; longevity; nocturnality; parental care; total sleep time.

### 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

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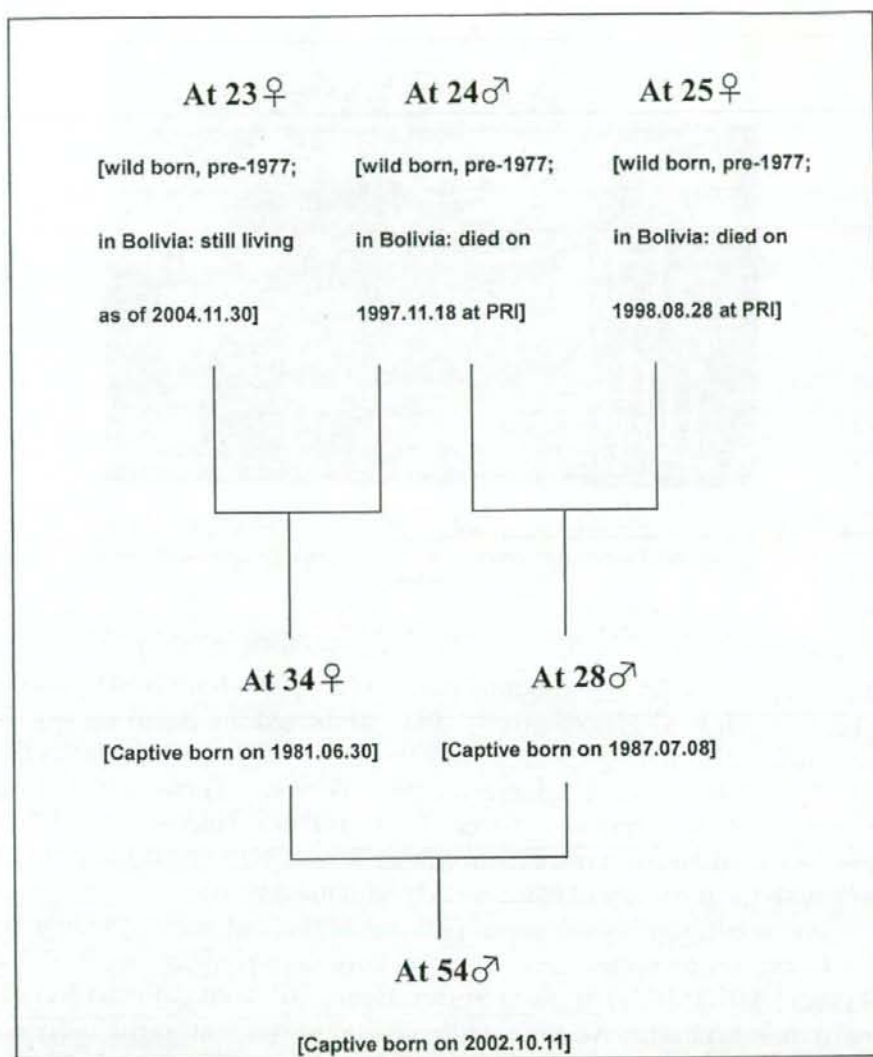
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Bolivia have described its sleeping sites such as tree holes and platforms in lodge trees (Aquino and Encarnacion, 1986; Garcia and Braza, 1993; Hershkovitz, 1983; Rathbun and Gache, 1980; Wright, 1978, 1983;). Wright (1983, 1994) observed that owl 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



**Fig. 1.** Genealogy of a 3-generational owl monkey family at the Primate Research Institute (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 $\sigma$  (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 accelerometer-type miniature transmitter (Actiwatch AW 64 model-MINIMITTER, Mini Mitter, Bend, OR, containing 64 KB of on-board 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<sup>®</sup> 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 actiwatchers 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 actiwatchers 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 actiwatchers 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 (Dixon, 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

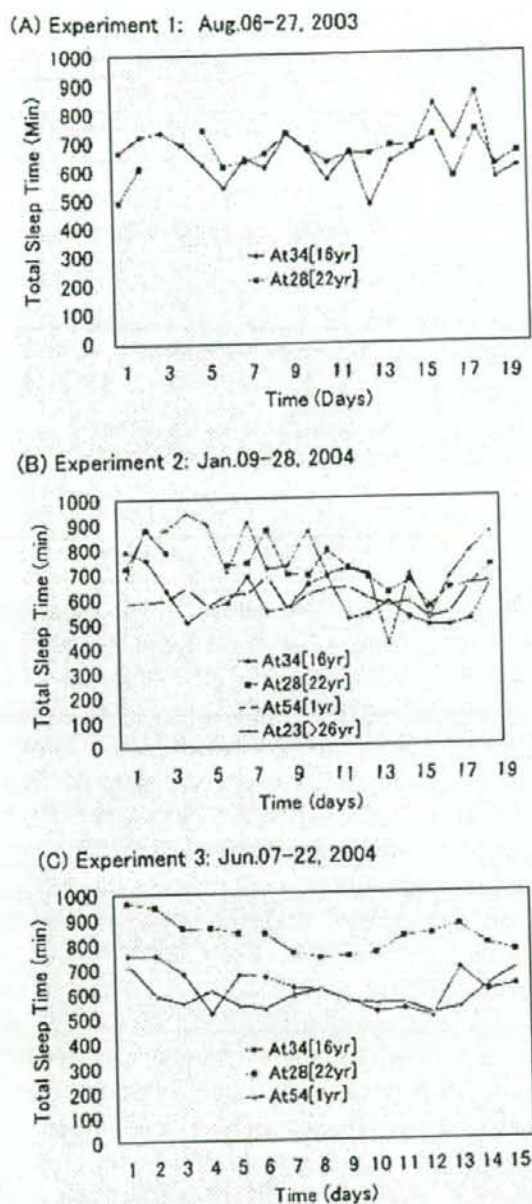
The fluctuations in daily TST for 20 d of continuous monitoring for At 28 and At 34 sharing the same cage are in Fig. 3A. The mean (+SD) values of daily TST for At 28 and At 34 are 658 (+64) and 665 (+92) min, respectively. Thus, on average the TST is *ca.* 11 h in the mating pair of owl monkeys. The 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 ( $\pm$ SD) value of daily TST, 820 ( $\pm$ 71) min, is markedly higher than the corresponding values for At 28 in Expt. 1 and 2 (Table I). Conversely, the mean ( $\pm$ SD) value of daily TST, 612 ( $\pm$ 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.



**Fig. 3.** Daily total sleep time (TST) determinations in owl monkeys. (A) Expt. 1 (August 6-27, 2003)—At 28 $\sigma$  and At 34 $\phi$ ; Expt. 2 (January 9-28, 2004)—At 23 $\phi$ , At 28 $\sigma$ , At 34 $\phi$ , and At 54 $\sigma$ ; Expt. 3 (June 7-22, 2004)—At 28 $\sigma$ , At 34 $\phi$ , and At 54 $\sigma$ . In all 3 experiments, mating pairs At 28 $\sigma$ , At 34 $\phi$ , and their 1-yr-old offspring At 54 $\sigma$  shared the same cage. During Expt. 3, At 28 $\sigma$  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 <sup>a</sup>	Daily mean TST (min) <sup>b</sup>		
	Expt. 1	Expt. 2	Expt. 3 <sup>c</sup>
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

<sup>a</sup>At 28, At 34 and At 54 occupied the same cage during the period covered in 3 experiments.

<sup>b</sup>Expressed as mean ± SD.

<sup>c</sup>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 <sup>a</sup>	12–20?	Hearn and Dixon (1984)
(unidentified) <sup>b</sup>	18	Scott (1992)
California Institute of Technology <sup>c</sup>	>20	Baer (1994)
University of Tübingen	>20	Rappold and Erkert (1994)
Lincoln Park Zoo, Chicago <sup>c</sup>	~25	Margulis (2004) <sup>d</sup>
(unidentified) <sup>b</sup>	~26–27	Allman <i>et al.</i> (1998)
University of Tübingen	>25	Erkert (1999)
(unidentified) <sup>b</sup>	25.3	Carey and Judge (2000)
Kyoto University, Inuyama <sup>e</sup>	>27	Present study (2004)

<sup>a</sup>Location not specifically indicated; appears to be composite information. The question mark following the numbers is as in the original.

<sup>b</sup>Cites the source as M. L. Jones (1980).

<sup>c</sup>Unpublished data.

<sup>d</sup>Personal correspondence from Sue Margulis (Primates Curator, Lincoln Park Zoo, e-mail, November 18, 2004).

<sup>e</sup>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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