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Sleep Patterns of Aging Chimpanzees

(*Pan troglodytes*)

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Abstract

Diurnal primates spend around half of their lifetime sleeping or inactive. These nocturnal behaviors are considerably understudied compared to daytime activities. While it is well established that sleep quality diminishes with age in humans, little is known about the effects of advanced age on sleep in our closest primate relatives. We aimed to describe captive chimpanzee (*Pan troglodytes*) sleep patterns and examine whether individual sleep quality changed over an 11-yr period. We recorded the individual night rooms of 12 chimpanzees for six nights using infrared video cameras and analyzed 72 nights (936 h) of video. To evaluate long-term changes, we compared our data from 2018–2019 with previously published data from 2007–2008 on the same individuals living under the same conditions. We used complete inactivity and a head-down, lying posture as a proxy measurement for sleep. Each night individuals slept a mean of 10.5 (\pm SD 1.8) h and woke up 15.1 (\pm 3.6) times. The mean duration of sleep bouts was 45.4 (\pm 16.8) and the mean duration of awake bouts was

10.2 (\pm 8.2) min. We found that as chimpanzees aged they experienced significantly more frequent awakenings and shorter sleep bouts (i.e., more fragmented sleep), but nightly sleep duration and the length of awake bouts did not differ significantly between the two study periods. Our results suggest that chimpanzees experience some changes in sleep with age similar to those in humans and other animals.

Keywords Aging. Chimpanzee. Sleep. Sleep patterns. Welfare

Introduction

Sleep is essential for all primates, and substantial evidence exists linking sleep to the maintenance of the body and the brain including neurogenesis, oxidative stress defense, energy restoration, and cognitive processing (e.g., Samson and Nunn 2015; Samson *et al.* 2019; Siegel 2005; Walker 2008). Primate sleep duration varies greatly across species, from around 7 h in humans (*Homo sapiens*) to 17 h in owl monkeys (*Aotus trivirgatus*), with chimpanzees (*Pan troglodytes*) sleeping around 10 h, just below the average for primates (Nunn and Samson 2018; Nunn *et al.* 2010). While humans sleep fewer hours than their closest primate relatives, chimpanzees and bonobos (*Pan paniscus*), they obtain overall deeper sleep and a higher proportion of rapid eye movement (REM) sleep, the stage in which dreams typically occur and when animals experience a maximal disconnect from their external environment (Nunn and Samson 2018; Samson and Nunn 2015).

Sleep quality diminishes with healthy aging in humans, with a decrease in total sleep duration, more frequent awakenings, shorter sleep bouts, and longer awake bouts (e.g., Floyd *et al.* 2000; Gulia and Kumar 2018; Li *et al.* 2018; Mander *et al.* 2017; Vitiello 1997, 2006). A wide range of species, including geladas (*Theropithecus gelada*: Noser *et al.* 2003), rhesus macaques (*Macaca mulatta*: Zhdanova *et al.* 2011), Asian elephants (*Elephas maximus*: Walsh 2017) and even fruit flies (*Drosophila melanogaster*: Koh *et al.* 2006) also exhibit characteristics of decreasing sleep quality with age such as less or more fragmented sleep. However, we do not know if similar changes occur in our closest evolutionary relatives, with whom we share similar life history patterns and long periods of sleep. Moreover, because most human sleep studies have focused on individuals from industrialized populations, the sleep behavior of people living in nonindustrial or small-scale societies is less well understood. In one study,

opposite changes were observed among pastoralists in a small-scale society where labor demands shifted to younger individuals, possibly freeing more time for the elders to sleep (Prall *et al.* 2018), illustrating that diverse sleep patterns exist across human populations (Rattenborg *et al.* 2017).

Although sleep is an essential activity that can occupy around half of an individual's lifetime, the sleep behaviors of chimpanzees and most other primates are not well understood. In the wild, chimpanzees typically select a site suitable for building sleeping platforms in trees usually around 8–20 m high, but up to 48 m high, and sleep in those platforms from dusk to dawn (Goodall 1962; McCarthy *et al.* 2017). Although chimpanzees are diurnal, various nighttime activities have been reported such as vocalizing, urinating, feeding, crop raiding, and socializing (Krief *et al.* 2014; Pruetz 2018; Zamma 2014). Given the sleeping habits of wild chimpanzees, they have never been recorded in detail. Collecting unobstructed night recordings in captive environments can also be challenging, and scoring videos is tedious and time consuming. Recent advances may facilitate captive sleep studies (e.g., Melvin *et al.* 2019), but describing sleep architecture in the wild will likely remain a challenge for many primate species (*cf.* Reinhardt *et al.* 2019 for the first detailed sleep study of a primate in the wild using actigraphy). Despite this, the study of sleep in natural environments is encouraged to measure its patterns and functions in the ecological contexts animals evolved in (Rattenborg *et al.* 2017; Reinhardt 2020).

Although captive chimpanzee sleep patterns have been described noninvasively (Morimura *et al.* 2012; Videan 2006), little is known about the potential effects of advanced age on their sleep, and no study has followed the same individuals over an extended period of time (i.e., longitudinal study). In one study, older chimpanzees (33–44 years, $N = 10$) slept longer and had fewer sleep disruptions than younger, prime adults (14–28 years, $N = 10$), suggesting that they experienced higher overall sleep qu

ality (Videan 2006). In another report, increasing age resulted in more frequent awakenings, but not a decrease in total sleep time; however, this study did not include individuals old enough (only one, 37 yr old) to address potential age effects comprehensively (Morimura *et al.* 2012).

We studied the sleep of captive chimpanzees living at Kumamoto Sanctuary in Japan and present a cross-sectional and longitudinal investigation of the effects of aging on sleep. Our first aim is to expand the literature on chimpanzee sleep patterns with new data including aged individuals by describing four sleep variables and comparing two age classes (prime and old adults) cross-sectionally. To do this, we video recorded 12 long-term resident male chimpanzees over six, 13-h nights (resulting in 936 h of data) and analyzed the videos following Morimura *et al.* (2012), using instantaneous sampling at 1-min intervals. Our second aim is to examine whether individual sleep quality changes with increasing age, and for this we took a long-term, or follow-up, approach. To do this, we compared our data collected from 2018 to 2019 with data collected from 2007 to 2008 on the same 12 individuals living under the same conditions (Morimura *et al.* 2012). Thus, we compared repeated measures on the same individuals at two points in time separated by *ca.* 11 yr.

We hypothesize that as chimpanzees age, their sleep quality decreases. Specifically, we predict the following differences in older individuals (cross-sectional comparisons) and changes within individuals after aging (long-term comparisons): 1) a decrease in the total nightly sleep duration, 2) an increase in the number of nightly awakenings (sleep fragmentation), 3) a decrease in the mean sleep-bout duration (used as a proxy for the depth of sleep), and 4) an increase in the mean awake-bout duration (time spent awake after sleep disruption).

Methods

Subjects and Site

We observed chimpanzees living at Kumamoto Sanctuary (previously named Chim-panzee Sanctuary Uto, a former laboratory facility) in Kumamoto, Japan. All individuals ($N = 12$) were males aged 23 to an estimated 48 (± 1) yr at the time of data collection (October 2018–May 2019; Table I). In the earlier study, which took place between October 2007 and April 2008, these same individuals were around 11 yr younger, aged 12 to an estimated 37 (± 1) yr (Morimura *et al.* 2012). During the day, the chimpanzees lived in three all-male groups. Group composition changed daily, and chimpanzees had access to one of three outdoor enclosures of either 413 m³ (W: 8.5 m, D: 12.8 m, H: 3.8 m, two enclosures) or 486 m³ (W: 10.0 m, D: 12.8 m, H: 3.8 m, one enclosure) in area. One day every 2 weeks the three outdoor enclosures and a 150 m long corridor were open for all males to interact, if they chose to do so. Keepers separated individuals into individual indoor night rooms, each 10.8 m³ in area (W: 2.0 m, D: 2.0 m, H: 2.7 m), before giving them dinner. While the chimpanzees remained socially isolated each night from the evening until the following morning (16:00 h to around 08:00 h), they were able to communicate with neighboring individuals visually and physically through a small section of iron bars. Indoor rooms were brightened by automatic lights set from 07:00 h to 19:00 h providing a light–dark condition of 12:12 each day, in addition to daylight reaching each night room through ceiling windows. While rooms were temperature controlled to 20–28° C, outside air reached the rooms through a small gap in the door so outdoor seasonal changes may have slightly affected indoor conditions.

Previous studies have typically classified chimpanzees as “aged,” “old,” or “elderly” from 30 or 33 yr (e.g., Baker 2000; Videan 2006), but recently this boundary was increased to 35 and 37 yr (Hopkins *et al.* 2020; Neall Webb *et al.* 2019). We classified chimpanzees aged 36 yr or older as “ol

d” adults because individuals in our study fell into two clear groups based on age; the oldest “prime” adult was 31 yr of age (Table I).

Data Collection

We recorded the chimpanzees’ nocturnal activity during 4 mo (October 13–November 24, 2018, April 17–May 2, 2019) using a custom-built apparatus attached securely to the top of indoor night enclosures. We used infrared night vision cameras (Wyze Cam V2 1080p; Wyze Labs, Inc.) which we installed and maintained daily, rotating between two and six rooms per night. For the entirety of an individual’s night activity to be visible, one camera and one external infrared light (F8150_940nm; EnergyPower, Inc.) were required per room, placed on the center of the enclosure top and pointing down thus providing a “bird’s-eye view” (Fig. 1). In total we collected 123 recorded nights; of these we analyzed six per individual (72 in total) and compared our data with data from the the 72 nights in Morimura *et al.*’s (2012) study.

Following Morimura *et al.* (2012), we used instantaneous sampling at 1-min intervals throughout the 13-h period (17:00–06:00 h) to record sleep. We defined sleep using behavioral criteria: a completely inactive posture with the body lying down and head on the floor or nesting materials. If an individual was in the same state (i.e., asleep or awake) at two consecutive time points, we assumed that they were in that state for the intervening period. Thus “sleep” as defined here may not have always been true sleep (i.e., the behavior we observed may not always have been accompanied by the full physiological manifestation of sleep, especially sleep bouts of shorter durations). To identify sleep states precisely and noninvasively, allowing a thorough understanding of sleep architecture, requires techniques such as scoring behavioral signatures (e.g., respiration, random eye movement; Samson and Shumaker 2013), which was not possible in this study.

We generated descriptive statistics of four variables for each individual each night:

- 1) *total sleep duration* was the sum of all sleep bouts for each 13-h observation period,
- 2) *number of awakenings* was the count of all awake bouts occurring between sleep bouts, 3) *mean sleep bout duration*, and 4) *mean awake bout duration*. We report means in the text for comparison with previous studies, although not all data were normally distributed and so we also provide medians and plot the data. We generated these variables, for both our data and for the data from Morimura *et al.* (2012), in two different ways: the first including all 1-min sampled data, which we term *high-resolution* sleep, and the second considering only sleep bouts >5 min in duration which we call *no tossing-turning* sleep. We used 5 sequential minutes of complete inactivity because the number of sleep bouts <5 minutes was highly skewed and following Videan (2006). Although a 1-min awake bout may have more accurately identified an individual as truly awake (e.g., sitting up or standing to urinate in the night), it is unlikely that “true” sleep occurred during sleep bouts of only 1–4 min. Due to our use of infrared videography, rather than polysomnography or actigraphy, we could not be sure whether an individual entered actual sleep in any sleep bout, especially bouts of short duration, so we removed some of the noise present in the *high-resolution* sleep data by using *no tossing-turning* data for some analyses.

Whereas Morimura *et al.* (2012) reported the maximum duration of sleep and awake bouts, we report their mean durations, due to potential variability across nights (e.g., a disruption from a neighboring chimpanzee could result in a particularly long awake bout). We did not consider the effect of day length or external temperature on sleep behaviors because Morimura *et al.* (2012) found no effect of these variables and because indoor night rooms were on a time-controlled light and temperature setting.

Statistical Analysis

We used R to conduct statistical analyses (R Core Team 2017). To examine interindividual variability in sleep patterns, we compared the four dependent sleep variables across individuals (2018–2019 data only) using Kruskal–Wallis tests due to violations of the assumptions of the one-way analysis of variance (ANOVA), followed by Bonferroni *post hoc* tests. To examine the relationship between age category and sleep variables cross-sectionally (2018–2019 data only), we ran a Welch two-sample *t*-test for *number of awakenings* (data normally distributed and variances homogeneous) and two-sample Wilcoxon rank tests with continuity correction for the other three variables. We used Welch two-sample *t*-tests to compare intraindividual changes between 2007–2008 and 2018–2019 data.

To perform linear mixed effects analyses of the relationship between age and the four sleep variables, we used the *lme4* (Bates *et al.* 2015) and *lmerTest* (Kuznetsova *et al.* 2016) packages. The data for *number of awakenings* was count rather than continuous so we used a Poisson generalized linear mixed model. We entered age as a fixed effect (we subtracted the minimum age from all ages), and as random effects we included intercepts for individuals to control for repeated measures (i.e., a random intercept model) and by-individual random slopes for the effect of age to allow individuals to show differing slopes. We used the *summary* function in R to compare the null (intercept only) models with the full models (Pinheiro and Bates 2000). We considered values of $P < 0.05$ to be statistically significant, and report fixed-effects estimates and confidence intervals.

Ethical Note

For this study, we implemented no changes apart from installing cameras above six of the indoor night rooms. Food and water were available *ad libitum*. The care and study of the chimpanzees complied with the Guide for Animal Research Ethics provided by the Wildlife Research Center, Kyoto University and the Guide for the Care and Use of Great Apes of Kumamoto Sanctuary. The study was conducted in a manner commensurate with the ethical policy of the Wildlife Research Center, Kyoto University, as well as domestic and international laws related to the welfare and management of animals and was approved by the Institutional Animal Experimentation Committee (#WRC-2018KS004A). The authors declare that they have no conflict of interest.

Data Availability The data sets analyzed in the current study are available from the corresponding author on reasonable request.

Results

Sleep Characteristics and Cross-Sectional Comparison (2018–2019 data only)

Twelve male captive chimpanzees, ranging from 23 to an estimated 48 yr old in 2018–2019, slept for a nightly mean duration of $10.5 \pm \text{SD } 1.8$ h, or $631.6 \pm \text{SD } 108.5$ min, and showed individual differences (Kruskal–Wallis test: $H = 42.98$, $df = 11$, $P < 0.001$; Table II). The oldest individual, Lennon, slept a mean of 744 min (12.4 h) each night, the longest of all individuals, whereas Mizuo slept 492 min (8.2 h) per night. Shirou and George were the only two other individuals who slept < 10 h per night. Chimpanzees experienced a mean of $15.1 \pm \text{SD } 3.6$ awakenings each night, and this also differed across individuals ($H = 31.13$, $df = 11$, $P = 0.$

001; Table II). Whereas Lennon woke up 11 times per night, Naoya woke up 20 times and had the most fragmented sleep.

The mean sleep bout duration was $45.4 \pm \text{SD } 16.8$ min and differed among chimpanzees (Kruskal–Wallis test: $H = 31.48$, $df = 11$, $P < 0.001$; Table II). Naoya exhibited the shortest mean sleep bout, 33 min, whereas Lennon slept 40 min longer (73 min) per bout. The mean awake bout duration was $10.2 \pm \text{SD } 8.2$ min and also differed among individuals ($H = 37.38$, $df = 11$, $P < 0.001$; Table II). Lennon experienced the shortest mean awake bout (4 min) and Shirou the longest (22 min). The mean of the maximum sleep bouts was 120 min (2 h); Mizuo experienced the shortest maximum sleep bout of 103 min (1.7 h) and Takaboh the longest of 288 min (4.8 h). The mean maximum awake bout was 50 min; George once stayed awake for 252 min (4.2 h) whereas Takaboh's longest period awake was 29 min.

We found no significant differences between “prime” and “old” adults in any of the four measured sleep variables: *total sleep duration* (Wilcoxon rank-sum test: $W = 582.5$, $P = 0.591$; Fig. 2a); *number of awakenings* (Welch two-sample t -test: $t = -0.590$, $P = 0.557$; Fig. 2b); *mean sleep bout duration* (Wilcoxon rank-sum test: $W = 589.5$, $P = 0.648$; Fig. 2c); *mean awake bout duration* (Wilcoxon rank-sum test: $W = 563$, $P = 0.448$; Fig. 2d).

Long-Term Comparison (2007–2008 and 2018–2019 Data)

Nine individuals exhibited a significant change in at least one of the sleep measures across the 11-yr period, whereas three individuals (Mizuo, Shirou, Takaboh) showed no significant changes in any of the four variables (Fig. 3a–d and Electronic Supplementary Material [ESM] Table SI). As chimpanzees aged they experienced significantly more frequent awakenings (Table III, Fig. 3b) and shorter sleep bouts (Table III, Fig. 3c), so

overall more fragmented sleep. Overall, the mean number of awakenings in 2007–2008 was $11.6 \pm \text{SD}$

3.8 and increased to $15.1 \pm \text{SD } 3.4$ in 2018–2019, and mean sleep bout duration decreased from $64.9 \pm \text{SD } 27.8$ to $45.4 \pm \text{SD } 16.8$ min (Table II).

Neither total nightly sleep duration (Table III, Fig. 3a) nor the length of awake bouts (Table III, Fig. 3d) differed significantly between the two study periods after chimpanzees aged. Overall, the mean total sleep duration in 2007–2008 was $670 \pm \text{SD } 91.5$ min ($11.2 \pm \text{SD } 1.5$ h) and decreased to $632 \pm \text{SD } 108$ min ($10.5 \pm \text{SD } 1.8$ h) in 2018–2019, and mean awake bout duration showed little change from $9.9 \pm \text{SD } 8.6$ to $10.2 \pm \text{SD } 8.2$ min (Table II). When we included only chimpanzees that transitioned from “prime” to “old” age between the two periods ($N = 6$; Table I) in the model, there was again no significant relationship between age and total sleep duration (LMM: $\chi^2 = 3.524$, $df = 6$, $P = 0.060$) or mean awake bout duration (LMM: $\chi^2 = 1.072$, $df = 6$, $P = 0.300$), whereas the number of awakenings (GLMM: $\chi^2 = 6.307$, $df = 5$, $P = 0.012$) and mean sleep bout duration again showed a significant relationship with age (LMM: $\chi^2 = 7.647$, $df = 6$, $P = 0.006$).

Discussion

Sleep Characteristics

The 12 adult male captive chimpanzees in the current study, all of which were included in Morimura *et al.*'s (2012) study, slept a mean of 10.5 h per night. Variation in sleep time has been reported across captive chimpanzee groups, from a mean of 8.8 to 11.3 nightly hours (noninvasive studies only; Morimura *et al.* 2012; Videan 2006), and our findings fall within this range. Across populations, humans also show variation in sleep duration from as little as a mean 5.5 h of sleep per night among Himba N

amibian agropastoralists (Prall *et al.* 2018) to 7.9 h per night among Melanesian horticulturalists (Smit *et al.* 2019). For a wider primate comparison, captive orangutans (*Pongo* spp.) slept a nightly mean of 9.3 h and captive baboons (*Papio papio*) slept a nightly mean of 7.3 h (Samson and Shumaker 2015).

Similar to what has been observed in the wild (Zamma 2014), chimpanzees in our study often woke up to defecate, urinate, drink, or adjust their posture or sleeping location due to the vocalizations of other individuals or for other reasons. They experienced a mean of 15 awakenings per night, considerably more than the 3–5 awakenings reported in a different group of captive chimpanzees, although in that study awake bouts were counted from a minimum of 2 min instead of 1 min as in the current study (Videan 2006). Fifteen nightly awakenings was also more frequent than the 12 previously reported in Morimura *et al.* (2012), but nearly the same as orangutans who woke up a mean of 14 times per night, and less frequent than baboons that woke up 18 times (Samson and Shumaker 2015).

The mean nightly sleep bout duration, or period of undisturbed rest, may partly characterize the depth of sleep obtained. The mean sleep bout duration of the 12 chimpanzees was 45 min and the mean maximum sleep bout each night was 120 min. Chimpanzees' sleep bouts may be considerably shorter than humans', who typically spend 70 to 100 min in their first NREM-REM sleep cycle with subsequent cycles lasting longer (Institute of Medicine 2006). The mean awake bout duration of the chimpanzees was 10 min (awake bouts were most often only a single minute) and the mean maximum awake bout each night was 50 min. Because individuals were physically separated throughout the night, there may have been fewer engagements or opportunities to keep them awake for as long as the mean 20 min reported in a captive group where chimpanzees remained together with indoor and outdoor access throughout the night (Videan 2006). One individual who stood out in our data was George, w

hose habit of licking his lips sometimes appeared to prevent him from falling asleep (maximum of 252 min), although once asleep he stopped engaging in this behavior. Our continuous data were nonnormal, and data for similar variables in other studies may also not be normal; in such cases we recommend reporting medians in future work.

Similar to Morimura *et al.* (2012), we found high intra- and interindividual variability in sleep patterns in chimpanzees, illustrating that repeated measures and several individuals are required for to characterize sleep in chimpanzees. This is likely the case for other primates as well. Our data suggested that the oldest individual included in our study, 48-year-old Lennon, experienced higher-quality sleep than most other individuals as he showed longer total sleep, fewer awakenings, longer sleep bouts, and shorter awake bouts. Thirty-year-old Mizuo, by contrast, showed the opposite patterns. Three individuals—Mizuo, Shirou, and Takaboh—showed highly consistent sleep patterns across the 11-year period, with no significant changes across any of the four sleep measures, whereas the other nine experienced significant changes. Mizuo and Shirou exhibited poorer sleep quality than most other individuals during both observation periods.

Cross-Sectional Comparison

In a cross-sectional comparison using only data from 2018–2019, we hypothesized that old chimpanzees (≥ 36 years, $N = 7$) would experience lower sleep quality than young adults (23–31 years, $N = 5$). However, we found no age-related significant differences across any of the four measured sleep variables. Our findings contrast with the only other study comparing sleep between age classes, where old chimpanzees ($N = 10$) slept more and woke less frequently than prime adult individuals ($N = 10$), suggesting that they experienced higher quality of sleep (Videan 2006). The relatively small sample size may have influenced results in bo

th studies, especially in light of the high interindividual variation observed.

Long-Term Comparison

One of our aims was to reassess the sleep of the same individuals living under the same conditions 11 years after Morimura *et al.* (2012; videos recorded in 2007–2008). We hypothesized that as chimpanzees aged, they would experience lower sleep quality. Similar to the poorer quality of sleep observed among aging humans (e.g., Mander *et al.* 2017; Vitiello 2006), we found that as chimpanzees aged, they experienced more frequent awakenings and shorter sleep bouts. Greater disruption in sleep continuity may have contributed to the shortening of sleep bouts, which could suggest that individuals obtained less deep sleep at an older age. The sleep–wake cycle of mammals is partly regulated by circadian rhythms and homeostatic processes, along with environmental and various other factors, which change with increasing age and may influence sleep patterns in similar ways across species (Froy 2011; Gulia and Kumar 2018; Vitiello 2006). Humans and their ape relatives share other late-life changes, for example cardiovascular disease and other medical illnesses, which have been linked to decreases in human sleep quality (Doane *et al.* 2006; Vitiello 2006; Videan *et al.* 2009). Reanalyzing sleep data in light of health outcomes and survivorship of chimpanzees could reveal whether similar relationships are to be found in humans' nearest evolutionary neighbors.

In contrast to humans (e.g., Mander *et al.* 2017; Vitiello 2006), the effect of increasing age on the chimpanzees' total nightly sleep duration and the duration of their awake bouts was variable and nonsignificant. Overall, chimpanzees did not significantly lose or gain sleep in older age, and they did not stay awake longer after awakening (e.g., to urinate, change position). One explanation for this may be simply that chimpanzees do not experience all of the same changes as humans as they age. Another exp

lanation may be that because these chimpanzees were separated each night with little to do other than sleeping or resting, a decrease in total sleep and increase in awake bout duration was not observed.

Although we found no evidence of a population-level trend in changes in sleep quality as a function of age in the cross-sectional data, long-term data revealed decreasing quality in some sleep variables within individuals. However, five individuals were still prime-aged adults at the end of this study and thus not all individuals had reached “old” age. The precise time course of sleep changes in humans is not well established. Although it is often stated that as age increases, sleep quality decreases (e.g., Floyd *et al.* 2000; Gulia and Kumar 2018), a review concluded that most changes in humans’ sleep occur during early and middle adulthood (age 19–60 yr), whereas fewer changes occur in old age (60+ years) (Vitiello 2006). When we considered only chimpanzees who transitioned from “prime” to “old” age between the two time periods ($N = 6$) in analyses, the results were similar to those including all individuals, although they showed slight differences such as less nightly sleep. In summary, results from our long-term data showed that adult chimpanzees experienced some changes which suggest a decrease in sleep quality as they aged by 11 yr.

Limitations

Our study is a small step toward a better understanding of the potential effects of age on sleep in great apes. Although the chimpanzees’ caretakers, living conditions, and routines remained mostly consistent between the two study periods, factors other than age may have influenced sleep (e.g., social rank, stress level, daily events or changes), especially given our relatively small sample size, which was limited to males. When possible, future studies should include females, especially because human males show greater sleep impairments in old age than females (Mander *et al.*

2017). Another shortcoming of our study is that our attempt to study age-related changes on sleep was not truly longitudinal, as individuals were not observed regularly over an extended period of time, but during two periods of time 11 yr apart. Additionally, our data collection method was restricted to the use of noninvasive infrared video recording and so we could not describe sleep architecture because we did not use polysomnography or actigraphy techniques. However, direct observation allowed us to obtain nightly postural and other nocturnal behavioral data for future analyses.

The comparability of observations of sleep behaviors in a captive group of apes and those in the wild or more ecologically relevant environments is not clear. The only study directly comparing sleep in wild and captive primates, in a nocturnal species, suggests that such comparisons may not be useful due to ecological differences shaping this behavior (Reinhardt *et al.* 2019). However, it has also been argued that it is possible to obtain species-typical sleep durations from captive animals based on the consistency of sleep observed in humans across various environments, and phylogenetically consistent sleep patterns across species (Capellini *et al.* 2008; Nunn and Samson 2018). Still, captive animals receive plentiful and consistent food, live in spaces where temperature and other ambient conditions may be controlled, and experience daily routines unlike those living in natural habitats. Such conditions could allow captive individuals to allocate more time to sleep, which may also be less disturbed.

Welfare Considerations

Primates, like many other animals, spend half of their lifetime sleeping and resting, yet sleep-related behavior is considerably understudied compared to their waking activities (Anderson *et al.* 2019). Caretakers, resea

rchers, and staff working in a captive setting should strive to provide the best possible care to animals throughout their lives. We suggest that examining sleep is important for a fuller understanding of animal behavior; noninvasive studies are needed to draw appropriate conclusions of sleep physiology and behavior due to the pain, suffering, and stress involved in invasive studies. Monitoring sleep may also identify individual preferences and behaviors that may not be evident during the day, but that might be useful for improving welfare (see Samson and Nunn 2015 for cost-effective technologies). Providing species-appropriate sleeping sites is critical to positive welfare (Brando and Buchanan-Smith 2018). One change derived from the current study is that after sharing a selection of videos with care staff, they decided to increase the number of washable burlap sacks provided as bedding each night, especially to individuals that clearly used them. Additional changes to enhance the welfare of animals living in various captive environments may emerge from more focused studies on sleep in more species, and future research should highlight the role of sleep in health for captive primates. Failing to adequately address sleep behavior could be restricting our understanding of primate biology and behavior, as well as our ability to assess individual welfare needs.

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Author Contributions K. H. conceived the idea building from N. M.'s previously published study. N. M. provided the data published in 2012. K. H. designed the method for data collection, collected and analyzed the data, and wrote the manuscript. S. H. revised the manuscript and supervised the study.

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Figures

Table I Description of captive chimpanzees at Kumamoto Sanctuary, Japan included in a study of sleep (2007–2008, 2018–2019)

Individual	Birthplace	Year born	Age at start of first study (Oct. 2007)	Age at start of current study (Sept. 2018)	Age class at start of study	Age class at end of study
Satoru	Captivity	1995	12	23	P	P
Minato	Captivity	1992	15	26	P	P
Kanao	Captivity	1990	17	28	P	P
Mizuo	Captivity	1989	18	30	P	P
Norihei	Captivity	1987	20	31	P	P
Gorou	Unknown	e. 1982	25	36	P	O
Shirou	Unknown	e. 1982	25	36	P	O
Naoya	Wild	e. 1981	26	37	P	O
Norio	Wild	e. 1981	26	37	P	O
George	Wild	e. 1979	28	39	P	O
Takaboh	Wild	e. 1978	29	40	P	O
Lennon	Wild	e. 1970	37	48	O	O

Age classes are prime-aged adults (P; 12–31 yr) and old-aged adults (O; ≥ 36 yr).

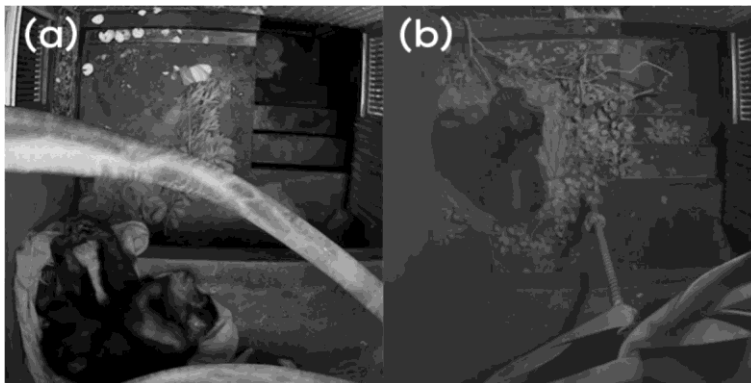


Fig. 1 Bird's eye views of chimpanzee Gorou sleeping at Kumamoto Sanctuary, Japan. (a) Gorou sleeping on the upper platform of an indoor night room during the night of April 20, 2019. (b) Gorou sleeping on the floor on November 23, 2018.

Table II Mean \pm SD and [median (IQR)] of four sleep variables in 12 captive chimpanzees at Kumamoto Sanctuary, Japan (six nights per individual per period) for *high-resolution* and *no tossing-turning* data (2007–2008, 2018–2019)

Data	Total sleep duration (min)	Total sleep duration (h)	Number of awakenings	Mean sleep bout duration (min)	Mean awake bout duration (min)
2018-2019 <i>highres</i>	635.7 \pm 10 8.2 [674.0 (101.5)]	10.6 \pm 1.8 [11.2 (1.7)]	16.7 \pm 3.9 [17.0 (5.0)]	41.2 \pm 16.1 [37.2 (15.2)]	8.9 \pm 7.3 [6.1 (5.4)]
2018-2019 <i>notossing</i>	631.6 \pm 10 8.5 [671.0 (101.3)]	10.5 \pm 1.8 [11.2 (1.7)]	15.1 \pm 3.4 [16.0 (4.0)]	45.4 \pm 16.8 [40.4 (17.0)]	10.2 \pm 8.2 [6.7 (4.9)]
2007-2008 <i>highres</i>	673.7 \pm 90.2 [706.5 (123.0)]	11.2 \pm 1.5 [11.8 (2.1)]	13.1 \pm 4.4 [13.5 (5.0)]	58.3 \pm 28.1 [48.5 (27.6)]	8.2 \pm 6.7 [6.0 (7.1)]
2007-2008 <i>notossing</i>	670.4 \pm 91.5 [704.0 (123.0)]	11.2 \pm 1.5 [11.7 (2.1)]	11.6 \pm 3.8 [11.0 (5.0)]	64.9 \pm 27.8 [58.7 (31.9)]	9.9 \pm 8.6 [6.8 (9.7)]
Combined <i>highres</i>	654.7 \pm 101.1 [683.0 (122.3)]	10.9 \pm 1.7 [11.4 (2.0)]	14.9 \pm 4.5 [15.0 (6.0)]	49.8 \pm 24.4 [41.5 (21.0)]	8.6 \pm 7.0 [6.1 (6.3)]
Combined <i>notossing</i>	651.0 \pm 101.9 [681.5 (122.3)]	10.9 \pm 1.7 [11.4 (2.0)]	13.3 \pm 4.0 [13.0 (5.3)]	55.1 \pm 24.8 [48.3 (22.9)]	10.0 \pm 8.4 [6.8 (7.6)]

High-resolution data include all 1-min samples, whereas sleep bouts <5 min were added to the previous awake bout in *no tossing-turning* data.

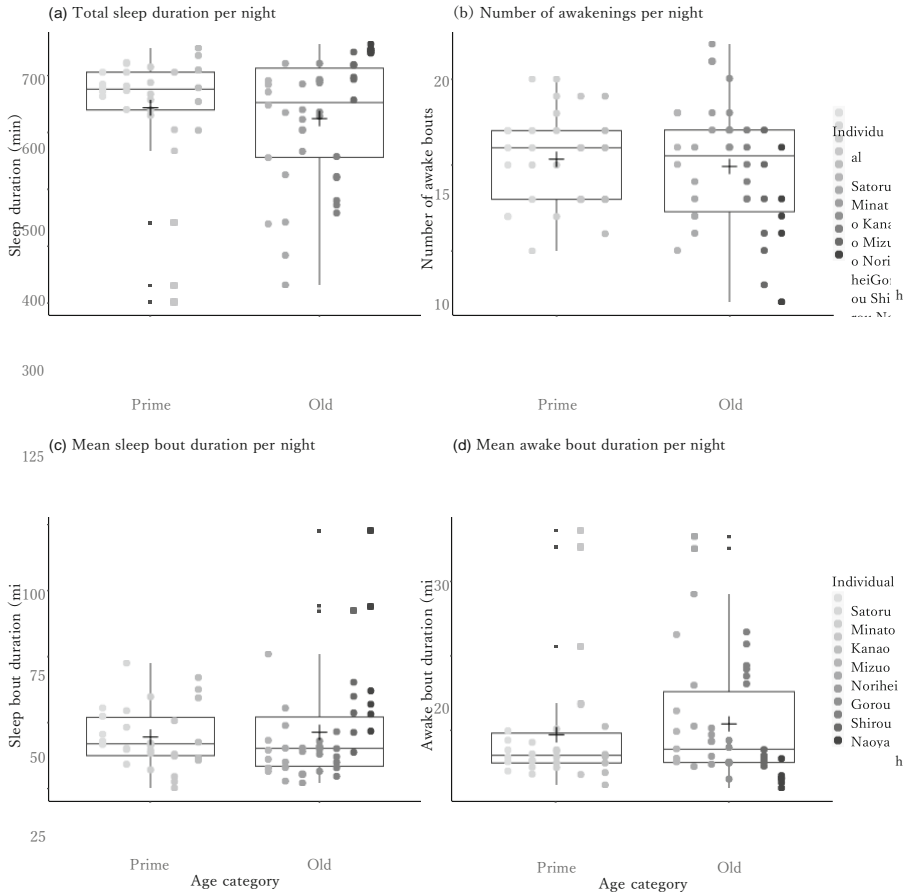


Fig. 2 Sleep patterns of 12 captive chimpanzees at Kumamoto Sanctuary, Japan by age category (“prime” and “old” adult) using 2018–2019 data. Individuals are listed by age in ascending order in legend (left to right in boxplot). Boxplot lines represent the median value, crosses (+) display the mean, box edges are the interquartile range, and farthest points from the whiskers are the minimum and maximum values in the data.

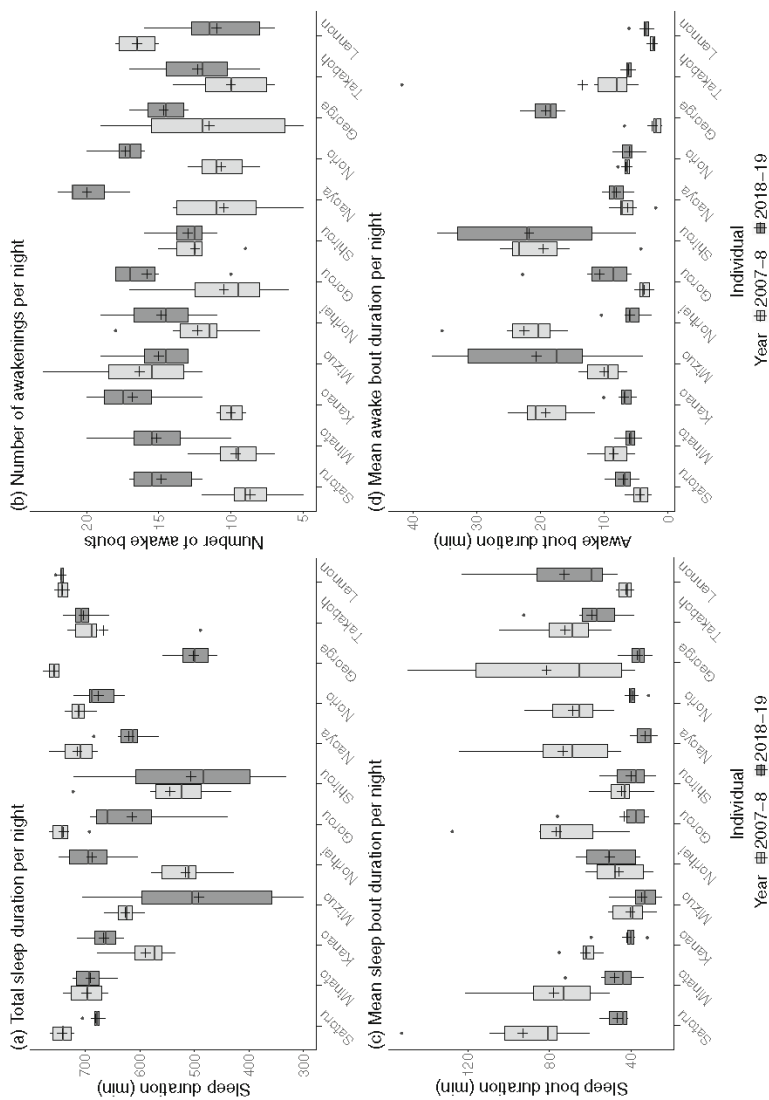


Fig. 3 Sleep patterns in 12 captive chimpanzees at Kumamoto Sanctuary, Japan in 2007–2008 and 2018–2019. Individuals are listed by age in ascending order from left to right. Boxplot lines represent the median value, crosses (+) display the mean, box edges are the interquartile range, and farthest points from the whiskers are the minimum and maximum values in the data.

Table III Results of linear mixed models investigating the influence of age on sleep variables in 12 captive chimpanzees at Kumamoto Sanctuary, Japan (2007–2008, 2018–2019)

Dependent variable	Predictor variable	Estimates	SE	<i>t</i> / <i>Z</i>	<i>P</i>
Total sleep duration (min)	Intercept	709.741	50.056	14.179 (<i>t</i>)	
	Age	-3.152	2.656	-1.186 (<i>t</i>)	0.259
Number of awakenings	Intercept	2.294	0.119	19.262 (<i>Z</i>)	
	Age	0.019	0.006	2.874 (<i>Z</i>)	0.004
Mean sleep bout duration (min)	Intercept	76.573	11.187	6.845 (<i>t</i>)	
	Age	-1.382	0.504	-2.744 (<i>t</i>)	0.018
Mean awake bout duration (min)	Intercept	-9.302	3.899	-2.386 (<i>t</i>)	
	Age	-0.008	0.214	-0.036 (<i>t</i>)	0.972