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Wild orangutans maintain sleep homeostasis through napping, counterbalancing socio-ecological factors that interfere with their sleep

Highlights

- Wild orangutans nap longer on days preceded by shorter overnight sleep periods
- Shorter naps are associated with a higher number of naps on the same day
- Associating with conspecifics is linked to shorter overnight sleep and nap periods
- Other behavioral and ecological factors also shape wild orangutans' sleep behavior

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In brief

Using long-term observational data, Ashbury et al. show that wild orangutans compensate for lost nighttime sleep with next-day napping and for shorter naps with more frequent napping. Orangutans' sleep patterns are also shaped by social and ecological factors. They trade off between sleep and other vital activities, such as travel and socializing.

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Wild orangutans maintain sleep homeostasis through napping, counterbalancing socio-ecological factors that interfere with their sleep

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SUMMARY

Sleep is a vital physiological process that lab-based studies of model species, including humans, have shown is homeostatically regulated—i.e., pressure to sleep builds during wakefulness and dissipates during sleep. However, how wild animals maintain sleep homeostasis and how socio-ecological pressures interfere with their sleep remain understudied. Here, we investigated sleep homeostasis and the factors that influence sleep duration among wild Sumatran orangutans (*Pongo abelii*), leveraging a comprehensive long-term dataset of their behavior, sociality, and ecology. We quantified sleep in 53 adult individuals using the time that an individual spent in a sleeping nest—i.e., its sleep period—as an indicator of time spent sleeping. We found that, after shorter nighttime sleep periods, orangutans' next-day cumulative nap period duration was longer and that shorter nap periods were associated with a higher number of naps on the same day. We also found that orangutans had shorter sleep periods (night and day) when they associated with more conspecifics. Orangutans also had shorter nighttime sleep periods when they traveled farther the day before, and they had longer cumulative nap periods on days when (1) they ate fewer calories, (2) the ambient temperature was cooler, and (3) it rained. Our results suggest that multiple factors shape wild orangutans' sleep behavior and that orangutans compensate for lost sleep via daytime napping. This supports the hypothesis that social and ecological pressures interfere with sleep among wild animals and that they must balance the costs and benefits of sleep with those of other critical activities.

INTRODUCTION

Sleep is a complex physiological process that is widespread across the animal kingdom.[1] Lab-based studies of model species, including humans, have shown that sufficient sleep is vital for effective physiological and cognitive functioning. Sleep deprivation weakens the immune system and impairs attention, working and long-term memory, and decision-making.[2–4] To guard against potentially detrimental sleep loss, animals experience a homeostatic drive to sleep: the pressure to sleep gradually increases during wakefulness and then decreases during sleep, and periods of insufficient sleep are followed by so-called "rebound" sleep.[1,5] Rebound sleep can manifest as a longer sleep duration or increased sleep intensity (i.e., a higher proportion of sleep time spent in deep sleep, also known as slow-wave sleep, as measured via electroencephalogram, EEG) during the subsequent sleep period or as naps during the subsequent active period.[6–8] Among humans, such daytime napping has been shown to reduce the homeostatic pressure, as well as the cognitive and physical impairment, that follows sleep restriction, and thus compensate for a previous night's limited sleep.[8–10]

Given the restorative energetic, physiological, and cognitive functions of sleep,[2,11–13] obtaining sufficient sleep should be especially important in animals that experience strong energetic constraints (such as seasonality in resource availability) and/or inhabit cognitively demanding niches (such as those requiring behavioral flexibility in response to unpredictable ecological and social challenges) (e.g., Aureli et al.,[14] Sueur et al.,[15] van Woerden et al.,[16] and Martin-Ordas and Call[17]). Studies in wild

Figure 1. An orangutan in a day nest
A female orangutan in the Suaq Balimbing research area naps in a day nest. Picture by Ellen Meulman.

animal populations suggest that ecological and social processes can affect individuals' sleep-wake schedules and interfere with sleep: prevailing weather conditions,[18] mating competition,[19] density of nearby conspecifics,[20,21] and familiarity and location of the sleep site[20] have been shown to lead to variation in individuals' sleep durations.[22] Moreover, studies on humans and captive animals provide evidence that nighttime sleep duration is influenced by the temperature and comfort of the sleep site[23–26] and activity levels during the day[27] and that the homeostatic regulation of sleep and food/energy intake are intertwined.[28] The extent and variability with which animals across taxa trade off sleep to satisfy other social and ecological needs, and the mechanisms used to restore sleep homeostasis, could provide integral insight into the costs, benefits, and adaptive functions of sleep.

Sumatran orangutans (*Pongo abelii*), semi-solitary great apes living on the Indonesian island of Sumatra,[29,30] are an ideal study system for investigating sleep trade-offs in a wild animal that occupies an energetically and cognitively demanding niche. Orangutans face significant energetic costs because of their large brains, large bodies, and arboreal lifestyle.[31] Also, they live in habitats with generally low and fluctuating food availability,[32] which exacerbates these energetic costs and presents cognitive challenges.[16] Orangutans need to locate food whose availability is spatially and temporally variable, and they need to recognize and process hundreds of different food items that often require extractive foraging, including—in some populations—tool use.[33–35] Furthermore, orangutans exhibit fission-fusion sociality,[36] which is hypothesized to be cognitively demanding because it requires individuals to maintain social relationships through absence and to flexibly adjust social behavior to the presence and absence of particular conspecifics.[37] When orangutans do associate with each other, it is energetically costly for them but also offers vital benefits, such as social learning and mating opportunities, and for females, protection from harassing males and socialization of their infants.[36,38–41]

The deep and uninterrupted sleep needed for orangutans to fulfill their cognitive and energetic demands may be, in part, facilitated by their use of sleeping nests (also called "sleeping platforms").[42,43] Unlike most other diurnal primates who usually sleep on bare branches at night, orangutans build bowl-shaped nests of branches, twigs, and leaves on which to sleep, enabling them to obtain safe, deep, and lengthy sleep, despite being high up in the forest canopy.[24,42,44–47] It takes an adult orangutan, on average, 7 to 9 min to build a night nest, and these structures include a basic frame of branches bent and broken into a platform, a "mattress" made of leafy branches, and a rim of interwoven branches.[48,49] Night nests also often include comfort elements, such as leafy pillows and detached leafy branches pulled over the orangutan's body as a blanket. Although the frequency varies across populations, and they often lack comfort elements, orangutans also build nests for short sleeps during the day (Figure 1).[48–50] Orangutans' propensity for constructing and using day nests rather than simply sleeping on a bare branch suggests that safely obtaining deep and uninterrupted sleep even during these daytime naps may be energetically, physiologically, and/or cognitively important.

Here, we investigate factors that influence sleep period duration among wild Sumatran orangutans (*Pongo abelii*) in the Suaq Balimbing research area, Indonesia, and look for evidence of homeostatic mechanisms to regulate sleep under ecologically and socially relevant conditions. We used a long-term dataset of direct observation nest-use data, which included 53 adult individuals, over 276 nights and 455 days between 2007 and 2021. We define the time that an orangutan spent in a nest as a *sleep period*, i.e., a contiguous window of time during which the orangutan's primary activity was most likely sleep. We define an orangutan's *nighttime sleep period* as the time between when observable movement, activity, or vocalizations ceased and the orangutan became inactive in its night nest in the evening and when observable movement, activity, or vocalizations began the next morning. We extend this definition of sleep period also to *daytime nap periods*: the times during which an orangutan was in a day nest and did not move or vocalize, and thus its primary activity was most likely sleep. Our measures of nighttime sleep periods and daytime nap periods are not synonymous with *time spent sleeping*, as they likely include short bouts of wakefulness (e.g., evidence of nighttime activity in apes[51–53]), as well as quiet rest before and after the onset and offset of actual sleep. Among captive orangutans whose nighttime sleep was assessed via infrared videography[24,43] and wild baboons whose nighttime sleep was assessed via collar-mounted triaxial accelerometers,[20] total overnight time spent sleeping was significantly predicted by the duration of the nighttime sleep period (captive orangutans[24,42,43] and wild baboons:[20,54]; Figure S1), suggesting that sleep period is a non-invasive indicator—but not the equivalent—of time spent sleeping.

We focus our analysis on two main variables: the duration of orangutans' nighttime sleep periods and the cumulative duration of orangutans' nap periods each day, both quantified to the nearest minute. To investigate potential mechanisms to maintain sleep homeostasis, we tested for correlations between the duration of an individual's nighttime sleep period one night and the next, between its cumulative daytime nap period duration and its preceding and subsequent nighttime sleep period durations, and between its average nap period duration and total number of naps on a given day. Furthermore, we explored social, behavioral, and ecological factors that may affect the duration of an orangutan's nighttime sleep and daytime nap periods. For nighttime sleep period, these factors included the number of association partners (conspecifics within 50 m, not counting mothers' own current dependent offspring) that an orangutan was with at the night nest, the time the orangutan spent building the nest (as a proxy for the comfort of the nest[24]), the distance the orangutan traveled during the day before (i.e., day journey length, as a measure of an individual's physical exertion), the orangutan's caloric intake during the previous day, as well as the food availability level in their habitat (a metric that has previously been shown to influence orangutans' behavior and activity budgets[55–58]), minimum nighttime temperature (as nights can be very cool), and occurrence of rainfall during the night. For cumulative nap period duration, these factors included the orangutan's average association size that day, the distance the orangutan traveled that day, and the orangutan's caloric intake that day, as well as the prevailing habitat food availability, maximum daytime temperature (as days can be very hot), and occurrence of rainfall during the day. Because of known differences in the time they spend resting,[59] we controlled for differences in sleep period duration between the four adult age-sex classes: adult females (i.e., parous females without a dependent offspring), mothers (i.e., adult females with a dependent offspring), flanged males (i.e., adult males with secondary sexual characteristics, including cheek pads, a pendulous throat sac, longer hair, and overall larger body size), and unflanged males (i.e., adult males without secondary sexual characteristics). We also controlled for potential confounding effects of ambient darkness duration and moon fraction (in the case of nighttime sleep) and for the length of the active period (in the case of cumulative daytime napping). Our aim was to provide the first quantitative assessment of factors that shape orangutan sleep patterns in the wild.

RESULTS

Overnight, orangutans were in their night nests starting from 17:40 (mean, range = 13:42–19:53) until 6:28 (mean, range = 5:39–8:14) the next morning, giving an average sleep period duration of 12.83 ± 0.78 (or 12 h 50 min ± 47 min; mean ± SD) h per night ($n = 276$). Mean sunset time was 18:34 (range = 18:15–18:46), and mean sunrise time was 06:27 (range = 06:15–06:46).

The full *nighttime sleep period duration* model (linear mixed model, LMM) tested for sleep homeostasis over consecutive nights as well as the effects of social, behavioral, and ecological factors on nighttime sleep period and fit the data significantly better than the corresponding null model (likelihood ratio test [LRT]: $\text{Chi}^2 = 73.372$, $p < 0.001$), indicating that our predictor variables had an overall significant effect on the duration of orangutans' nighttime sleep period (Table S1). Over consecutive nights, the duration of an individual's nighttime sleep period was positively correlated with the duration of its sleep period the night before (11.0 min longer sleep for every hour increase in sleep the night before; $\beta \pm \text{SE} = 0.170 \pm 0.043$, $p < 0.001$, Figure 2C). In terms of the factors that may affect nighttime sleep, orangutans had significantly shorter night sleep periods when they had more nighttime association partners ($\beta \pm \text{SE} = -0.191 \pm 0.044$, $p < 0.001$, Figure 2A): for every additional association partner, the focal orangutan's sleep period was 13.7 min shorter. Our dataset did not include any observations of adult orangutans sharing night nests with each other, and only mothers shared nests with their dependent offspring. Also, the farther an orangutan traveled during the day, the shorter its sleep period that night ($\beta \pm \text{SE} = -0.189 \pm 0.043$, $p < 0.001$, Figure 2B): for every additional 100 m in day journey length, the focal orangutan's sleep period was 3.9 min shorter. The duration of an individual's nighttime sleep period was positively correlated with the minimum nighttime temperature (4.1 min shorter sleep period for every degree Celsius decrease in minimum nighttime temperature; $\beta \pm \text{SE} = 0.083 \pm 0.041$, $p < 0.05$, Figure 2D). Neither food availability, the time spent napping during the day, the time spent building the night nest, caloric intake, nor rainfall had significant effects on the duration of the nighttime sleep period (Table S1). Furthermore, there was no significant difference in nighttime sleep period duration between the age-sex classes (Table S1).

To better understand the mechanism linking the negative correlation between day journey length and nighttime sleep period duration, we performed a follow-up test to investigate the relationship between day journey length and the duration of the daytime active period. This test showed that orangutans have longer active periods on days when they travel farther (LMM; $\beta \pm \text{SE} = 0.194 \pm 0.047$, $p < 0.001$; Table S2).

With respect to daytime nap periods, almost half of all full day follows in our dataset (41% of $n = 455$ follows) had at least one instance of day nest use (range = 0–4) by the focal orangutan. For focal orangutans who did use a day nest, they had a cumulative daytime nap period duration of 76 ± 53 min (mean ± SD), divided over 1.43 ± 0.71 different day nests.

The full *daytime cumulative nap period duration* model (zero-inflated Poisson generalized LMM) tested for sleep homeostasis between night- and daytime sleep periods as well as the effects of social, behavioral, and ecological factors on daytime sleep period and fit the data significantly better than the corresponding null model (LRT: $\text{Chi}^2 = 527.92$, $p < 0.001$), indicating that our predictors had an overall significant effect on the cumulative duration of an orangutan's naps (Table S3). Orangutans had significantly longer cumulative nap periods on days when they had shorter nighttime sleep periods the night before ($\beta \pm \text{SE} = -0.103 \pm 0.010$, $p < 0.001$; Figure 3A): focal orangutans had a 12.3% longer cumulative nap period for every hour decrease in sleep period the night before. Orangutans had shorter cumulative nap periods on days when they had higher caloric intake (5.0% shorter nap period for every 500 kcal increase in intake; $\beta \pm \text{SE} = -0.192 \pm 0.012$, $p < 0.001$; Figure 3B), and on days when there was no rain (16.2-min shorter nap period than days without rain; $\beta \pm \text{SE} = 0.227 \pm 0.027$ $p < 0.001$; Figure 3C). Orangutans also had significantly shorter cumulative nap periods when they associated with more conspecifics (5.9% shorter nap periods for each additional social partner; $\beta \pm \text{SE} = -0.044 \pm 0.011$, $p < 0.001$; Figure 3D), and when the maximum daytime temperature was higher (2.6% shorter nap period for every additional degree Celsius; $\beta \pm \text{SE} = -0.046 \pm 0.009$, $p < 0.001$; Figure 3E). Our dataset did not include any observations of adults sharing day nests with each other, and only mothers shared nests with their dependent offspring. Orangutans trended toward shorter cumulative nap periods when they had longer day journey lengths ($\beta \pm \text{SE} = -0.023 \pm 0.012$, $p = 0.058$), but the effect size was extremely small (0.7% shorter nap periods for every additional 100 m of travel). Furthermore,

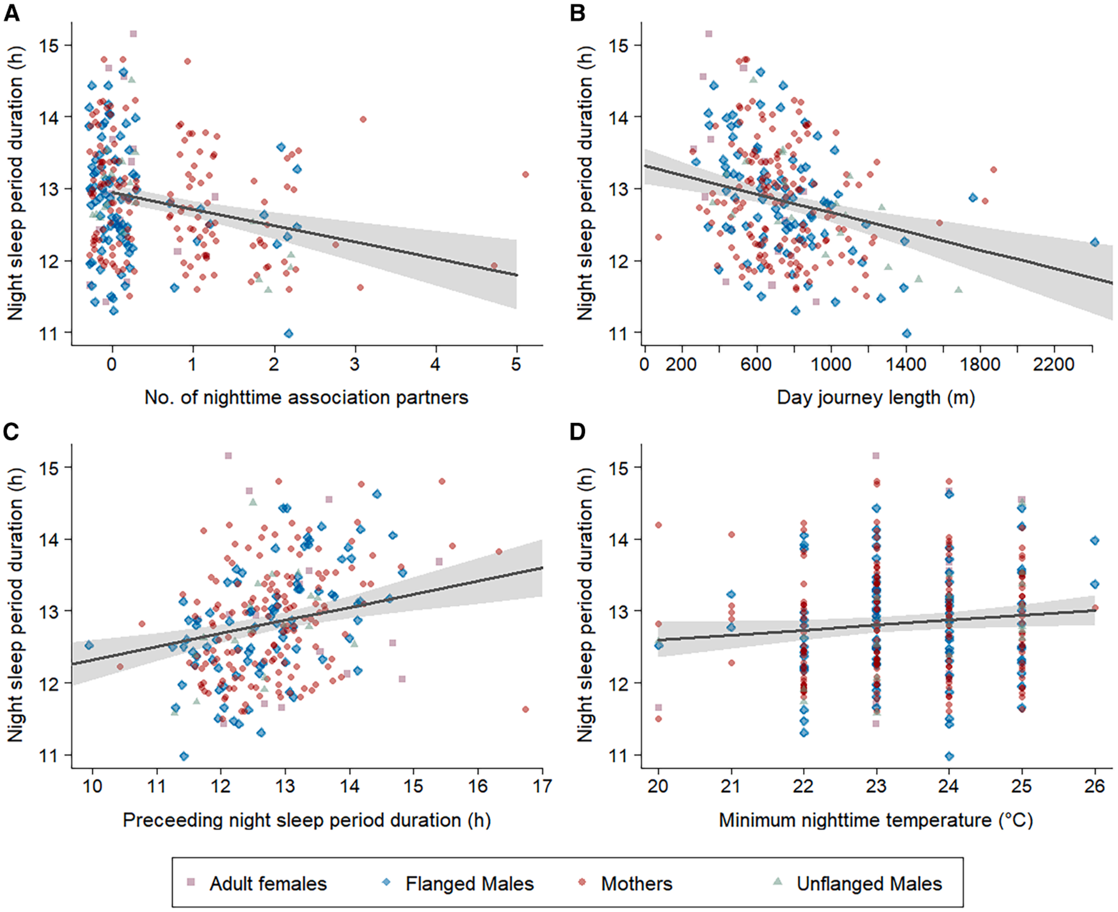

Figure 2. The duration of the nighttime sleep period is affected by social, behavioral, and ecological factors

(A–D) Orangutans had shorter nighttime sleep periods when (A) they had more nighttime association partners and (B) they traveled farther on the preceding day. They had longer nighttime sleep periods when (C) the duration of their nighttime sleep period during the preceding night was longer and (D) the minimum nighttime temperature was higher. The solid black lines represent the model predictions of the specified predictor, and gray ribbons show the confidence bands of the predicted value, while all other effects in the model are kept at their means. Predictors that were not statistically significant (food availability, the time spent napping during the preceding day, the time spent building the night nest, caloric intake, and rainfall) are not plotted.

See Table S1 for detailed model results and Table S2 for detailed model results showing that orangutans have longer active periods on days when they travel farther. For visualization purposes, the points in (A) were jittered horizontally.

there were significant differences in cumulative daytime nap period duration between the age-sex classes (Table S3): mothers (adult females with dependent offspring) had significantly longer cumulative nap periods than adult females without dependent offspring (mean predicted nap period for mothers = 62.8 min versus mean predicted nap period for adult females = 51.9 min; β ± SE = 0.190 ± 0.058, $p < 0.01$), and flanged males had significantly longer cumulative nap periods than unflanged males (mean predicted nap period for flanged males = 78.5 min versus mean predicted nap period for unflanged males = 54.5; min; β ± SE = −0.364 ± 0.117, $p < 0.01$). Food availability did not have a significant effect on cumulative nap period duration.

The full *average duration of nap periods* model tested for sleep homeostasis within daytime sleep and fit the data significantly better than the corresponding null model (LRT: $\text{Chi}^2 = 325.16$, $p < 0.001$). The full model indicated a significant negative relationship between the average duration of nap periods and the number of naps per day (LMM: β ± SE = −0.071 ± 0.031, $p < 0.05$; Figure 3F; Table S4).

To compare association sizes during the day versus at night, we performed a simple follow-up test: this showed that the average number of daytime association partners and the number of nighttime association partners did not significantly differ (daytime: mean ± SD = 0.44 ± 0.65, nighttime: mean ± SD = 0.50 ± 0.83, Welch two-sample t test: $t = -0.975$, $df = 518.58$, $p = 0.33$).

DISCUSSION

We found evidence that wild orangutans use napping as a mechanism to maintain sleep homeostasis: the shorter an orangutan's sleep period overnight, the longer its cumulative nap period the next day, suggesting that orangutans use daytime naps to compensate for lost nighttime sleep. Furthermore, orangutans took more naps on days when they had shorter nap periods, suggesting that they needed to satisfy some cumulative sleep

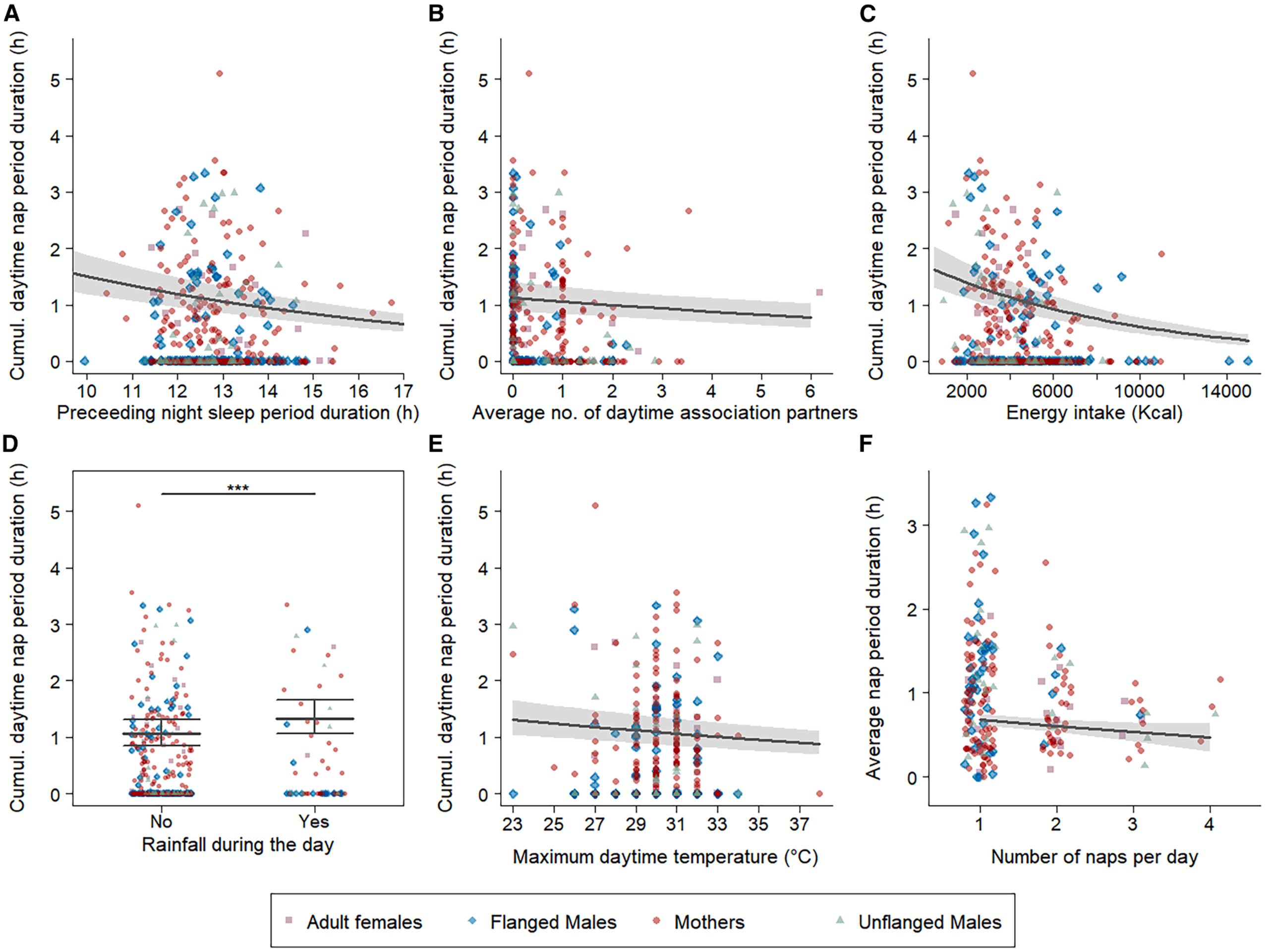

Figure 3. The cumulative duration of daytime nap periods is affected by social, behavioral, and ecological factors

(A–F) Orangutans had longer cumulative nap periods when (A) they had a shorter nighttime sleep period the preceding night, (B) they were in association with fewer association partners over the course of the day, (C) they had lower total energy intake, (D) there was rain during the day, and (E) the maximum daytime temperature was lower. (F) Furthermore, orangutans had more naps on days when their nap periods were, on average, shorter. The solid black lines represent the conditional model predictions of the specified predictor, and gray ribbons show the confidence bands of the predicted values, while all other effects in the model are kept at their means. Predictors that were not statistically significant (day journey length and food availability) are not plotted.
See Tables S3 and S4 for detailed model results. For visualization purposes, the points in (F) were jittered horizontally.

duration quota. We also found that social, behavioral, and ecological factors lead to substantial variation in the duration of nighttime sleep period and daytime nap periods among wild orangutans. Associations with conspecifics, in particular, were linked to shorter night sleep and daytime nap periods, suggesting that social interactions can interfere with sleep. Our findings are thus consistent with the hypothesis that, for animals in the wild, social and ecological pressures can interfere with sleep, and the costs and benefits of sleep are traded off with those of other critical activities, such as travel and sociality.

We found that on days when orangutans napped, they had a 12.3% longer cumulative nap period duration for every hour of nighttime sleep period lost, which translates to approximately 10 min longer nap period when the nighttime sleep period decreases from 11 to 10 h. In humans, napping for even just 10 min has been shown to reduce the homeostatic pressure that follows sleep restriction and compensate for a previous night's limited sleep.[8,10,60] Thus, orangutans may mitigate the negative effects of insufficient nighttime sleep—such as memory impairment and reduced foraging efficiency[61]—by napping. This strategy to compensate for lost nighttime sleep may be especially accessible to orangutans and other animals that do not live in cohesive social groups: because of their fission-fusion social dynamics,[36] they do not need to coordinate nap periods and navigate conflicts of interest in nap timing and duration with group members, and so they can rely on naps to maintain sleep homeostasis.

Napping has notable cognitive benefits among humans, promoting long-term memory, enabling learning,[62–64] and allowing restoration of the immune system.[8] The same may be true for orangutans, particularly for individuals in the population studied here who (1) build day nests at a much higher frequency than orangutans in other populations (who often simply rest on bare branches[48]) and (2) occupy a cognitively demanding niche, wherein they rely on vast cultural repertoires across multiple behavioral domains, including the flexible and habitual use of tools and other complex foraging techniques.[34,65,66] Sleeping in a nest (versus simply sleeping on a bare branch, as is standard for most diurnal arboreal primates[44]) has been shown to facilitate deeper and less fragmented sleep,[24,43,44] and thus these two phenomena may be linked: Suaq orangutans' high capacities for learning and memory that facilitate their large cultural repertoires may be linked to their ability to effectively compensate for lost nighttime sleep via nest-based naps. However, determining the presence and causality of this relationship on an ultimate level—whether buffering against sleep loss facilitated the evolution of cognitive capacities, or vice versa—will require phylogenetic comparative analyses of sleep regulation across species in the wild.

Adjusting the duration and the number of naps may be especially important mechanisms through which orangutans can compensate for lost sleep, as we also found that several behavioral, social, and ecological factors lead to variation in the duration of nighttime sleep and daytime nap periods.

Effects of associations

We found that associations with conspecifics interfered with orangutans' sleep periods. Indeed, both the duration of the nighttime sleep period and the cumulative duration of daytime nap periods were significantly shorter when more association partners were present. This result suggests a so far largely unknown dimension of the costs of association among orangutans: reduced sleep. Associations are already particularly costly for orangutans given their large body size and their preference for ripe fruit: feeding competition is high when multiple orangutans are foraging in the same, limited, food patches.[38] Despite these energetic costs, as well as the potential costs to sleep duration that we have shown here, orangutans regularly spend time in association with conspecifics, thus highlighting the importance of these associations for mating, social play, and social information transmission.[38,41,67–69] As we also found that daytime and nighttime associations were equally frequent, orangutans may gain as-of-yet undocumented benefits from sleeping near conspecifics. Among wild baboons, social pressures similarly interfere with sleep: individuals sleep less when more conspecifics are in their proximity, and they have shorter and more fragmented sleep when multiple groups share a sleeping site.[20,21] After sharing a sleeping site, however, there is increased social tolerance between groups—suggesting that sleep-site-sharing somehow facilitates affiliative social relationships, even between otherwise discrete social groups.[21] Similar processes could be occurring among orangutans, with nighttime proximity somehow facilitating beneficial inter-individual bonding, although further research is needed to test this hypothesis.

Effects of travel

We also found that longer travel distances were linked to shorter subsequent night sleep periods and trended toward being linked to shorter cumulative daytime nap periods. This suggests that the energetic expenditure needed for arboreal travel does not lead to increased sleep, as indicated by human sleep studies wherein more exercise leads to longer night sleep durations.[27] Rather, it is possible that orangutans trade off time that could be spent sleeping during the night—and to a less significant extent, also during the day—with time traveling in order to obtain other benefits, such as getting to high-quality fruit patches (which can be widely dispersed[70]), finding mates, or avoiding harassing males.[38,71] Since this trade-off seems stronger with nighttime sleep period than with daytime nap periods, we then predicted that days with more travel are generally longer than days with less travel. This was confirmed in our follow-up analysis, indicating that orangutans' nighttime sleep period begins later on days when they travel farther. These results show that extended daily travel in orangutans may be energetically costly not only because of the energetic expenditure itself and possible foraging opportunity costs but also via reduced opportunity to sleep.

Effects of food availability and caloric intake

Although daily travel distance, foraging effort, and food intake are generally linked among orangutans,[56,57] in our analysis we found no evidence that individuals' caloric intake or the habitat's prevailing fruit availability levels affected the duration of orangutans' nighttime sleep period. This suggests that orangutans' energetic intake per se does not have a strong effect on their night sleep duration. However, we found that orangutans had longer nap periods on days when they consumed fewer calories. There are two plausible, mutually non-exclusive explanations for this finding: (1) orangutans may nap more on days when they consume fewer calories in order to conserve and balance energy expenditure (energetic conservation explanation), and/or (2) orangutans may prioritize spending time napping at the expense of spending time eating, particularly on days following a shorter nighttime sleep period (homeostatic regulation explanation). Because Suaq has relatively high food availability year-round, the caloric intake of this population is higher than other orangutan populations living in more variable habitats,[32] and thus the second explanation is likely more probable. Investigating the interplay between energy intake and nap durations in species that experience more pronounced fluctuations in energy intake would help to disentangle these effects and their underlying causality.

Effects of temperature and rain

We found that cumulative daytime nap period durations were affected by both ambient temperatures and rainfall, and orangutans spent more time in their day nests when it rained during the day and on hotter days. We also found that orangutans had shorter nighttime sleep periods when the minimum nighttime temperature was lower. Among humans, ambient temperature has a quadratic effect on sleep quality, with both too high and too low temperatures leading to reduced sleep quality,[23] and our orangutan findings accord with this: orangutans have longer nighttime and nap periods when nights are not too cold and days are not too hot. Rain during the day, however, leads to longer nap periods, suggesting that the cooling effects of rain may offset the heat of hot days and that orangutans may be using day nests to protect themselves against the rain itself.[44,49] Among humans, increasing global temperatures are associated with widespread reduced sleep quality.[72,73] Our results suggest that the orangutans' ability to buffer against short nighttime sleep using daytime napping will be increasingly compromised as rainforests become hotter. Given the importance of sufficient sleep for effective cognitive and physiological functioning, climate change leading to reduced sleep quality is an underappreciated avenue through which anthropogenic pressure may contribute to population decline in wild animals.[74]

Other effects

Against our prediction, nest construction time did not have an effect on nighttime sleep period duration. Captive orangutans have less fragmented sleep when they sleep in more complex (and presumably comfortable) sleeping platforms,[24] and thus it is possible that nest comfort affects wild orangutans' sleep efficiency (which we could not measure), rather than the overall duration of their sleep period. Alternatively, it is possible that, for wild orangutans, the time it takes to construct a nest is not an accurate reflection of the presence or experience of comfort elements and is rather a function of other variables, such as the mechanical and structural properties of the tree in which it is being constructed, the needs of the builder, and/or the architectural structure of the nest's frame.[49] The positive correlation between the durations of an orangutan's nighttime sleep periods from one night to the next suggests that there may be coarse fluctuations in orangutans' baseline sleep needs over time. Because we did not find an effect of habitat fruit availability, and we controlled for the duration of ambient darkness and the illuminated fraction of the moon, we hypothesize that these fluctuations are not due to any external pressures but may be related to individual intrinsic (e.g., physiological) pressures instead. Among humans and other animals, individual factors, such as age, sex, reproductive status, hormone levels, stress levels, and otherwise-unexplained individual variation, have been shown to influence the duration and quality of sleep.[74–77] Given our limited sample size and the challenges of collecting such data on wild great apes, we were unable to test the effects of such detailed intrinsic factors on orangutans' sleep period durations, nor could we investigate sleep behavior and regulation over larger time scales (i.e., >24 h, multiple days, seasons, etc.[78]), but increasingly detailed data collection protocols and growing sample sizes may allow for this in the future.

Limitations

"Time spent in a nest," i.e., sleep period, is only an indicator of time spent sleeping, and because nests often obscure visual observation of sleeping apes—ruling out night-vision cameras and other methods of direct observation—and equipping orangutans with on-body sensors is not currently possible (nor ethical) given available technologies, understanding their sleep patterns requires a certain degree of interpolation. Sleep is, however, behaviorally defined: it is a rapidly reversible state of diminished responsiveness and behavioral quiescence.[1] Previous studies investigating sleep in wild animals have used body posture and inactivity as evidence of sleep,[79] and orangutans—although out of sight—who are in nests with no discernible vocalizations or leaf rustling, fulfill these criteria. We found a mean (±SD) nighttime sleep period duration of 12.83 ± 0.78 h (12 h 50 min ± 47 min), which is barely different from the mean (±SD) sleep period duration of 12 h 46 min (±60 min) found for adult orangutans in captivity,[24,42,43] suggesting that wild orangutan nighttime sleep patterns are similar to those of their captive counterparts. Importantly, captive adult orangutans have a mean (±SD) sleep efficiency value of 0.75 (±0.07), meaning that they are only actually asleep for 75% of the duration of their nighttime sleep period, on average.[24,42,43] Applying the mean sleep efficiency value from captivity to our wild dataset yields an actual nighttime sleep duration of 9.63 ± 0.59 h (mean ± SD). Captive and wild orangutans may well have different sleep efficiencies, and thus this extrapolation may not be accurate, but it underscores that our measure of wild orangutans' sleep period certainly includes periods of wakefulness and is not synonymous with time spent sleeping. The strong correlation between time in nest and actual time spent sleeping in captive orangutans (Figure S1A), where sleep was assessed via infrared videography,[24,42,43] supports the use of sleep period, i.e., time in a nest, as an indicator of actual time spent sleeping and its variability in this study.

Our approach, however, cannot determine the precise onset or offset of sleep, nor can it assess other dimensions of sleep, such as sleep efficiency, sleep fragmentation (the frequency and duration of awakenings between initial sleep onset and final waking), sleep depth (the reduction in responsiveness to external stimuli), or sleep architecture (the timing, duration, and patterning of rapid eye movement [REM] and non-REM sleep stages). Environmental factors could further influence not only the duration of the sleep period but also other aspects of sleep, as observed among wild boars wherein elevated daytime temperatures are linked to increased sleep fragmentation.[74] If, for example, factors associated with shorter sleep periods—such as extended daily travel distances—also reduce the latency from nest entry to sleep onset, the impact of these factors on orangutans' actual time spent sleeping may be less pronounced than our time-in-nest-based sleep period estimates suggest. We hope that future technological development will enable more detailed study of orangutans'—and other currently untaggable animals'—sleep. In particular, innovative technologies enabling non- or minimally invasive collection of high-quality (night) video, accelerometry, or EEG data from more species of wild animals (e.g., Loftus et al.,[20] Williams et al.,[80] Van Hasselt et al.,[81] and Burger et al.[82]) would enable a phylogenetically broader understanding of the factors that affect the duration, efficiency, depth, and architecture of sleep in the wild.

Conclusions

Wild orangutans compensate for shorter nighttime sleep periods with longer cumulative nap periods the next day and by napping more frequently when they have shorter nap periods. This mechanism to buffer against lost sleep time is important given that a range of social, ecological, and behavioral factors interfere with day- and nighttime sleep (Figure 4). Because of their cognitively demanding ecological niche[35,50,65] and the significant energetic constraints that they face,[31,32] reduced sleep may be particularly detrimental for orangutans. These disproportionately negative potential consequences of sleep loss may be linked to the evolution of mechanisms that promote sleep homeostasis, such as napping, and that ensure safe, high-quality sleep, such as nest use.[43] Our study sheds a first light on the links between sociality, travel, energetic intake, weather conditions, and sleep in wild orangutans. Expanding the study of sleep to more wild populations and species, as well as developing new technologies for measuring sleep in wild animals, will allow for a

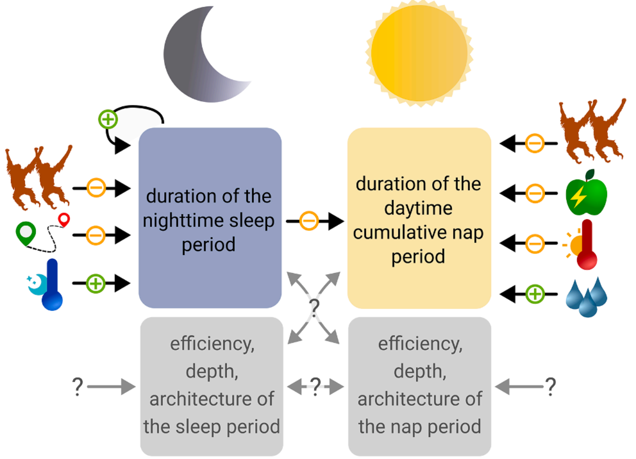

Figure 4. Factors influencing the duration of wild orangutans' sleep periods

Green plus signs indicate significant positive correlations, and yellow minus signs indicate significant negative correlations. The duration of an orangutan's nighttime sleep period was positively predicted by the duration of its sleep period the night before and the minimum nighttime temperature. Its nighttime sleep period was negatively predicted by the number of conspecifics with whom it was in association at night and the distance that it had traveled the day before. The cumulative duration of an orangutan's daytime nap periods increased as the duration of its sleep period the night before decreased and was negatively predicted by the average number of conspecifics with whom it associated, the total number of calories that it ingested, and the maximum temperature that day. Rain during the day predicted longer cumulative nap periods. Our behavioral study focused on the duration of wild orangutans' sleep periods and did not measure the efficiency, depth, or architecture of the sleep period. The development of new technologies for quantifying detailed sleep metrics among wild animals would enable the study of the factors that influence these other characteristics of orangutan sleep, as well as how these sleep characteristics all interact to maintain sleep homeostasis.

better understanding of sleep processes at the proximate and evolutionary levels.

RESOURCE AVAILABILITY

Lead contact

Requests for further information and resources should be directed to and will be fulfilled by the lead contact, Caroline Schuppli (cschuppli@ab.mpg.de).

Materials availability

This study did not generate new, unique reagents.

Data and code availability

- All data used in this analysis have been deposited in the Harvard Dataverse and are publicly available as of the date of publication at https://doi.org/10.7910/DVN/ERGAZ5.
- All original code has been deposited in the Harvard Dataverse and is publicly available at https://doi.org/10.7910/DVN/ERGAZ5 as of the date of publication.
- Any additional information required to reanalyze the data reported in this paper is available from the lead contact upon request.

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AUTHOR CONTRIBUTIONS

Conceptualization, A.M.A., M.C.C., and C.S.; methodology, C.S., S.S.U.A.; formal analysis, A.M.A. and C.S.; investigation, F.L., A.L.P., T.R., and C.S.; resources, T.R., S.S.U.A., and C.S.; data curation, F.L., D.R.S., and C.S.; writing – original draft, A.M.A. and C.S.; writing – review and editing, A.M.A., F.L., A.L.P., T.R., D.R.S., S.S.U.A., M.C.C., and C.S.; visualization, A.M.A. and C.S.; supervision, C.S.; project administration, T.R., S.S.U.A., and C.S.; funding acquisition, M.C.C. and C.S.

DECLARATION OF INTERESTS

The authors declare no competing interests.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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SUPPLEMENTAL INFORMATION

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
Repository data	This paper	https://doi.org/10.7910/DVN/ERGAZ5
Experimental models: Organisms/strains		
Pongo abelii	Wild Sumatran orangutans: Suaq Balimbing monitoring station, Gunung Leuser National Park, South Aceh, Sumatra, Indonesia	www.suaq.org
Software and algorithms		
R 4.2.2[83]	R Foundation for Statistical Computing, www.r-project.org	RRID:SCR_001905
suncalc[84]	https://CRAN.R-project.org/package=suncalc	N/A
lme4[85]	https://cran.r-project.org/web/packages/lme4/index.html	RRID:SCR_015654
glmmTMB[86]	https://cran.r-project.org/web/packages/glmmTMB/index.html	RRID:SCR_025512
Multcomp[87]	https://cran.r-project.org/package=multcomp	RRID:SCR_018255
ggeffects[88]	https://cran.r-project.org/package=ggeffects	RRID:SCR_022496
Performance[89]	https://cran.r-project.org/web/packages/performance	N/A
DHARMa[90]	https://cran.r-project.org/web/packages/DHARMa/	RRID:SCR_022136
Analysis code	This paper	https://doi.org/10.7910/DVN/ERGAZ5
Other		
Established protocol for focal data collection of wild orangutans at Suaq Balimbing	Caroline Schuppli; ab.mpg.de/571325/standarddatacollectionrules_suaq_detailed_jan204.pdf	N/A

EXPERIMENTAL MODEL AND STUDY PARTICIPANT DETAILS

Study site

We collected data from June 2007 to December 2021 at the Suaq Balimbing monitoring station in the Gunung Leuser National Park in South Aceh, Indonesia. The study area is a 5.2 km^2 area consisting predominantly of lowland peat-swamp forest, with surrounding mixed dipterocarp, riverine, and seasonally-flooded freshwater swamp forests. More detailed information about the ecology of the study area can be found in van Schaik.[36]

Study subjects

At Suaq, orangutans are found opportunistically, and then followed for up to 10 days. We have included data from 53 individuals in total, from four age-sex classes: adult females (i.e., parous females that had no current dependent offspring, n = 7), mothers (i.e., adult females with a dependent offspring, n = 12), flanged males (i.e., adult males with secondary sexual characteristics, n = 20), and unflanged males (i.e., adult males without secondary sexual characteristics, n = 20). Three females transitioned from adult females to mothers (or vice versa), and 4 males transitioned from unflanged to flanged, during the study period. We included only adult individuals in our analysis as we do not have robust data for all predictor variables (e.g., reliable estimation of daily caloric intake) for immatures.

Ethics approval and consent to participate

This study was strictly observational and non-invasive, and observers did not handle or interact with and kept a minimal distance of 7 meters to our study animals. Our research protocols were approved by the Indonesian Badan Riset dan Inovasi Nasional (BRIN, formerly RISTEK; Research Permit No.: 152/SIP/FRP/SM/V/2012 and following) and complied with the legal requirements of Indonesia.

METHOD DETAILS

Focal data collection

Behavioral data were collected during full-day nest-to-nest focal follows, following an established protocol (ab.mpg.de/571325/standarddatacollectionrules_suaq_detailed_jan204.pdf). During these follows, the activity of the focal orangutan as well as the presence of, and distance to, association partners (i.e., any other orangutans within 50 meters of the focal individual) were recorded at two-minute intervals. Whenever the focal activity was feeding, the food item (species and part) being eaten was recorded. Furthermore, detailed all-occurrence data were collected on behaviors of special interest, including nest building and use. We also collected GPS locations of the focal individual at 30-minute intervals, as well as GPS locations of all nests, using hand-held GPS devices (Garmin GPSMAP 78, GPSMAP 62s, and GPSMAP 64s).

Detecting sleep and nap periods

We used periods of inactivity in a nest as an indicator of orangutan sleep. Orangutan nests are constructions consisting of branches, twigs, and leaves that have been bent, broken, and manipulated to create a resting platform in a tree[44,47] (Figure 1). A night nest is the nest that a focal individual stays in overnight, while a day nest is a nest that it uses for some period of time during the day. Once in a nest, the orangutan itself may be out of sight from the observers, but any movement within the nest is still visible to observers on the ground, as the leaves and branches in and around the nest shake and swish even with the slightest movement of its occupant. Whenever an orangutan was in a nest, and there was no discernable movement, vocalizations, or other signs of activity, we considered this to be a sleep period. Orangutans at Suaq usually build a new nest every night (although, they occasionally add to, and fix up, an older nest rather than building a new one), as well as a nest for every significant period of rest during the day,[49] thus our quantification of sleep period is unlikely to have missed any night- or daytime sleep. In other study systems, total overnight time spent sleeping is significantly predicted by the duration of the nighttime sleep period (captive orangutans:[24,42,43]; wild baboons:[20,54]; Figure S1), suggesting that sleep period is a reliable non-invasive indicator – but not the equivalent – of time spent sleeping.

Measuring sleep and nap period durations

Whenever a focal individual built a nest, we recorded the details of the nest-building process, including: the time at which the individual started building the nest, the time at which the individual became inactive in the nest, and the time at which the individual showed signs of activity again. We defined the **nighttime sleep period** as the time between when an individual became inactive in its night nest in the evening and when apparent or observable movement and activity began the next morning. We measured the nighttime sleep period duration in minutes. Similarly, we defined **nap periods** as the time between when an individual became inactive in a day nest and when it subsequently showed signs of movement and activity. To calculate the **daytime cumulative nap period duration**, we summed the durations (in minutes) of all of an individual's nap periods during the day, and to calculate the **average nap period duration**, we divided a day's cumulative daytime nap period duration by the **total number of day nests** that the individual built and used on that day. All durations were recorded with a precision level of 1 minute, as observers would write down start and end times as HH:MM.

Measuring caloric intake

As part of Suaq's long-term database, we have compiled average adult orangutan feeding rates (number of items ingested per minute) for each for the 4 age-sex classes, for each specific food item, as well as the average macronutrient and caloric content of these items (see Rahmaeti et al. *in prep* for details). Feeding rates for items were calculated from video recordings of feeding bouts with clear and prolonged visibility. Macronutrient and caloric contents of every common food item are obtained through the regular collection, processing, and analysis of food item samples in accordance with the methods outlined in.[56,91,92] From this, we have calculated the average (mean) energy content (in kcal) for each food item. For food items for which we did not have a feeding rate or caloric content available, we substituted values from the most similar item available (i.e., the same plant part of similar size of a closely related species; these substitutes made up 29% of the feeding time of the focal animals of this study). For each focal follow, we used the durations of time that the focal was observed feeding on each specific food item, and the average adult feeding rates and the average caloric values for those food items, to obtain a total caloric intake value for that focal on that day.

Measuring predictor and control variables

In our analysis, we included the following behavioral, ecological, and social variables:

1) Number of conspecific association partners, which we quantified as the **number of nighttime association partners**, i.e., the number of conspecifics that were in association with the focal individual when it became inactive in its night nest, and the **average number of daytime association partners**, i.e., the average number of conspecifics in association with the focal individual across all 2-minute intervals of the daytime active period. Number of nighttime association partners and average number of daytime association partners ranged from 0 to 6. For mothers, their own dependent offspring were excluded from both counts of association partners, but these dependents were included in the counts for other conspecifics.
2) **Day journey length**, which we calculated by summing the Euclidean distances between successive GPS locations over the course of the focal follow, using the TrajLength function in the *trajr* package in R.[93]

3) Prevailing **habitat food availability**, which we quantified monthly as the percentage of fruit-bearing trees in two phenology plots that cross the study area from North to South and East to West, consisting of *ca.* 1500 stems with DBHs of at least 70 cm.[56]
4) Daily **energy intake** (in Kcal), which we measured by integrating the nutritional composition of the consumed food items, the mean rates at which they were ingested, and the cumulative duration of time that the focal spent feeding on each item each day (see above for details).
5) Rainfall, which we measured every morning at 6:00 for **rainfall during the night**, and every evening at 18:00 for **rainfall during the day**, by reading a rain gauge that was installed at the research camp. Due to occasional issues with the rain gauge, and the inability of our measurement to distinguish between a short duration of intense rain and a longer duration of light rain, we binarized rainfall measures to 0 (no rain) and 1 (rain) in all analyses.
6) Ambient temperature, which we measured every morning at 6:00 for **minimum nighttime temperature**, and every evening at 18:00 for **maximum daytime temperature**, by reading a min-max thermometer installed near the research camp.
7) **Nest construction duration**, which we calculated as the time between the start of the nest-building activity and the end of the nest-building activity. Nest construction duration was only reliably collected for night nests, and ranged from 1 to 24 minutes (mean = 7:18 minutes).
8) **Duration of ambient darkness** and the **illuminated fraction of the moon** for each night, which we obtained using the getSunlightTimes and the getMoonIllumination functions, respectively, of the *suncalc* package.[84]
9) **Length of the active period**, which we calculated using the time at which individuals showed signs of movement, activity, and/or vocalizations in the morning and the time at which they became inactive in their new night nests in the evening.
10) **Age-sex class** of the focal individual (mother, adult female, flanged male, or unflanged male).
11) **Number of day nests built per day**, which is simply the number of unique day nests that the focal orangutan built (or fixed up and reused) each day.

QUANTIFICATION AND STATISTICAL ANALYSIS

General approach

We used the R programming language (v4.2.2) for all statistical analyses and all plots.[83] To avoid issues caused by differences in the distribution and scales of our predictor variables, we z-transformed all continuous variables. We always included the identity of the focal individual as a random effect to avoid pseudo-replication issues caused by the fact that individuals occurred multiple times in the dataset. To assess the overall significance of the predictors in our three primary models, we compared each of the three full models (random effects, as well as all predictor and control variables as fixed effects) to their equivalent null model (containing only random effects and control variables as fixed effects), via likelihood ratio tests (LRT) using the anova function.[94,95] If this comparison indicated that the full model explained significantly more variance in the data than the null model, then we assessed the significance of the fixed effects in the full model through the cftest function of the *multcomp* package (for the LMERs[87,96]) or the model output (for the GLMM). We used the glht function in the *multcomp* package to perform Tukey's all-pair comparisons tests of the 4 age-sex classes.[87,96] Throughout our analyses, we used a significance criterion of $p < 0.05$. We computed and plotted model predictions for each significant fixed effect using the ggeffects function of the *ggeffects* package.[88] Due to missing data in our predictor and response variables, sample sizes varied between our statistical models.

Analyzing nighttime sleep period duration

To analyze ***nighttime sleep period duration***, we used Linear Mixed Effects Models (LMER) via the lmer function of the *lme4* package[85] (Table S1). The ***nighttime sleep period duration*** model included duration of sleep the night before, total nap time the day before, number of nighttime association partners, day journey length, habitat food availability, energy intake, rainfall during the night, minimum nighttime temperature, and nest construction duration as predictor variables, as well as duration of ambient darkness, illuminated fraction of the mood, and age-sex class as control variables. This model included included $n = 276$ focal-nights with one night nest each.

Analyzing daytime cumulative nap period duration

To analyze ***daytime cumulative nap period duration***, we used zero-inflated Generalized Mixed Models (GLMM) with a Poisson family distribution (using the discrete number of minutes as a response) via the glmmTMB function of the *glmmTMB* package[86] (Table S3). We chose a zero-inflated model due to the large number of zeros in the dataset (stemming from days when no napping occurred). The ***daytime cumulative nap period duration*** model included duration of sleep the night before, average number of daytime association partners, day journey length, habitat food availability, energy intake, rainfall during the day, and maximum daytime temperature as predictor variables, as well as length of the active period and age-sex class as control variables. Model predictions and effect sizes reported in the main text are for the conditional part of the model only. This model included n=455 focal-days.

Analyzing average duration of nap periods

To test for a link between the ***average duration of nap periods*** per day and the number of day nests built per day, we used an LMER via the lmer function of the *lme4* package (Table S4). The ***average duration of nap periods*** model included only a single predictor: the number of day nests built per day. This model included *n* = 213 focal-days, i.e., only focal-days on which the focal individual napped at least once.

Checking the models

We checked all models for multicollinearity issues via the VIF factor using the check_collinearity function as implemented in the *performance* package.[89] For the LMERs, we visually assessed the distribution of the model residuals and for the Poisson GLMM, we tested for zero inflation and overdispersion issues using the testDispersion and testZeroInflation functions of the *DHARMa* package.[90] For all models, we calculated conditional R2 values via the r2_nakagawa function of the *performance* package.[89]

Follow-up analyses

In two small follow up analyses, we 1) compared the average number of daytime association partners versus the number of nighttime association partners per follow using a Welch two sample t-test, and 2) tested whether the duration of an orangutan's active period was predicted by the distance it travelled that day using an LMM with active period duration as the outcome variable, day journey length and age-sex class as fixed effects, and focal ID as a random effect (***duration of the active period*** model, Table S2).