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Where to sleep next? Evidence for spatial memory associated with sleeping sites in Skywalker gibbons (*Hoolock tianxing*)

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Abstract

Finding suitable sleeping sites is highly advantageous but challenging for wild animals. While suitable sleeping sites provide protection against predators and enhance sleep quality, these sites are heterogeneously distributed in space. Thus, animals may generate memories associated with suitable sleeping sites to be able to approach them efficiently when needed. Here, we examined traveling trajectories (i.e., direction, linearity, and speed of traveling) in relation to sleeping sites to assess whether Skywalker gibbons (*Hoolock tianxing*) use spatial memory to locate sleeping trees. Our results show that about 30% of the sleeping trees were efficiently revisited by gibbons and the recursive use of trees was higher than a randomly simulated visiting pattern. When gibbons left the last feeding tree for the day, they traveled in a linear fashion to sleeping sites out-of-sight (> 40 m away), and linearity of travel to sleeping trees out-of-sight was higher than 0.800 for all individuals. The speed of the traveling trajectories to sleeping sites out-of-sight increased not only as sunset approached, but also when daily rainfall increased. These results suggest that gibbons likely optimized their trajectories to reach sleeping sites under increasing conditions of predatory risk (i.e., nocturnal predators) and uncomfortable weather. Our study provides novel evidence on the use of spatial memory to locate sleeping sites through analyses of movement patterns, which adds to an already extensive body of literature linking cognitive processes and sleeping patterns in human and non-human animals.

Keywords Spatial memory · *Hoolock tianxing* · Sleeping sites · Revisitation analysis · Linear movement

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Introduction

As animals move through space, they generate memories associating specific locations with relevant biological events (Fagan et al. 2013; Spiegel and Crofoot 2016). Yet, there is significant interspecific variation in the capacity of animals to store, recall, and integrate environmental information as memories (Janmaat et al. 2021; Morrison et al. 2021). It has been argued that the functionality of spatial memory varies in relation to the targeted food resources' spatiotemporal patterns (Riotte-Lambert and Matthiopoulos 2020). Thus, animals foraging for highly ephemeral and dispersed food items, such as fruits, have likely benefitted from evolving sophisticated cognitive skills to forage across rainforests (Milton 1981; DeCasien et al. 2017). However, animals experience multiple ecological pressures in addition to foraging, which may have also contributed to the emergence of sophisticated spatial skills (Dunbar and Shultz 2017).

Even though choosing suitable sleeping trees can affect animal survival, sleeping sites are often limited, which indicates that being able to remember the location of such

sleeping sites is highly advantageous. From bees to humans, sleeping patterns have been shown to vary in their duration, timing, architecture, and intensity (Keene and Duboe 2018; Reinhardt 2020). Despite this variation, there is an underlying association between qualitative sleep and enhanced cognitive processes (Paller et al. 2021), maturation of the central nervous systems (Blumberg 2015), and energy homeostasis (Schmidt 2014). Since sleeping individuals are in a state of reduced awareness and responsiveness, an important factor determining sleep quality is the environment where they sleep (Samson and Nunn 2015). Sleeping sites that provide protection against predators (Lima et al. 2005), favor thermoregulation (Reinhardt et al. 2019), and prevent the risk of falling (i.e., muscle tone decreases during REM sleep; Siegel 2004) are often selected. Therefore, by memorizing the location of favorable sleeping sites, individuals would benefit from increasing the quality of their sleep, which in turn would promote the performance of their cognitive processes (Fruth and Hohmann 1996; Samson and Nunn 2015).

Non-human primates (hereafter primates) are study models frequently used to understand the evolution of cognition because of their close phylogenetic relatedness to humans and their wide range of behavioral adaptations (Shettleworth 2010). Sleeping site selection varies across primate species, including tree holes (e.g., Lemuridae, Kappeler 1998), dense tangles (e.g., Lorisidae, Svensson et al. 2018), or cliffs (e.g., Cercopithecinae, Hamilton 1982). Most great apes build a different nest every night, which, in addition to enhancing their sleep quality, supports flexible movement patterns (Janmaat et al. 2014; Fruth et al. 2018; but see Stewart and Pruetz (2013), for evidence on recursive use of nests in chimpanzees at Fongoli, Senegal). Janmaat et al. (2014) showed that female chimpanzees in Tai Forest, Ivory Coast, decided where to build their sleeping nest at the end of the day in relation to the fruit tree where they were planning to forage in the next morning. Primates relying on fixed sleeping sites need to return to specific locations before sunset, which constrains their movement decisions (Markham et al. 2016). By memorizing the location of suitable sleeping sites, individuals might be able to return to these sites efficiently but also to select the most beneficial sleeping site depending on where they are planning to forage the next day. Even though recursive use of sleeping sites has been widely documented across primates (Poirotte et al. 2017), the use of spatial memory to reach such sleeping sites has not been reported yet.

Inferring spatial memory can be done by examining recursive movements to previously visited locations (Bar-David et al. 2009) and, subsequently, examining variations in specific metrics extracted from the traveling trajectories towards revisited locations under different conditions (e.g., linearity, speed, revisiting intervals; Janmaat et al. 2021). For instance, black howler monkeys (*Alouatta pigra*) in southern Mexico increased the linearity of their traveling trajectories when returning to fruit trees where they had been observed foraging previously, but only when fruits were ripening (de Guinea et al. 2021a, b). Similarly, tufted capuchin monkeys (*Sapajus nigritus*) increased their traveling speed to feed on revisited ripening fruit trees under conditions of increased intragroup competition or after prolonged starvation periods (Tujague and Janson 2017). Therefore, exploring the recursive use of sleeping sites and the trajectories used to reach such revisited sleeping sites will be indicative of spatial memory associated with sleeping site location (Janmaat et al. 2014). We expect that animals increase the linearity and speed of their trajectories while traveling towards sleeping sites close to sunset to avoid predators or when weather is unfavorable.

Gibbons are particularly interesting models to study the relationship between sleeping site selection and spatial memory because they are the only ape that sleeps in fixed-location sleeping sites instead of nests (Anderson 1998). They need to return to specific locations to avoid predators (*Nomascus concolor jingdongensis*, Fan and Jiang 2008; *Hylobates pileatus*, Phoonjampa et al. 2010; *Hylobates albibarbis*, Cheyne et al. 2012) and to promote thermoregulation (*Nomascus nasutus*, Fei et al. 2012; *Hoolock tianxing*, Fei et al. 2019). Since temperature decreases and predators are more active during twilight (Caine 1987; Anderson 1998; Reichard 1998; Fan and Jiang 2008; Phoonjampa et al. 2010; Fei et al. 2012), the relevance of approaching a suitable sleeping site will increase as sunset approaches. Asensio et al. (2011) revealed that white-handed gibbons (*Hylobates lar*) were able to anticipate the emergence of fruits in preferred tree species and plan travel bouts longer than their visibility distance to feed on them. Similarly, Javan gibbons (*Hylobates moloch*) showed the skills to keep track of both synchronous and asynchronous fruit productivity cycles within small home ranges (Jang et al. 2021). Given the importance of sleeping site selection, gibbons likely evolved similar spatial memory skills associated with sleeping sites.

Here, we explore spatial memory skills in relation to sleeping sites in endangered skywalker gibbons (*Hoolok tianxing*) in Mt. Gaoligong. Skywalker gibbon was described as a new specie in 2017 (Fan et al. 2017) and its total population was estimated to be less than 200 individuals in China (Zhang et al. 2021). All populations in China live in seasonal montane forests. Skywalker gibbons occupy home ranges four to five times larger than those of tropical gibbons (Zhang et al. 2014; Yin et al. 2016), and they can travel hundreds of meters from their last feeding site to their sleeping tree (Fei et al. 2017). Despite traveling such long distances, skywalker gibbons have been shown to frequently reuse specific sleeping sites characterized by being large, tall trees (Nankang: mean height = 22.3 m; Banchang: mean height = 32.9 m) surrounded by many other trees taller than

20 m (Nankang, 68 individual/ha; Banchang, 137 individual/ha), which can provide protection against terrestrial predators (Fei et al. 2017). They avoided aerial predators using branches away from the tree top but also by moving fast and directly to sleeping sites to subsequently stay quiet after settling (Fei et al. 2017). In addition, sleeping site selection has been documented to change as a function of the environmental temperature, suggesting flexibility in the movement decisions of wild gibbons (Fei et al. 2019). Thus, we hypothesize that skywalker gibbons possess spatial skills that they use to memorize the location of suitable sleeping sites and plan their trips at the end of the day before sleeping. First, we expect that the observed frequency of revisiting sleeping trees will be higher than randomly simulated visiting patterns of sleeping trees during the same time period. Second, traveling linearity towards out-of-sight sleeping sites is expected to not differ significantly from traveling linearity towards sleeping sites in-sight. Third, we expect that the linearity and speed of the traveling trajectories towards sleeping sites out-of-sight will increase as time to sunset decreases.

Methods

Study sites and subjects

We observed two groups of skywalker gibbon at Mt. Gaoligong National Nature Reserve, China. The first group (Group BB) was observed at Banchang (N25°12′, E98°46′) between May 2013 and October 2018, and the second group (Group NA) was observed at Nankang (24°49′ N, 98°46′ E) between June 2017 and October 2018 (Fei et al. 2017, 2019). The vegetation at these sites is characterized by mid-montane evergreen broad-leaved forests between 1600 – 2700 m above sea level (Fan et al. 2011). The climates at these sites were similar: annual rainfall was 1633 mm and 1655 mm and mean temperature was 13.2° and 13.1° at Banchang and Nankang, respectively.

Data collection

We observed each group for 5–10 consecutive days each month (Group BB: 613 days; Group NA: 126 days). We started collecting behavioral observations *ca.* 30 min before sunrise and when possible continued until the gibbons entered their sleeping tree at the end of the day (Banchang: $9.8 \pm SD$ 1.2 h/day, N = 415 full days, Range = 6.5–13.1 h/day; Nankang: $10.6 \pm SD$ 1.0 h/day, N = 119 full days, Range = 8.2–12.6 h/day). We used a GPS unit to collect the location of the group BB every 30 min from May 2013 to December 2014 (Garmin eTrex Legend HCx), every 10 min from January 2015 to December 2016 (Garmin

eTrex 20), and every 5 min from January 2017 to October 2018 (Garmin GPSMAP 62sc). Similarly, we collected the location of Group NA using Garmin GPSMAP 62sc every 5 min from June 2017 to October 2018. We only recorded GPS locations when the inaccuracy was smaller than 10 m. In addition, whenever a gibbon was feeding on a tree, we used all occurrences sampling to collect feeding data and recorded the arrival and departure time to the feeding tree for each individual, the item in which gibbons fed on (i.e., non-fig fruit, fig, leaves, flower, fauna, and others) and the tree species. If an adult fed on a tree (including lianas on the tree) for ≥ 5 min during a single visit, we defined this individual feeding tree as an important feeding tree (Asensio et al. 2011). Subsequently, we determined the last important feeding tree of the day (hereafter "dinner tree"; Janmaat et al. 2014). We used handheld GPS units to record the location of all important feeding trees and marked each tree using an aluminum tag with a unique number after all gibbons left the tree.

When gibbons left their dinner trees, they often moved very fast to different sleeping trees (Fei et al. 2017). We tried to follow and record travel trajectories of different individuals to their sleeping trees. Infants and juveniles often cling to their parents when they sleep and subadults are peripheral to the group (see Fei et al. 2019 for details). Therefore, we focused on sleeping behavior of adult individuals in this study (adult male AM and adult female AF in group NA, and adult male BM and adult female BF in group BB). We recorded the arrival time of each individual to their sleeping trees and marked all sleeping trees with a number plate. We recorded the location of each individual sleeping tree. To describe in detail the travel path used while moving to sleeping trees, we recorded the numbers on the aluminum tag of every important feeding tree and sleeping tree traveled through together with locations of short rest, locations where gibbons changed their travel direction, and locations where individuals were separated from each other > 20 m.

Data analyses

Adult gibbons of group NA rarely shared sleeping trees, but the adult male and female of group BB often slept together in the same tree (Appendix table S1). To make sure the analysis did not lead to pseudo-replication, we retained data only when individuals slept alone or was first entering sleeping trees when they shared sleeping trees with others (BM: 270 days out of 470 days; BF: 322 days out of 466 days; AM: 108 days out of 116 days; AF: 109 days out of 117 days).

(a) Revisiting analysis

We used ArcGIS 10.3.1 to transform the GPS point data into projected coordinate points (WSG 84 coordinate system

was converted into Beijing 54 GK Zone-17 projected coordinate system) and used the minimum convex polygon (MCP) method to calculate home range size for each group.

We counted the accumulated number of new sleeping trees and the accumulated number of revisits to sleeping trees in relation to the number of days that group was followed. To test if the recursive use of sleeping sites was higher than randomly simulated revisit patterns, we estimated the number of potential sleeping trees within each group's home range. Since we previously determined that tree height was the main factor driving sleeping site selection in skywalker gibbons (Fei et al. 2017), we estimated the number of potential sleeping sites with similar heights within the home ranges (group BB: $N = 283$, mean $29.4 \pm$ SD 6.4 m; group NA: $N = 102$, mean $23.7 \pm$ SD 4.9 m). A habitat survey revealed that the density of trees taller than 29.4 m at Banchang was 13/ha and trees taller than 23.7 m at Nankang was 7/ha (Yuan et al. 2014). Group BB has a home range of 255 ha (May. 2013–Oct. 2018) and NA's home range was 126.5 ha (Jun. 2017–Oct. 2018). There were 3315 potential sleeping trees within group BB's home range, and 885 trees within group NA's home range. Subsequently, we ran a random revisited model using the packages "dplyr (version 1.0.4: Wickham et al. 2021)", "foreach (version 1.5.1: Calaway et al. 2020)", and "doParallel (version 1.0.16: Wallig et al. 2020)" in R 3.5.1 to calculate how many potential trees would have been revisited twice, three times, or more by chance during the same observational days (Appendix. 1). The observed frequency of revisiting sleeping trees (Of_n) and simulated frequency (Sf_n) of revisiting have the following formulas:

$$Of_n = \frac{R_n}{P} \times 100\%$$

$$Sf_n = \frac{S_n}{P} \times 100\%,$$

where: Of_n is the observed frequency of sleeping trees being used n times; Sf_n is the simulated frequency of sleeping trees being used n times. R_n is the number of observed sleeping trees being used n times. S_n is the number of simulated sleeping trees being used n times. P is the number of potential sleeping trees. $n = 1, 2, 3, 4$

For example, we created a dataset including 885 IDs that represents the 885 potential sleeping trees within group NA' home range. We then randomly picked one ID from the dataset 108 times to simulate that sleeping tree being used during our 116 observational days of AM. Finally, we counted the number of each ID being selected to obtain the S_n for AM. We repeated the simulation 10,000 times. Since our data was independent and normally distributed, we used the One-Sample t test to examine whether the observed frequency of revisited sleeping trees was different from the simulated frequency under the same observational days.

(b) Travel direction analysis

We selected travel paths for which GPS locations were collected at 5 min intervals to analyze travel direction, speed, distance and linearity from the dinner tree to the sleeping tree (Fig. 1). To test if gibbons travel to sleeping trees directly after leaving dinner trees, we built a deviation angle model and calculated the travel direction of two successive
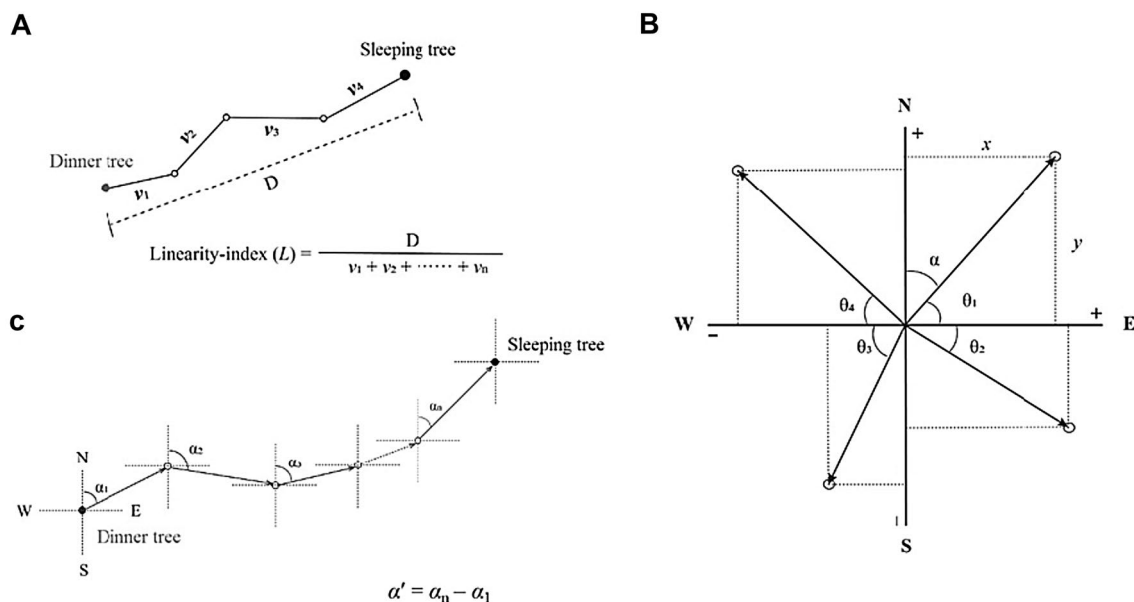
Fig. 1 The calculation model of moving linearity index (**A**), moving direction (**B**), and deviation angle (**C**)

GPS locations (each step) (Valero and Byrne 2007). By subtracting the two values of longitude and latitude of two successive GPS locations, the differences in longitude (x) and latitude (y) were obtained. Then we calculated θ by the tangent function ($\tan \theta = y/x$) or arctangent function (arctan θ) (Fig. 1B). If x and y are both positive, we obtained the travel direction $\alpha = 90° - \theta_1$; if x is positive and y negative, $\alpha = 90° + \theta_2$; if x is negative and y positive, $\alpha = 270° - \theta_3$; if x and y both negative, $\alpha = 270° + \theta_4$ (Fig. 1B). We then defined the first azimuth from the dinner trees to the next point as α_1, and so on to $\alpha_2, \alpha_3, …, \alpha_n$ (Fig. 1C). We calculated the deviation angle (α') of each step to the original travel direction using the following formula:

$$\alpha' = \alpha_n - \alpha_1.$$

We predicted that if gibbons move directly to known sleeping trees, α' should not deviate much from 0° or 360° (match the original orientation). On the contrary, if gibbons were randomly searching for sleeping while traveling, α' could deviate appreciably from 0° or 360°.

(c) Travel linearity analysis

We calculated distance traveled (V) by summing up the distances between successive locations ($V = v_1 + v_2 + ⋯⋯ + v_n$) (Fig. 1A), and travel speed (S) by dividing the travel distance by travel time duration. We calculated the linearity index (L) by dividing the Euclidean distance (D) by travel distance (V) from dinner tree to sleeping tree using the following formula (Normand and Boesch 2009) (Fig. 1A):

$$L = \frac{D}{v_1 + v_2 + \cdots + v_n}$$

This ratio varies between 0 and 1, with L close to 1 approaching straight-line traveling. Estimating the visual range of an arboreal animal in the wild is strikingly difficult because it depends not only on the species' physiological adaptations and the environmental properties of the landscape, but it also varies according to the traveling momentum (i.e., speed, height and angular deviation of the animal at a given moment in time, Janson and Di Bitteti 1997). The only available estimates on gibbons' visual range within dense tropical forest was on average 21 m, and the maximum was 40 m (Brockelman 2009). Previous estimates in other primate species' visual range across different landscapes varied from 30 to 50 m (30 m, *Gorilla gorilla*, Salmi et al. 2020; 35 m, *Alouatta palliata*, Hopkins 2011; 40 m, *Alouatta pigra*, de Guinea et al. 2021a, b; 50 m, *Sapajus libidinosus*, Presotto et al. 2018). Thus, we decided to keep 40 m as threshold to be both consistent with previous research and to guarantee the replicability of this study in other taxa lacking information on visual range. We calculated linearity index for sleeping trees in-sight (10–40 m, L_{in}) and out-of-sight (≥ 40 m, L_{out}) separately, then used the Mann–Whitney U test to test if L_{out} was lower than L_{in} because this data was not normally distributed (Appendix Fig. S1).

(d) Dinner tree departure model

The histogram and Shapiro–Wilk normality test found none of our variables were normally distributed (Appendix Fig. S1). We used the log transformation: $y = \log(x)$ to normalize the speed of traveling to sleeping sites out-of-sight. We used the $y = (max - x)/(max - min)$ to transform the linearity index (L_{out}) of traveling to sleeping sites out-of-sight from a left-skewed distribution to a right-skewed distribution to fit the Generalized Linear Mixed Models (GLMM) (Appendix Fig. S1). We also used $y = (x - min)/(max - min)$ to standardize the daily mean temperature, the daily rainfall, time leaving the dinner tree relative to sunset, and the Euclidean distance from dinner trees to sleeping sites. Then we built two GLMM based on "lme4 (version 1.1-26: Bates et al. 2015)" and "MuMIn (version 1.43.17: Burnham and Anderson 2002)" package to test if the speed (Travel Speed Model: verbose = 2; family = gaussian; Model residuals: Shapiro–Wilk normality test, $W = 0.993$, $P = 0.638$) and linearity (Travel Linearity Model: verbose = 2; family = Gamma (link = "log"), Model residuals: Shapiro–Wilk normality test, $W = 0.878$, $P < 0.001$) of the traveling trajectories between the dinner tree and the sleeping site increased as sunset approached. To ensure the stability of Travel Speed Model and Travel Linearity Model, we ran a series of GLMM in which each model removed one different individual. In these models, the speed and linearity index (L_{out}) of traveling to sleeping sites out-of-sight were selected as the response variables. We determined daily mean temperature (TEMP), daily rainfall (RAIN), time leaving the dinner tree relative to sunset (LEA), and the Euclidean distance from dinner trees to sleeping sites (DIS) as fixed factors and individual ID as a random factor. In addition, TEMP and RAIN also were considered as random slopes (Appendix Table S2). The Akaike Information Criterion corrected for small sample sizes (AICc) was used to evaluate model performance (Burnham and Anderson 2002). We found no single model superior to the others in both the GLMMs (Appendix Table S3, S4). Subsequently, a model-averaging approach was applied to derive coefficients of variables from the set of top models that had a cumulative Akaike weight (ωi) over 0.9 (Appendix Table S5). There were no issues of multicollinearity in our models since all VIF values were below 3 (Fox and Weisberg 2018).

We use the ArcGIS 10.3.1, R 3.5.1, and SPSS 21.0 for analyses. All research reported in this manuscript has met the appropriate national and institutional guidelines for the

legal acquisition and was permitted by the Yunnan Forestry and Grassland Administration and Gaoligong Nature Reserve Administration Bureau. All research reported in this manuscript adhered to the legal requirements of China.

Results

Frequency of revisiting sleeping trees

The accumulated number of new sleeping trees and accumulated revisits to sleeping trees continued to increase throughout the study period without reaching an asymptote (Fig. 2A); however, nearly 30% of all sleeping trees were revisited (AM: 21 trees: 36.2%, 21/58; AF:17 trees, 28.3%, 17/60; BM: 56 trees, 33.9%, 56/165; BF: 67 trees, 37.6%; 67/178) (Fig. 2B). A single sleeping tree was each revisited 9 times by the adult female at Banchang and 10 times by the adult female at Nankang (Fig. 2B). Although many trees were revisited, only five trees at Banchang and three trees at Nankang were revisited on consecutive days by the same individual.

The observed frequency of sleeping trees being used twice (AM: $t = -7.237$, $df = 9999$, $P < 0.001$; AF: $t = -4.731$, $df = 58$, $P < 0.001$; BM: $t = -15.753$, $df = 9999$, $P < 0.001$; BF: $t = -6.569$, $df = 9999$, $P < 0.001$) (Fig. 3B), three times (AM: $t = -18.215$, $df = 9999$, $P < 0.001$; AF: $t = -15.686$, $df = 58$, $P < 0.001$; BM: $t = -56.189$, $df = 9999$, $P < 0.001$; BF: $t = -30.494$, $df = 9999$, $P < 0.001$) (Fig. 3C), or four times (AF: $t = -43.280$, $df = 58$, $P < 0.001$; BM: $t = -866.051$, $df = 9999$, $P < 0.001$) (Fig. 3D) are all significantly higher than the frequency produced by the simulated random revisitation model under the same observational days (BM: 270 days; BF: 322 days; AM: 108 days; AF: 109 days). The simulated frequency of revisiting a tree four times by chance was close to zero for all four individuals (Fig. 3D). These results indicate that gibbons did not randomly revisit their sleeping trees.

Fig. 2 Cumulative number of new sleeping trees and accumulated revisits to sleeping trees (**A**), frequency of reused sleeping trees (**B**) by two groups of skywalker hoolock gibbon at Nankang and Banchang, Mt. Gaoligong, China
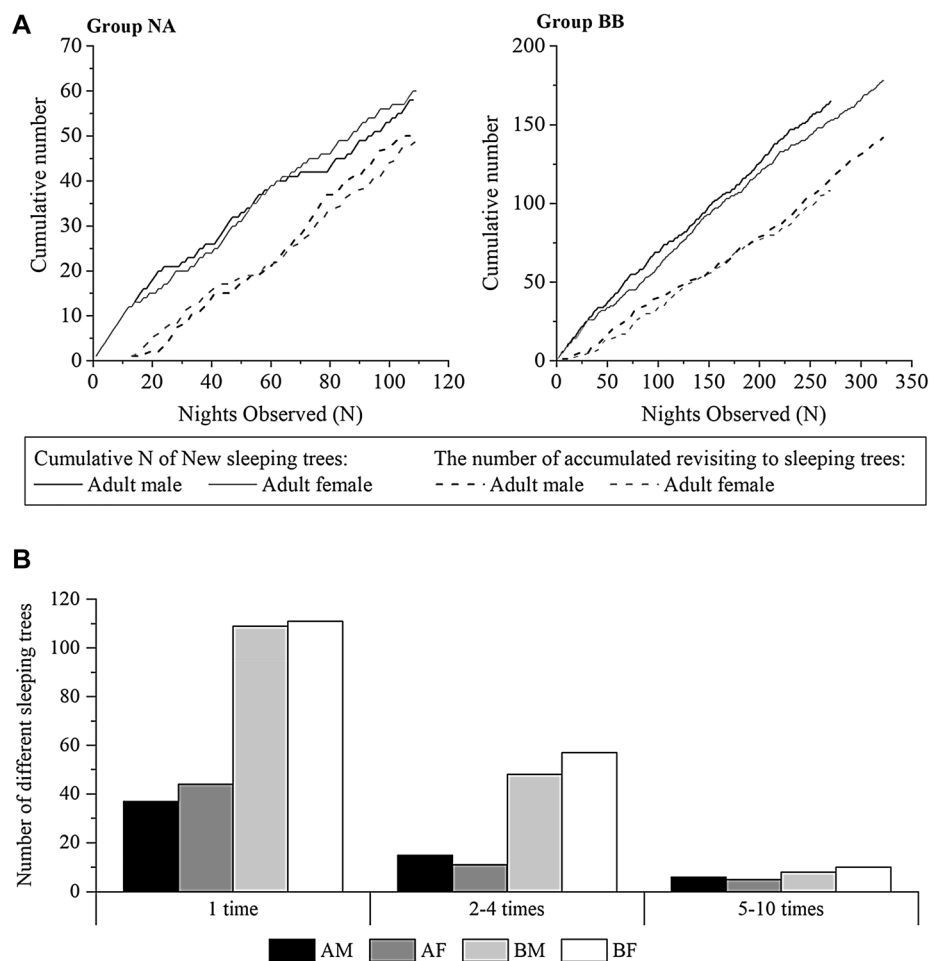
Fig. 3 Observed (in blue square) and simulated frequency (in box figure: line cap: upper/lower extreme; upper/lower quartile; cross: mean value; dots: outlier data point) of sleeping trees being used once (**A**); twice (**B**); three times (**C**); or four times (**D**) by four adult skywalker hoolock gibbons in two groups at Nankang and Banchang, Mt. Gaoligong, China
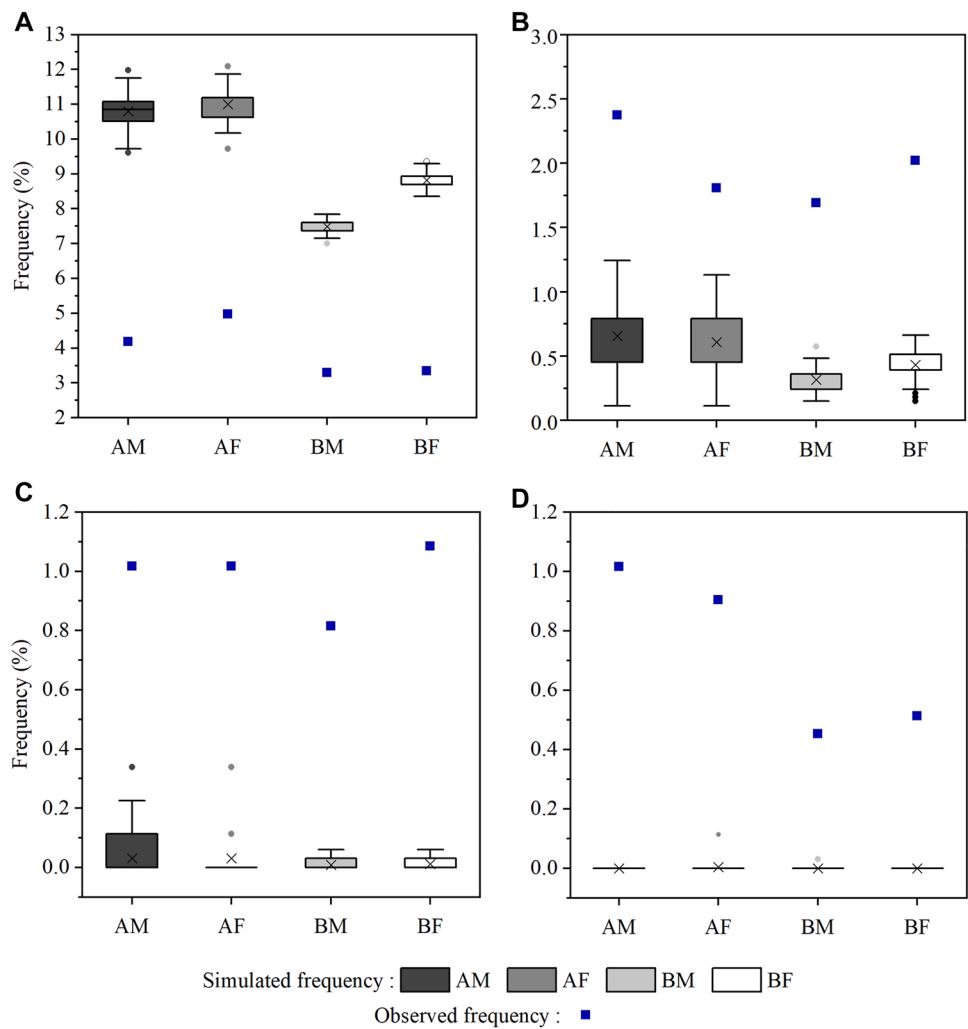
Assessment of traveling trajectories

(a) Deviation angle of from last feeding tree to sleeping tree

Gibbons rarely make a U turn (180°) or T turn (90°) on the way to sleeping trees. The deviation angle from the original orientation when leaving the dinner tree was typically less than 10° (Banchang: BM, 114/108, 53.7%; BF, 84/147, 57.1%. Nankang: AM, 110/235, 46.8%; AF, 166/269, 61.7%; Fig. 4).

(b) The linearity of travel path to sleeping trees in-sight and out-of-sight

We found that gibbons occasionally selected dinner trees of the day as sleeping trees (Banchang: BM, 4.8%, 13/270; BF, 7.5%, 24/322; Nankang: AM, 1.8%, 2/108; AF, 4.6%, 5/109). The Euclidean distances between dinner and sleeping trees were about 45 m and 90 m for group BB and

group NA, respectively (Table 1). Although the linearity of travel to sleeping trees out-of-sight of three individuals was significantly lower than that to sleeping trees in-sight (Mann–Whitney U test: BM, $Z = -0.946$, $P = 0.344$; BF, $Z = -3.538$, $P < 0.001$; AM, $Z = -3.205$, $P = 0.001$; AF, $Z = -5.059$, $P < 0.001$), linearity of travel to sleeping trees out-of-sight was higher than 0.8 for all individuals (Table 1).

(c) Departure time and traveling speed

The latest time leaving dinner trees relative to sunset of group BB and group NA was 97.7 min and 67.1 min, and the latest time entering sleeping trees relative to sunset of group BB and group NA was 90.2 min and 42.7 min, respectively (Table 1). The speed of travel to out-of-sight sleeping trees was $11.4 \pm SD\ 6.3$ m/min for adult male BM and $9.4 \pm SD\ 5.9$ m/min for adult female BF in group BB, and was $12.7 \pm SD\ 9.2$ m/min for adult male AM and $13.5 \pm SD\ 11.6$ m/min for adult female AF in group NA (Table 1).
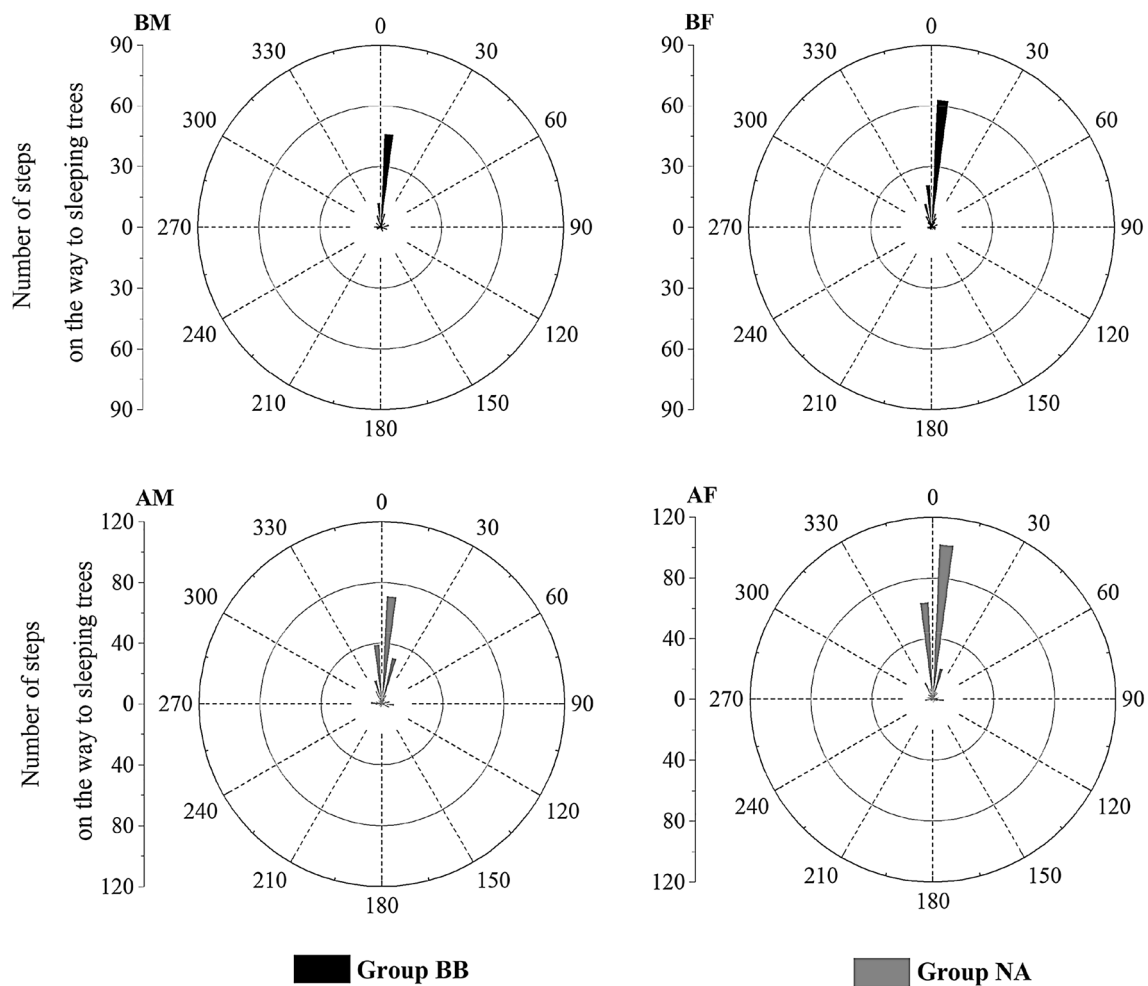
Fig. 4 Distribution of deviation angle from the original orientation on the way from the last feeding trees to sleeping trees by four adult individuals in two groups of skywalker hoolock gibbon at Nankang and Banchang, Mt. Gaoligong, China. The length of bars represents the accumulated number of steps with the same angular deviation in which 0° is the goal direction

(d) The departure model

The Travel Speed Model showed that traveling speed increased when sunset approached and when daily rainfall increased (Table 2). However, the Travel Linearity Model showed that these fixed factors did not significantly affect travel linearity from dinner tree to the out-of-sight sleeping site (Table 3). We found the main conclusions remained the same after removing one individual from the model (Appendix Table S6).

Discussion

Our results indicate that skywalker gibbons at Mt. Gaoligong were goal-directed on the way to sleeping sites. To reach such sleeping trees before sunset, gibbons increased the speed of their traveling trajectories when the departure time at the dinner tree was closer to sunset. Altogether, we reveal novel evidence using naturalistic observations suggesting an association between sleeping behavior and spatial memory in a wild primate.

Despite occupying large home ranges, skywalker gibbons selected a small subset of trees as sleeping locations among all the potential sleeping locations suitable in the study area. Thus, commuting from dinner to sleeping trees over potentially long distances implies an additional energy expenditure on a daily basis. Since skywalker gibbons inhabit montane forests in Mt. Gaoligong where food availability varies seasonally (Fan et al. 2013), maintaining such additional daily energy expenditure during periods of food scarcity might challenge the fitness and survival of the individuals (Wright 1999; Fan et al. 2008). We show that gibbons are cognitively able to optimize the trajectories (i.e., linearity) and adjust the speed of their travel bouts depending on the urgency of reaching their sleeping sites. By developing

Table 1 Descriptive results of the Euclidean distance from dinner trees to sleeping trees (m), time leaving dinner trees relative to sunset (min), time entering sleeping trees relative to sunset (min), speed (m/min) and linearity of travel path to sleeping sites in-sight and out-of-sight

		Mean	N	SD	Min	Max
Euclidean distance from dinner trees to sleeping trees (m)	BM	45.4	59	59.4	0.0	392.1
	BF	47.1	75	42.9	0.0	170.2
	AM	83.3	100	76.4	0.0	477.3
	AF	88.7	100	89.9	0.0	492.8
Time leaving dinner trees relative to sunset (min)	BM	213.8	174	45.1	97.7	330.0
	BF	216.2	226	45.7	99.0	333.0
	AM	173.6	97	48.1	67.1	285.9
	AF	181.8	98	49.2	74.0	297.7
Time entering sleeping trees relative to sunset (min)	BM	202.9	265	44.3	90.2	316.0
	BF	202.4	320	42.6	98.0	315.3
	AM	163.2	104	52.6	54.2	278.5
	AF	167.9	107	52.9	42.7	282.9
Speed of travel to sleeping trees out-of-sight (Euclidean distance > 40 m) (m/min)	BM	11.4	24	6.3	2.9	22.9
	BF	9.4	34	5.9	0.8	23.0
	AM	12.7	62	9.2	2.1	61.7
	AF	13.5	60	11.6	2.4	68.1
Linearity of travel path to sleeping sites in-sight (L_{in}) (Euclidean distance 10–40 m)	BM	0.837	19	0.226	0.310	1.000
	BF	0.947	22	0.108	0.630	1.000
	AM	0.898	27	0.173	0.380	1.000
	AF	0.956	29	0.103	0.590	1.000
Linearity of travel path to sleeping sites out-of-sight (L_{out}) (Euclidean distance > 40 m)	BM	0.831	24	0.1445	0.590	1.000
	BF	0.819	37	0.163	0.440	1.000
	AM	0.842	65	0.131	0.430	1.000
	AF	0.851	64	0.159	0.290	1.000

Table 2 The fixed effects of Travel Speed Model analyzing the effect of daily mean temperature (℃), daily rainfall (mm), time leaving dinner trees relative to sunset (min), and the Euclidean distance from dinner tree to sleeping tree out-of-sight (m) on the speed (m/min) of travel to sleeping trees out-of-sight

Fixed effect	Estimate	Std. Error	t-value
Intercept	2.564	0.280	9.143
Daily mean temperature (℃)	0.330	0.403	0.820
Daily rainfall (mm)	1.156	0.548	2.111
Time leaving dinner trees relative to sunset (min)	−1.234	0.252	−4.987
Euclidean distance from dinner tree to sleeping tree out-of-sight (m)	0.071	0.293	0.241

Table 3 The fixed effects of Travel Linearity Model analyzing the effect of daily mean temperature (℃), daily rainfall (mm), time leaving dinner trees relative to sunset (min), and the Euclidean distance from dinner tree to sleeping tree out-of-sight (m) on the linearity index of travel to sleeping trees out-of-sight

Fixed effect	Estimate	Std. Error	t-value
Intercept	−1.826	0.378	−4.832
Daily mean temperature (℃)	−0.006	0.501	−0.012
Daily rainfall (mm)	−0.601	0.867	−0.694
Time leaving dinner trees relative to sunset (min)	0.594	0.491	1.208
Euclidean distance from dinner tree to sleeping tree out-of-sight (m)	0.294	0.614	0.471

the cognitive skills necessary to anticipate the locations of sleeping sites, gibbons likely minimize the costs of traveling. The absence of cognitive skills would lead gibbons to engage in random search at the end of each day to find a suitable sleeping site, likely leading to higher energetic costs than purposeful travel to familiar sleeping sites.

The most parsimonious explanation for our findings is that skywalker gibbons rely on memory to locate sleeping trees. Not only did gibbons travel towards out-of-sight sleeping sites (> 40 m away) from dinner trees using highly linear trajectories (Table 1), they also rarely changed directions on the way to sleeping trees. Straight, efficient, and goal-directed paths when traveling between out-of-sight locations to engage in specific behaviors are often interpreted as the animal's ability to anticipate events previously experienced at that location (Janson 1998; Noser and Byrne 2007; Cheke and Clayton 2010). Previous research has focused on goal-directed revisiting patterns towards ephemeral food resources (i.e., hummingbirds foraging on nectar in flowers, González-Gómez and Vasquez 2006; chimpanzees foraging on fruits in trees, Janmaat et al. 2013) and locations where social events took place (i.e., intergroup encounters in black howler monkeys, de Guinea et al. 2021a). Here, we expand our knowledge on goal-directed revisitation patterns by showing that gibbons approached sleeping sites where they likely had experienced suitable sleeping conditions before.

Even though we did not explicitly demonstrate that gibbons memorize sleeping trees to enhance the quality of their sleeping patterns, we found evidence suggesting that memorizing the location of sleeping trees provided protection against predators. Travel speed increased as sunset approached, which may be part of a predator-avoidance strategy. Gibbons are small apes characterized by a body weight that ranges between 6 and 9 kg, which makes them vulnerable to predation by nocturnal cats (Jiang et al. 1994; Morino 2010; Fei et al. 2012). Entering sleeping trees before sunset is thought to be a strategy to avoid being tracked and attacked by nocturnal predators who are more active around sunset (Caine 1987; Anderson 1998; Reichard 1998; Fan and Jiang 2008; Phoonjampa et al. 2010; Fei et al. 2012). Therefore, the closer sunset is, the more vulnerable gibbons are to nocturnal predators. In addition, we found that travel speed increased when daily rainfall increased. During days with heavy rain, it is also important for gibbons to enter sleeping trees faster to minimize energy cost.

By remembering the locations of sleeping trees, gibbons can rapidly and directly approach such locations and minimize the risk of detection by predators (Pochron 2001; Fei et al. 2017). In addition, sleeping at trees that provided protection against predators will indirectly increase the sleep quality of animals by supporting continuous, unaltered sleep throughout the night (Lima et al. 2005). We suggest future research to focus on measuring sleep quality across different sleeping trees in relation to the landscape of fear in the area (i.e., gradient of predation risk and disturbance derived from anthropogenic pressures across the study area, Coleman and Hill 2014) to better understand the relationship between sleeping patterns, predation risk and cognition.

Lastly, we found that gibbons did not randomly revisit their sleeping sites. For instance, while the frequency of randomly revisiting a tree four times was close to zero in our simulations, there were dozens of sleeping trees being revisited more than four times by gibbons. A single tree was even revisited 10 times at Nankang. However, gibbons rarely revisited sleeping trees on consecutive nights, which makes it difficult to predict their sleeping site and possibly minimizes the risk of detection by predators (Reichard 1998; Von Hippel 1998; Teichroeb et al. 2012; Feilen and Marshall 2014; Fei et al. 2017). Thus, in addition to accurately locating and approaching sleeping trees, gibbons were able to alternate and combine their visits among multiple sleeping locations. Likely, gibbons remember when they last visited a specific sleeping site, suggesting that they also incorporate a temporal layer of information in their movement decisions (Janson and Byrne 2007; Trapanese et al. 2019). The complexity underlying the cognitive process of "where to sleep next" potentially increases beyond selecting a subset of spatial locations (i.e., sleeping trees) to memorize by continuously updating the sequential order in which these sites were visited (Conway and Christiansen 2001). We encourage future research to explore non-human primates' ability to employ a statistical combinatory approach in the movement decisions associated with the selection of sleeping sites since it would add to previous evidence describing statistical botanical knowledge in great apes (Janmaat et al. 2013; 2021; Trapanese et al. 2020).

Conclusion

Safe and comfortable sleeping trees/sites were limited resources within both skywalker hoolock gibbon groups' home ranges. The gibbons displayed a series of behaviors indicating spatial memory in relation to sleeping site use. By remembering the locations of sleeping trees, these gibbons rapidly and directly moved to suitable sleeping trees that were out-of-sight to potentially minimize the costs of traveling while reducing the risk of detection by predators. In sum, our study suggests that sleeping behavior is a good system to investigate spatial memory in primates, a system that is largely overlooked in the current literature.

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