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Influence of Weather Conditions on Sleeping Patterns and Selection of Foliage Cover of Sleeping Trees in Black-and-Gold, Howler Monkeys (*Alouatta caraya*) in Northern Argentina

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Abstract

Sleeping behaviors, such as sleeping in clusters and sleeping-tree selection, are affected by several social and ecological factors simultaneously, among which weather conditions are suggested to be the most important. We evaluated the relationship between weather conditions (temperature and rainfall) and sleeping-cluster patterns, body posture, and foliage cover at sleeping sites in four groups of black-and-gold, howler monkeys (*Alouatta caraya*) inhabiting San Cayetano (27° 30 'S-58° 41'W), Corrientes, Argentina. During 12 months (between June 2012 and July 2013), we collected clustering, postural, and weather data on 185 days. The number of individuals in sleeping clusters was higher at low temperatures and lower at higher temperatures. At low temperatures, the curled posture was the most frequent, whereas the spread posture increased in frequency as temperatures increased. We did not find a significant relationship between rainfall and sleeping body postures. At low and medium temperatures, individuals selected sleeping trees with dense foliage cover and used open-crowned sleeping trees on rainy days. Consistent with what was found in previous studies, our findings suggest that howler monkeys used behavioral thermoregulation strategies that reduce the exposition to adverse climatic conditions.

Keywords Behavioral thermoregulation · Sleeping habits · Ambient temperature · Rainfall

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Introduction

Sleeping habits may affect the health, ecology, and behavior of nonhuman primates (Anderson, 1984). Selection of adequate sleeping sites and clustering patterns, for example, can be a strategy to reduce the costs associated with long resting periods, such as reduced reaction time to unpredictable variation in the environment and inability to detect the presence of predators, affecting the survival of individuals (Anderson, 1984; Gilbert *et al.*, 2010; Nunn *et al.*, 2010; Reichard, 1998). Numerous nonmutually exclusive hypotheses have been proposed to explain the social and ecological factors influencing the use and selection of sleeping tree and sleeping-cluster patterns at night: parasite avoidance (Brividoro *et al.*, 2019; Hausfater & Meade, 1982; Kowalewski & Zunino, 2005), comfort or a stable body position during sleep (Anderson & McGrew, 1984; Brividoro *et al.*, 2019; Reichard, 1998), daytime social interactions (Anderson, 1984; Brividoro *et al.*, 2021; Brotcorne *et al.*, 2014; Di Bitetti *et al.*, 2000), proximity to feeding sites (Albert *et al.*, 2011; Brividoro *et al.*, 2019; Phoonjampa *et al.*, 2010; von Hippel, 1998), predator avoidance (Albert *et al.*, 2011; Barnett *et al.*, 2012; Di Bitetti *et al.*, 2000; Fei *et al.*, 2012; Matsuda *et al.*, 2008), and thermoregulation (Anderson & McGrew, 1984; Reichard, 1998; Takahashi, 1997).

Among the many factors that affect sleeping patterns in primates, weather conditions are considered some of the most important (Anderson, 2000). The behavioral thermoregulation hypothesis suggests that several mechanisms exist to regulate body heat and minimize individual exposure to adverse weather conditions (Bicca-Marques & Calegaro-Marques, 1998; Savagian & Fernandez-Duque, 2016; Takahashi, 1997; Terrien *et al.*, 2011; Urbani *et al.*, 2020). These strategies include microhabitat selection (Caine *et al.*, 1992; Di Bitetti *et al.*, 2000; Smith *et al.*, 2007; Thompson *et al.*, 2014), changes in body postures and orientation, protection from exposure to adverse weather conditions (Bicca-Marques & Calegaro-Marques, 1998; Dausmann *et al.*, 2000; Fan & Jiang, 2008; Lopes & Bicca-Marques, 2017; Reichard, 1998), and increasing the number of individuals in sleeping clusters to conserve body heat during cold seasons (Aquino & Encarnacion, 1986; Bicca-Marques & Calegaro-Marques, 1998; Fan & Jiang, 2008; Gaulin & Gaulin, 1982; Reichard, 1998; Savagian & Fernandez-Duque, 2016; Takahashi, 1997; Terrien *et al.*, 2011; Thompson *et al.*, 2014).

Black-and-gold, howler monkeys (*Alouatta caraya*) are arboreal with a wide distribution across Paraguay, Brazil, Bolivia, and Argentina. Northern Argentina and southern Brazil are the southern-most part of their range (Oklander *et al.*, 2019). The southern limit of their distribution in Argentina encompasses an area where there is a marked difference between the winter and summer seasons, with a decline in food availability, lowest temperatures, and shortest day lengths in the cold season (Brividoro, 2018; Zunino *et al.*, 2017). Rainfall shows only a slight decrease in winter so it is not possible to differentiate between a rainy and dry season (Zunino *et al.*, 2007). Black-and-gold, howler monkeys are folivorous-frugivorous, with a diet based mainly on foliar structures (mature and immature leaves and buds), flowers, and fruits (Bravo & Sallenave, 2003; Fernández, 2014).

Black-and-gold, howler monkeys sleep in clusters in sleeping trees at night (Bicca-Marques & Calegaro-Marques, 1998; Brividoro *et al*., 2019, 2021). Cluster composition is affected by social factors; for example, individuals with more diurnal social interactions sleep together (Brividoro *et al*., 2021). Howlers select the largest sleeping trees (larger diameter at breast height, total height, and height of the lowest branch), and this pattern of selection is related to strategies for reducing parasitic infection, increasing the opportunity to adopt relaxed and stable body position, and facilitating access to food and range defense (Brividoro *et al*., 2019; Kowalewski & Zunino, 2005; Urbani *et al*., 2020).

Our study is a partial replication of previous ones that examined the effect of temperature on clustering patterns and body postures, and it extends previous studies by incorporating the analysis of temperature on the selection of sleeping trees and the effect of rainfall on clustering patterns, body postures, and sleeping trees selection in four groups of black-and-gold, howler monkeys that inhabit fragmented forests in northeastern Argentina. This work will provide information on the behavioral strategies developed by primates to reduce the costs associated with adverse weather conditions, which could be used to optimize success in conservation and reintroduction strategies for primates.

We tested the following hypotheses and predictions:

- Hypothesis 1: The clustering patterns (Individuals in sleeping clusters) vary according to weather conditions, as a strategy to conserve body heat and to avoid the cooling effects produced by the body as water evaporates. We predicted that the proportion of individuals sleeping in clusters in physical contact would increase with decreasing ambient temperature class or in the presence of rainfall.
- Hypothesis 2: Body postures vary according to weather conditions as a strategy to reduce the adverse effects of weather conditions at night, through loss of body heat. We predicted that body postures that decrease the number of body regions exposed (a curled posture) will be more frequent when the temperature is low or when it rains, whereas body postures that increase the number of body regions exposed (a spread posture) will be more frequent during high temperatures.
- Hypothesis 3: Selection of sleeping trees varies according to weather conditions to reduce exposure to rain and low temperature. We predicted that individuals would select sleeping trees with dense foliage cover on rainy days or when the temperature is low.

Methods

Study Site

The study site is composed of fragments of semideciduous, gallery forest in the basin of the Riachuelo River (a tributary of Paraná River) close to Corrientes Biological Field Station (EBCo) and San Cayetano Provincial Park (27°30′S, 58°41′W), Corrientes, Argentina (Fig. 1). The climate is subtropical (close to the limit of the warm temperature zone), with an average annual temperature of 21 °C, and an average

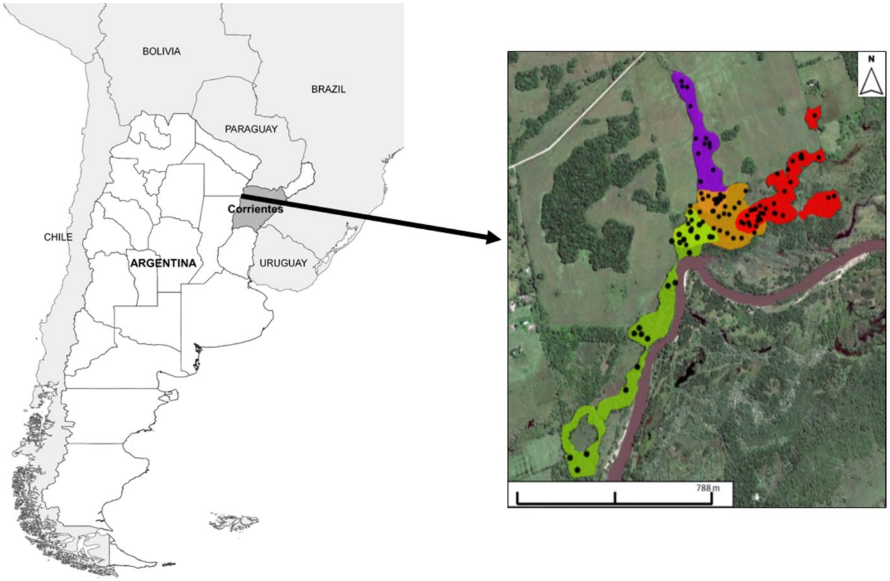

Fig. 1 Home range, overlap area, and sleeping trees of four study groups of black-and-gold howlers (*Alouatta caraya*) in Corrientes Province, Argentina (27°30′S, 58°41′W), between June 2012 and July 2013. Black circles indicate the spatial location of sleeping trees. Home ranges: green: GA; orange: GCN; red: GT; and violet: GS.

annual rainfall of 1,440 mm (Zunino *et al.*, 2017). In the study site, the summer season has maximum temperatures, transitional seasons have intermediate temperatures, and the winter season has minimum temperatures (Zunino *et al.*, 2017). The average annual temperature (June 2012 to July 2013) at the study site was 20.3 ± SD 5.6 °C. The lowest temperature recorded was − 2.8 °C in the winter (June to August), and the maximum temperature was 38.7 °C in the summer (December to February). We recorded 22 days with rainfall and 163 without rainfall. We recorded ambient temperature and the presence/absence of rainfall each morning at the sleeping tree.

Study Groups

We observed four habituated uni-male/multi-female and multi-male/multi-female neighboring groups of black-and-gold, howler monkeys (GT, GS, GCN, and GA groups; Table I, Fig. 1). We obtained 185 total days of observations: GT: $N = 47$ days; GS: $N = 48$ days; GCN: $N = 48$ days; and GA: $N = 42$ days. We identified individuals by natural characteristics (e.g., body size, pelage coloration) and artificial marks placed during previous studies (e.g., anklets, ear tags) (Oklander *et al.*, 2007, 2010; Schmidt *et al.*, 2017).

We classified individuals by age/sex classes following Rumiz's criteria (1990): infant < 1 yr; female juveniles 1–3 yr; male juveniles 1–4 yr; female subadults 3–4 yr; male subadults 4–5 yr; female adults > 4 yr; male adults > 5 yr.

Table I Age-sex composition of four study groups of black-and-gold howler monkeys (*Alouatta caraya*) in Corrientes Province, Argentina (27°30′S, 58°41′W), between June 2012 and July 2013

Group	Adult		Sub-adult		Juvenile		Infant
	Male	Female	Male	Female	Male	Female	
GT	1	2	0	2	0	0	0 (+4, − 1)
GS	2	2	0	0	1	1	2 (+2)
GCN	2 (− 1)	2	0	0	1	1 (− 1)	0 (+2, − 1)
GA	2 (− 1)	4	0	0	2 (-2)	0	4 (+4, − 1)

Group: study group; (+): individuals born in the study periods; (−): individuals disappear in the study periods

We excluded one adult male and two juvenile males in group GA and the juvenile female in GCN from analyses, because they disappeared 1 month after the study began. We included one adult male in GCN and the two juveniles in GA, who disappeared a month before the study ended.

We excluded adult females with infants from the analysis of potential effect of ambient temperature and rainfall on sleeping body postures, because the presence of infants may affect the body posture adopted by females. We excluded infants from analyses, because they had never been seen sleeping alone (Brividoro *et al*., 2021).

Data Collection

Behavioral Data

We considered a howler monkey as sleeping when it was inactive and with closed eyes in the sleeping site (Brividoro *et al*., 2021). We defined a sleeping cluster as two or more individuals sleeping at night in physical contact, sleeping alone as one individual sleeping at night without physical contact with other individuals, and a sleeping tree as a tree used by one or more individuals at night (Brividoro *et al*., 2019, 2021).

We recorded the number of individuals sleeping in physical contact in a sleeping cluster and the body posture of each individual. We recorded these data in the morning, approximately 2 h before individuals moved and began their daily activities (in winter around 7:00 h and in summer around 4:30 h). We followed the monkeys throughout the day until they entered a sleeping site (Brividoro *et al*., 2019). We follow the protocol described in Brividoro *et al*. (2021) to record data in the sleeping tree: We identified individuals each morning at sleeping sites before they began to move. If that was not possible, for example, scarce natural light made it difficult to identify individuals, we assigned animals a number, followed them when they moved, and then identified them when possible. We used the morning records to represent the nocturnal spatial arrangement of individuals, because they moved around at the sleeping site at sunset until midnight (Brividoro *et al*., 2019; Di Bitetti *et al*., 2000). We recorded data for each study group for a mean of 3 ± SD 1 consecutive days per month between June 2012 and July 2013. MVB recorded data with the help of field assistants trained in data collection and individual identification.

We divided body regions into anterior and posterior limbs, back, ventral region, flanks, tail, and face to describe sleeping postures, following previous studies (Bicca-Marques & Calegaro-Marques, 1998; Paterson, 1981). We identified two sleeping postures descripted in Bicca-Marques and Calegaro-Marques (1998) (Fig. 2):

A) Curled (Fig. 2a): arms and legs are flexed and close to the body while the back is bent and the head is near the tail, giving the body a spherical shape in which the ventrum is completely hidden. This posture can be observed with the individual "sitting" (anterior–posterior axis perpendicular to the branch on which it is located, face facing the ventral region or exposed) or “lying” (anterior–posterior axis parallel to the branch, face exposed). This posture exposes few body regions (the back and the outer part of the limbs, both with dense hair).
B) Spread (Fig. 2b): individual with the ventral region supported and partially covered by a tree branch. Anterior and posterior limbs extended toward the ground or flexed over the branch. Face supported over a branch (exposed) and tail stretched over the branch. In the stretched posture the ventral region is the only covered or partially covered body region.

Foliage Cover of Sleeping Tree

We recorded sleeping tree foliage cover each morning. We visually estimated the foliage cover of all sleeping trees with values ranging from 0% (no foliage cover) to 100% (total crown covered), divided into 10% classes. We selected a quarter of the canopy of sleeping tree, calculated the percentage covered by vegetation, and then multiplied it by four (these data should be interpreted with caution as this measure is a subjective estimate). The same observer estimated foliage cover throughout the study to avoid interobserver differences in data recording.

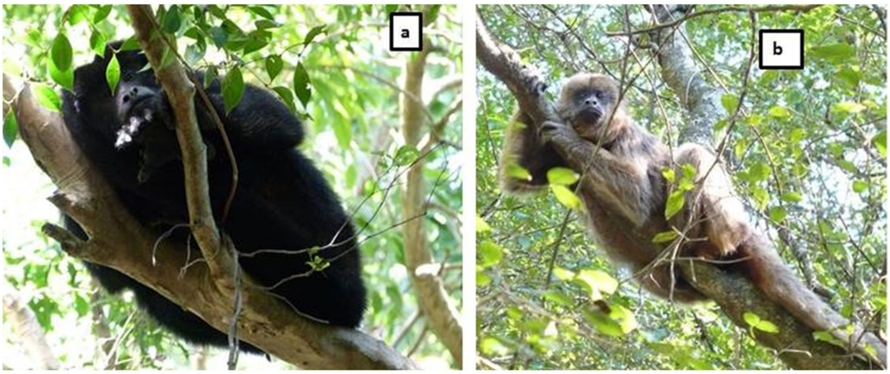

Fig. 2 Sleeping postures recorded in four study groups of black-and-gold howlers (*Alouatta caraya*) in Corrientes Province, Argentina (27°30′S, 58°41′W), between June 2012 and July 2013. (**a**) Curled posture; (**b**) Spread posture.

Temperature and Rainfall Data

We recorded temperature data every 10 min while the animals were inactive, starting in the morning shortly before individuals began their daily activities. We recorded ambient temperature with a portable meteorological station (Sinometer Ws1050) placed approximately at the height where the monkeys sleep (Brividoro et al., 2019) but in trees located 10 m from the sleeping trees to avoid disturbing the monkeys. We defined three ambient temperatures classes: low = −3 °C to 10.9 °C; medium = 11 °C to 20.9 °C; and high 21 °C to 38.7 °C. We used the modal class to categorize each day. We used a categorial variable for temperature to reflect the seasons at the study site. During the study period, the mean ambient temperature was 20.3 ± 5.6 °C (range = −2.8 °C to 38.7 °C), and we obtained 23 days corresponding to low, 70 days to medium, and 92 days to high temperature class. We recorded 22 days with rainfall and 163 without rainfall at the sleeping tree.

Statistical Analysis

We ran generalized linear mixed-effects model (GLMM) with a Binomial (link "logit") distribution using maximum likelihood (Laplace approximation, Zuur et al., 2009) with the "lme4" package (Bates et al., 2015). For each analysis, we ran the global model and the null model, and we used Akaike's Information Criterion (AIC) to compare the fit of the models (Bolker et al., 2009). We checked model assumptions (normality and homogeneity of residuals) by using graphical methods (QQ-plots) and statistical tests (Kolmogórov-Smirnov test) using "DHARMa" package (Hartig, 2022). For each statistical analysis, we used R software (v. 3.5.0; R Core Team, 2018) and a significance level for all statistical tests at 0.05.

To evaluate the relationship between the number of individuals in sleeping clusters and ambient temperature and rainfall, we used the proportion of individuals in sleeping clusters (number of individuals sleeping in clusters/total number of individuals in the social group) that were in physical contact as the response variable to standardize the value across groups. Ambient temperature class (low, medium, and high) and rainfall (presence/absence) were the explanatory variables. We included group identity as a random factor.

To evaluate the effect of ambient temperature and rainfall on sleeping postures, we included the sleeping posture (curled/spread) as the response variable, ambient temperature class and rainfall (coded as presence = 1 and absence = 0) as explanatory variables, and "individual identity" nested within "group identity" as a random factor.

To evaluate the effect of ambient temperature and rainfall on foliage cover, we used percentage of foliage cover of sleeping tree as the response variable, ambient temperature class, and rainfall (coded as presence = 1 and absence = 0) as explanatory variables, and sleeping tree and group identity as random factors.

Ethical Note This research adhered to the American Society of Primatologists Principles for the Ethical Treatment of Non-Human Primates (https://www.asp.org/society/resolutions/EthicalTreatmentOfNonHumanPrimates.cfm), complied with protocols approved by the appropriate Institutional Animal Care Committee from the author's home institution and adhered to the legal requirements of the country in which the research was conducted.

Data Availability The data that support the findings of this study are available from the corresponding author upon reasonable request.

Results

Individuals Sleeping in Clusters, Ambient Temperature and Rainfall

Of the 185 days of observation, all individuals slept clustered on 58% ($N=107$ days) and one or more individuals slept alone on 42% ($N=78$ days). We obtained 432 records of individuals sleeping in clusters (juveniles, subadults, and adults). The proportion of individuals sleeping in clusters was significantly higher at lower temperatures, significantly lower at higher temperatures and not significantly different between intermediate temperatures and either high or low temperatures (Table II; Fig. 3). Rain had no significant effect on the proportion of individuals grouped (Table II).

Table II Results of GLMM testing the effect of ambient temperature and rainfall on proportion of individuals in sleeping clusters, sleeping body postures and sleeping tree selection according to their foliage cover in four study groups of black-and-gold howler monkeys (*Alouatta caraya*) in Corrientes Province, Argentina (27°30′S, 58°41′W), between June 2012 and July 2013

Response variable	Explanatory variable		Est	Std. error	Z	*P*	AIC
Proportion of individuals in sleeping clusters	Temperature classes	*Low*	0.5	0.22	2.19	< 0.01	1397
		Medium	0.02	0.18	0.11	0.91	
		High	−0.4	0.18	−2.2	< 0.01	
	Rain	0.00	0.14	0.00	0.99		
	Null model	−0.2	0.2	−0.9	0.38	1432	
Sleeping body postures	Temperature classes	*Low*	−5.05	1.00	−5.05	< 0.001	554
		Medium	2.15	1.02	2.1	< 0.01	
		High	3.33	0.99	3.35	< 0.001	
	Rain	−0.11	0.4	−0.3	0.74		
	Null model	−2.3	0.26	−8.9	< 0.001	593	
Foliage cover of sleeping tree	Temperature classes	*Low*	0.46	0.1	4.7	< 0.001	10,354
		Medium	0.25	0.1	2.7	< 0.01	
		High	−0.02	0.1	−0.3	0.92	
	Rain	−0.4	0.03	−11.9	< 0.001		
	Null model	0.1	0.1	1.01	0.31	10,612	

Temperatures class: Low = −3 to 10.9 °C; Medium = 11 to 20.9 °C; High = 21 to 38.7 °C

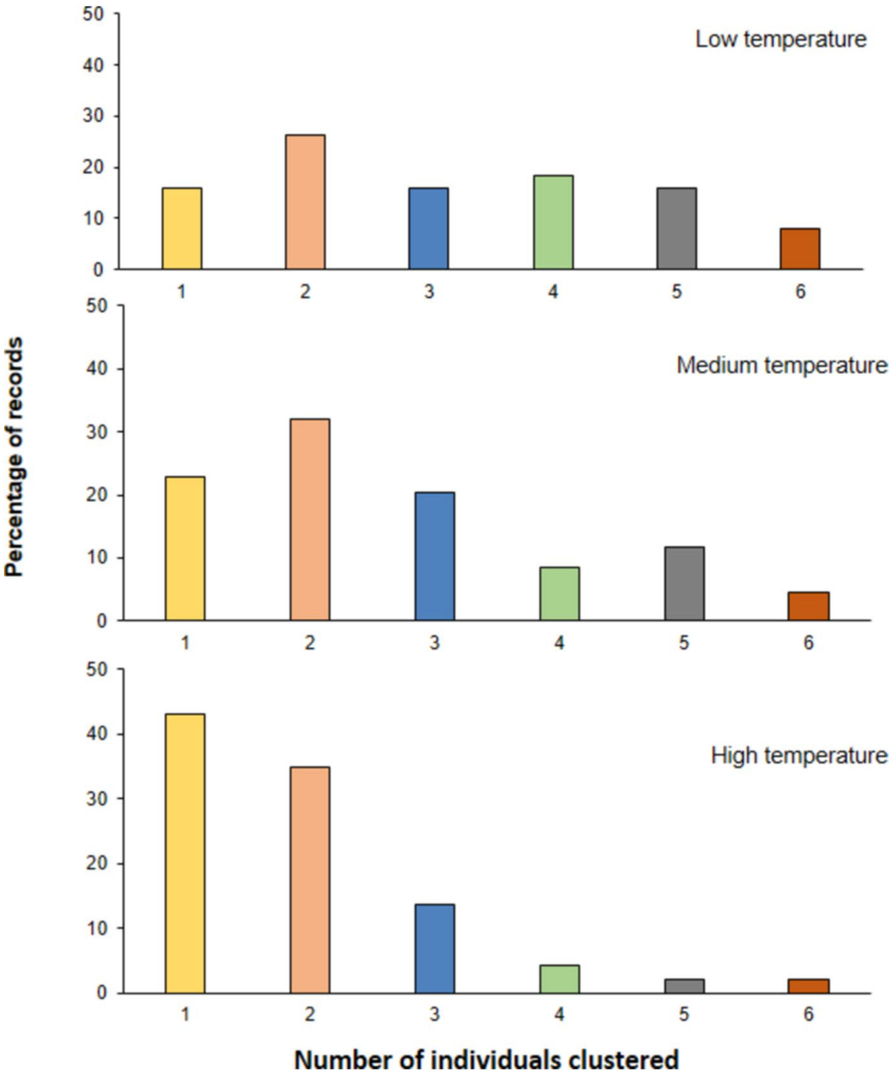

Fig. 3 Percentage of records of number of individuals sleeping in clusters in relation to ambient temperature class in four study groups of black-and-gold howlers (*Alouatta caraya*) in Corrientes Province, Argentina (27°30′S, 58°41′W), between June 2012 and July 2013. Number of individuals present in each group studied: GT $N=5$; GS $N=6$; GCN $N=5$; and GA $N=5$.

Body Postures, Ambient Temperature, and Rainfall

We obtained 903 records of sleeping body posture ($N=808$ records of curled posture and $N=95$ records of spread posture) by adult, subadult, and juvenile individuals (GT: $N_{curled}=183$, $N_{spread}=23$; GS: $N_{curled}=250$, $N_{spread}=16$; GCN: $N_{curled}=223$, $N_{spread}=19$; GA: $N_{curled}=152$, $N_{spread}=37$). Considering all sex and age classes except infants and adult females with infants, we obtained 139 records of body posture for the low temperature class, 328 records for the medium temperature class, and 436 records for high temperature class. The curled posture was the most frequent sleeping body posture (89%) in all temperature classes and for all sex-age classes (Fig. 4). The spread posture was recorded less often (11%) in all temperature classes and in the presence or absence of rain, but its frequency increased slightly in the high temperature class and without rain (Fig. 4). In the absence of rainfall, we obtained 709 records of curled posture and 85 records of spread posture. In the presence of rainfall, we obtained 99 records of curled posture and 10 of spread posture. Temperature was a significant predictor of sleeping posture: howler monkeys adopted the curled posture more frequently that spread posture at low temperatures (Table II). Rainfall had no significant effect on sleeping body posture (Table II).

Foliage Cover of Sleeping Trees, Ambient Temperature and Rainfall

We obtained 172 records of sleeping tree use and identified 104 trees in 185 days of study. Temperature and rainfall had significant effects on the percentage of foliage cover of the sleeping tree selected (Table II). Howler monkey selected trees with more foliage cover at low and medium temperatures than at high temperatures (Table II). Rainfall had an inverse effect: the probability of selecting a sleeping tree with greater foliage cover was lower on rainy nights (Table II; Fig. 5).

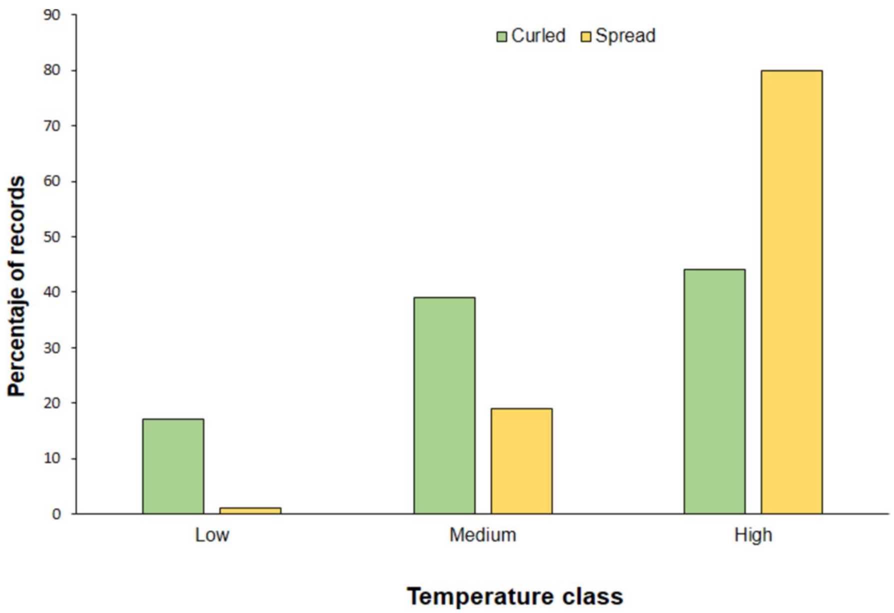

Fig. 4 Percentage of records of body postures (curled/spread) in different ambient temperature classes, adopted by four study groups of black and gold howlers (*Alouatta caraya*) in Corrientes Province, Argentina (27°30′S, 58°41′W), between June 2012 and July 2013.

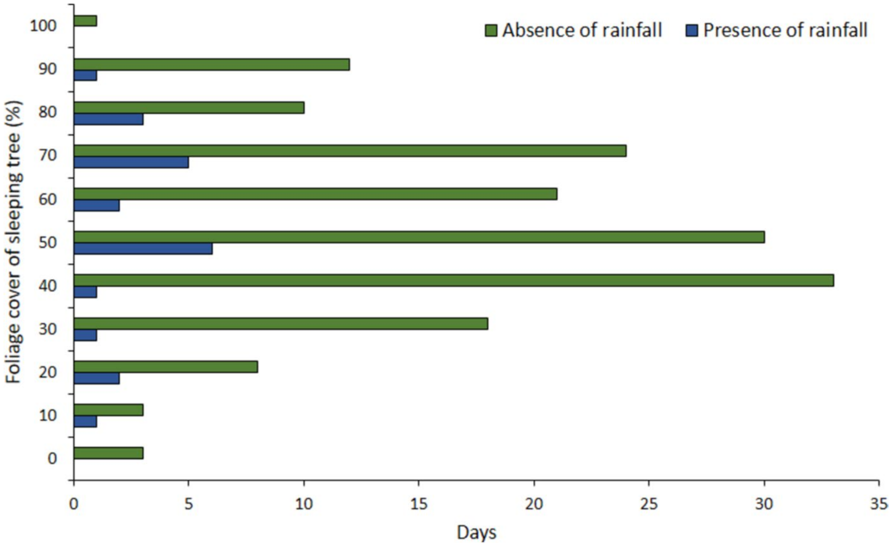

Fig. 5 Percentage of foliage cover of sleeping tree selected in presence/absence of rainfall by four study groups of black and gold howlers (*Alouatta caraya*) in Corrientes Province, Argentina (27°30′S, 58°41′W), between June 2012 and July 2013.

Discussion

Black-and-gold howler monkeys inhabiting a fragmented forest in northern Argentina showed differences in sleeping cluster patterns, sleeping position, and selection of sleeping tree foliage cover according to weather conditions. We found that thermoregulation had effect on the behavioral patterns associated with nocturnal sleep. We found that ambient temperature affected clustering patterns and selection of sleeping tree foliage cover: the proportion of individual in sleeping clusters was larger at low temperatures and lower at higher temperatures. The curled posture was more frequent than the spread posture at low temperatures and individuals selected sleeping trees with dense foliage cover at low and medium temperatures. The behavioral patterns recorded coincide with those of previous studies in howler monkeys (*A. palliata*: Paterson, 1981; *A. caraya*: Bicca-Marques & Calegaro-Marques, 1998), which suggest that howlers use energy-conserving posture, related to their folivorous diet, mainly based on the ingestion of mature leaves, and energy-poor (Bicca-Marques & Calegaro-Marques, 1998). The proportion of individuals in a sleeping group in physical contact varied with the ambient temperature, supporting the hypothesis that clustering is a social thermoregulation strategy (Savagian & Fernandez-Duque, 2016). Variation in the proportion of clustered individuals has been interpreted as a probable thermoregulatory strategy in other primate species, including Geoffroy's tamarins (*Saguinus oedipus*, Dawson, 1979), Azara's owl monkeys (*Aotus azarae azarae*, Savagian & Fernandez-Duque, 2016), and Japanese macaques (*Macaca fuscata*, Takahashi, 1997). These behavioral thermoregulatory mechanisms may occur during the day or night (Anderson, 1984; Bicca-Marques & Calegaro-Marques, 1998; Brain & Mitchell, 1999; Savagian & Fernandez-Duque, 2016; Takahashi, 1997). In addition, we found that individuals grouped together to sleep at high temperatures. This finding could be related to other functions of sleep clustering in addition to thermoregulatory function, such as facilitation of social interactions, reduction of predation risk, and favoring body stability during sleeping hours, as reported for this species (Brividoro et al., 2021) and other species (Anderson, 1998, 2000). Individuals sleeping in clusters must be tolerant of each other. In many cases, this clustering corresponds to the frequency and intensity of affiliative social interactions or genetic relationships (Brividoro et al., 2021; Takahashi, 1997; Terrien et al., 2011).

Body postures are another thermoregulatory mechanism that allows animals to conserve body heat in cold times and dissipate it on warm nights (Barnett et al., 2012; Bicca-Marques & Calegaro-Marques, 1998; Gestich et al., 2014; Gilbert et al., 2010; Morland, 1993; Paterson, 1981). Covering or exposing different body regions are an effective way to conserve or lose body heat, which, together with other behaviors, minimize thermal stress (Paterson, 1981; Stelzner & Hausfater, 1986; Thompson et al., 2014). We found that sleeping postures are affected by temperatures: the frequency of curled and spread body postures changed with temperature. We observed the curled posture (leaving few exposed body regions) more frequently at low temperatures and the spread posture (leaving many body regions exposed) more frequently as the temperature increased. However, we observed the curled posture in all temperature classes. This could be because a curled postures is a stable and safe position during periods of night sleep that facilitate spatial accommodation between clustered individuals (Anderson & McGrew, 1984) or may reduce the risk of vector-borne diseases (e.g., nocturnal mosquitoes), because this position reduces the exposure of body regions with less hair density (Nunn & Heymann, 2005). We did not find a relationship between rainfall and sleeping body postures and size of sleeping clusters, which would indicate that temperatures but not rainfall us a determining factor of sleeping habits.

Black-and-gold, howler monkeys selected sleeping trees with more dense foliage cover on medium and low-temperature days; this pattern could also represent a strategy to conserve body heat during the coldest nights, preventing individuals from being fully exposed to low temperatures. On rainy days and when the temperature was high, they selected open-crowned trees more often. As previously reported for this species (Brividoro et al., 2019), the selection of sleeping trees respond to several factors, including risk of parasitic infection, body stability, proximity to feeding sites, between others. Therefore, our results add the climatic variables to the previously reported factors. In the mornings of low-temperature days or after rainy nights, individuals moved to the top of the sleeping trees and exposed the body regions with sparse hair, including the ventral region and flanks to the sun. This "sunbathing" behavior, observed previously in *A. caraya* (Bicca-Marques & Calegaro-Marques, 1998) and in several other primate species, for example Azara's owl monkeys (Savagian & Fernandez-Duque, 2016), Japanese macaques (Hanya et al., 2007), and black-fronted titi monkey (*Callicebus nigrifrons*, Gestich et al., 2014), is thought to regulate body temperature (Savagian & Fernandez-Duque, 2016; Terrien et al., 2011). In addition, on mornings following rainy days, the monkeys sunbathed and rubbed their backs against the bark of the sleeping trees, possibly because the back was the body region most exposed to the rain. The selection of sleeping trees in relation to the weather conditions and according to their foliage has been observed in Azara's owl monkeys; nocturnal primates that sleep in trees with less foliage during the day to allow direct sun exposure in winter (Savagian & Fernandez-Duque, 2016). Sleeping tree selection by howlers also may respond to other factors, such as the risk of predation, body stability, and range defense (Brividoro et al., 2019; Jucá et al., 2020).

The gradual and constant increase in ambient temperature, more frequent and prolonged droughts, and wildfires that arise from global climate change (Abba et al., 2022; Tomas et al., 2021) increase the need for conservation strategies and the importance of information about the ecology and behavior of primates in their natural habitat. Our study is a partial replication and extension of previous studies of howler monkeys in other study sites. Unlike previous studies, in addition to evaluating the effect of temperature, we also evaluated the effect of rainfall on body posture and clustering and also on the selection of foliage cover of sleeping trees. Our results support those previously reported and show that howlers show behavioral thermoregulation strategies related to sleeping, mainly in response to low temperatures. On days with lower temperatures, the howlers grouped together more, adopted postures that facilitate the conservation of body heat and selected trees with greater foliage cover. Knowing that climatic conditions, mainly temperature, are one of the main pressures that shape behavioral patterns in primates, these should be considered when planning and executing conservation plans and management strategies for primate populations. For example, plans for a howler monkey rescue, breeding, and/or reintroduction center should include consideration of climatic variables, selecting areas that have a range and seasonality of temperature and a vegetation structure that allow the development of thermoregulation strategies reported for the species. The trees available should allow the grouping and shelter of individuals when they sleep, with branches or structures of adequate thickness for this purpose, and foliage cover should change with the season. Thermoregulation strategies also have a social component that must be considered when forming groups of howlers.

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Author Contributions All authors contributed to the study conception and design. MVB, MMK, LIO, and HRF originally formulated the idea. MVB conducted fieldwork and data collection. MVB, MMK, VIC, and MFP analyzed the data. All authors read and approved the final manuscript.

Declarations

Significance Statement The weather conditions are suggested to be one the most critical factors that model sleeping behaviors. We studied the relationship between weather conditions and nocturnal sleeping behaviors in black-and-gold, howler monkeys (*Alouatta caraya*)—one social primate species that grouped at night for sleeping. Therefore, we hope that howlers develop strategies related to clustering, body posture, and foliage cover of sleeping trees selection that reduce the costs associated with adverse weather conditions (low temperatures and rainfall). We found that at lower temperature the number of individuals in sleeping clusters were higher, curled posture was the most frequent and individuals selected sleeping trees with dense foliage cover. We did not find a relationship between rainfall and sleeping behaviors. Our results support that the weather conditions are selective pressures that model sleeping behaviors.

Inclusion and Diversity Statement One or more of the authors of this paper self-identifies as an under-represented ethnic minority in science. While citing references scientifically relevant for this work, we also actively worked to promote gender balance in our reference list. The author list includes women and men in similar proportions.

Conflict of Interest The authors have no conflict of interest to declare. The authors have no financial or proprietary interests in any material discussed in this article.

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