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Ecological and Social Pressures Influence Diel Activity Patterns in Wild Tibetan Macaques

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ABSTRACT

The nighttime behavior of diurnal species is a “black box.” Although diurnal animals spend approximately half their lives in the dark, research has, for too long, relied on the simplifying assumption that what we can't observe isn't important. Advances in our ability to monitor nighttime behavior reveal that this is incorrect; essential biological and behavioral processes play out in the dark which are critical for understanding a species' ecology and evolution. We conducted our study from November 2021 to January 2022, using noninvasive 4G solar-powered night-vision cameras to quantitatively assess the impact of environmental and social factors on the diel activity patterns of wild Tibetan macaques at Mt. Huangshan, China. We find that Tibetan macaques maintain high levels of sleep throughout the night, as is typical for diurnal animals. However, non-sleep activity still accounted for 18.28% ± 0.45% of the total nighttime period, with activity occurring throughout the night. Notably, there was a peak in activity at midnight, including resting, movement, and social. Low temperatures significantly reduced daytime activity levels, while increasing nighttime activity, indicating that extreme temperatures have divergent impacts on activity levels during the day versus the night. Additionally, social activities were more frequent among females during the day, whereas males were more socially active at night. The distinct patterns of social activities during the day and night highlight the crucial role of social factors in nocturnal activities. The night-vision cameras have proven to be an effective research tool, allowing for a deeper understanding of primate behavior patterns and social structures. This provides new avenues for future research into the drivers of nighttime behavioral patterns across species.

1 | Introduction

While many mammals are nocturnal, most primates are diurnal, with exceptions such as most strepsirhines, tarsiers (*Tarsius spp.*), the owl monkey (*Aotus spp.*), and certain lemurs. Our focus on diurnality has limited our understanding of nocturnal behavior in diurnal primates, resulting in the assumption that periods of inactivity are mostly spent sleeping (Santini et al. 2015). However, with advances in research technologies, particularly the use of infrared cameras, infrared video cameras, GPS collars, and night vision devices, studies have shown that some diurnal primates also engage in activities other than sleep

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Abbreviations: AICc, corrected Akaike information criterion; ERA5, fifth generation ECMWF reanalysis; GLMM, generalized linear mixed models; VIF, variance inflation factor.

Pei-pei Yang and Wen-bo Li contributed equally.

Summary

- Tibetan macaques are typically diurnal animals, yet they still exhibit 18.28% of their activity time during the night, with a peak in activity at midnight.
- Extreme temperatures have opposite effects on activity levels, with low temperatures reducing daytime activity levels but increasing nighttime activity levels.
- Social activities were more frequent among females during the day, whereas high-ranking and young individuals were more socially active at night.

at night. Tan et al. (2013) used infrared camera traps to capture footage of gray snub-nosed monkeys' (*Rhinopithecus brelichi*) movement along a fixed route at 03:00, exhibiting behavior similar to that observed during the day. Lacroux et al. (2022) found that chimpanzees (*Pan troglodytes*) avoid areas with human activity at night and raid farmlands for corn to supplement their diet. Ishikawa et al. (2017) discovered through telemetry that captive crab-eating macaques (*Macaca fascicularis*) spend 10.50% ± 2.00% of their night awake. Isbell et al. (2017) used collars with tri-axial accelerometers and GPS sensors along with camera traps to find that Kenyan vervet monkeys (*Chlorocebus sabaeus*) and olive baboons (*Papio anubis*) spend 13.00% and 15.00% of their night active, respectively, primarily in movement and foraging.

However, current research on primates has primarily focused on behavior during the daytime, while neglecting the occurrence of activity during the nighttime. Significantly, advancing research on nocturnal behavior is pivotal for understanding the overall survival and adaptability of the animals. For example, studying nocturnal activity patterns can reveal insights into animals' sleep patterns and quality, providing important clues for understanding human sleep and its evolution (Tagg et al. 2018; Loftus et al. 2022).

To fully understand the circadian activity patterns of animals, it is essential to consider various influencing factors. These rhythms are determined by intrinsic factors (such as age and sex) (Krizo and Mintz 2015), social factors (such as intragroup competition and social relationships) (Monterroso et al. 2014; Minasandra et al. 2023), and environmental factors (such as predators, rainfall, and temperature) (Šklíba et al. 2014; Kooros et al. 2022). Studying these factors is crucial as they directly affect behaviors such as foraging, resting, and reproduction, which in turn influence survival and reproduction (Hill 2006; Li et al. 2010; Chu et al. 2018). For example, changes in weather and light can significantly alter the activity rhythms of primates (Kennaway et al. 2012; Pruetz 2018). For social animals, social factors can be significant drivers of activity patterns. For instance, individuals might stimulate each other to transition from resting to more active states or they may rest together for safety or social bonding. This is also true at night, as olive baboons may wake up synchronously influenced by other individuals (Loftus et al. 2022). Additionally, low-ranking males might reduce their sleep time in dim night environments to increase interactions with females and gain mating opportunities (Tagg et al. 2018).

The Tibetan macaque (*M. thibetana*) is a nationally protected species in China. Our research team has conducted a long-term study on Tibetan macaques in Huangshan, Anhui Province, collecting data on their diurnal activity rhythms and behavioral patterns. We have systematically elucidated their social and life history strategies and the behavioral mechanisms of group stability (Li 1999; Li and Kappeler 2020), revealing the effects of different environmental conditions on their behavior and adaptation strategies (Zhou et al. 2022). However, due to the limitations of observation technology, current research has mainly focused on the influence of ecological factors on their diurnal activity patterns, with nocturnal activity patterns remaining largely unknown.

To fill this research gap, we studied the A1 group of wild Tibetan macaques in the Fish Scale Pit area of Huangshan using advanced nocturnal imaging technology (noninvasive 4G solar-powered night-vision cameras). This technology can provide high-resolution nocturnal activity data without disturbing the macaques, allowing us to quantitatively study their nocturnal activity patterns and time allocation and compare them with diurnal activities. By comprehensively studying the various factors that influence circadian rhythms, we can better understand the activity patterns of Tibetan macaques, particularly the influence of social factors on nighttime behavior. Understanding the differences between nocturnal and diurnal activities helps us better comprehend the strategies primates use to cope with social and environmental challenges at different times of the day.

2 | Material and Methods

2.1 | Ethics Statement

This work was purely observational in nature and no experiments or animal captures were performed. This work did not require ethical approval from a human subject or animal welfare committee.

2.2 | Study Site and Focal Animals

We conducted this study at the Huangshan National Wildlife Reserve, Wild Monkey Valley in Anhui, China (30°04′25.1” N, 118°08′59.3” E) from November 2021 to January 2022. The study focused on group Yulinkeng 1 (YA1) due to its well-documented demographic information, including ages, genealogical relationships, and population dynamics (Li 1999). Additionally, YA1 is habituated to human presence and cameras. Long-term historical data facilitated individual identification based on distinctive physical features such as scars, hair color patterns, and facial/body appearance. Group YA1 consisted of 14 adult females (≥ 5 years), 11 adult males (≥ 7 years), 1 female subadult (4–5 years), 3 male subadults (5–7 years), 1 male adolescent (3–4 years), 8 female immatures (0–3 years), and 15 male immatures (0–3 years). Given the challenges of visually identifying immatures at night, data analysis focused on 14 adult females (≥ 5 years), 11 adult males (≥ 7 years), 1 female subadult (4–5 years), 3 male subadults (5–7 years), and

1 male adolescent (3–4 years). Throughout the study, group members primarily inhabited forested areas. We provided regular maize feedings (3–4 kg) at specific times each day (08:00–11:00 and 16:00) in open areas with high visibility for monkeys. After consuming the maize, the monkeys typically remained in the feeding area for a period before returning to the forest.

2.3 | Data Collection

We tracked the focal group by following them to their nighttime sleeping site after their evening foraging session. “Nighttime” was defined as the period from astronomical twilight to astronomical dawn the following day. We define day range length as the duration of the daytime, which was calculated based on astronomical twilight. Specifically, it was determined by subtracting the previous day's astronomical twilight from the next day's astronomical twilight and then subtracting the result from 24 h. To collect nighttime data, we used solar-powered 4 G night-vision cameras (DS-2XS2T46XM, Hikvision Digital Technology Co., Hangzhou, China) composed of starlight-level lenses, infrared illuminators, motion detection lenses, and data storage modules (Chen et al. 2024). These cameras (Figure 1) are compact, easy to install, and are equipped with a 4G communication module for remote monitoring via an accompanying mobile application (Hikvision), making them suitable for use in off-grid outdoor environments. Based on observations of the monkey group at night and defecation areas during the day, we placed 16 cameras in known or likely sleeping regions. Additionally, these cameras are equipped with motion detection capabilities. When monkeys entered the monitored area, the cameras would send an alert. When we first detected an individual at the sleep site on a given night, we turned on the infrared camera using the mobile app, and let the camera record throughout the night.

To obtain daytime and nighttime activity levels, we employed scan sampling methods. We systematically observed and recorded the behavior of individuals visible within the group, with each scan including at least 3 individuals, representing at least one-tenth of the target group ($N = 30$). We used 5 min scan sampling intervals. During the daytime, we used an audio recorder (Lenovo China, Beijing, China), while at night, we used video recordings to capture all observed individuals' movements, resting, sleeping, foraging, and social activities. The definitions for various behavior types are as follows:

1. Resting: The individual remains in the same location, including sitting or lying on branches or rocks, self-grooming.

2. Movement: Any behavior that causes a change in spatial location, such as walking, climbing, jumping, and running.

3. Feeding: Involves the intake or chewing of food.

4. Sleep: The presence of closed eyes, absence of bodily movement, decreased neck muscular tone, and facial/limb twitching (Samson and Shumaker 2015).

5. Social: Categorized as affiliative, aggressive, and sexual behaviors (Li 1999).

We acquired hourly climate data including ambient temperature, wind speed, rainfall, and cloud cover from the ERA5 reanalysis data set provided by the Copernicus Climate Change

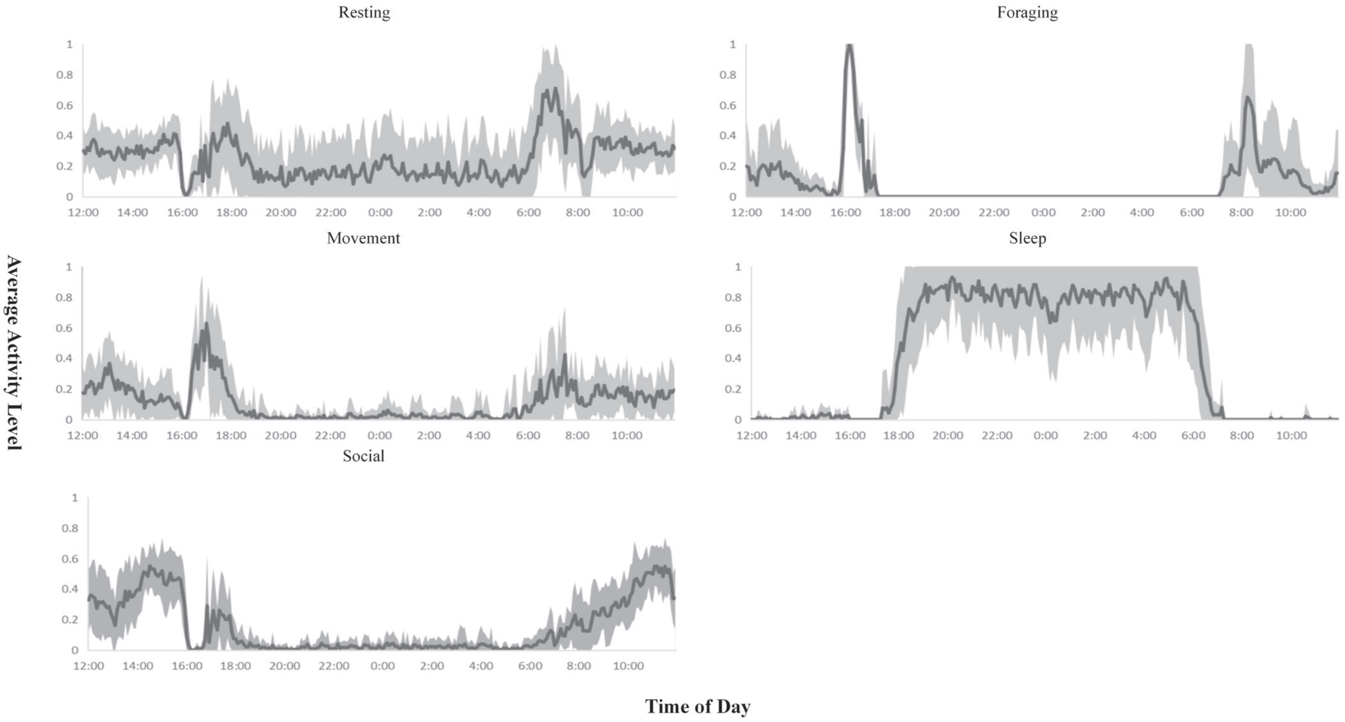

FIGURE 1 | Average activity levels throughout the 24-h in YA1 group. The black line represents the mean value of the activity, and the gray area includes the standard deviation range. The X axis represents time, and the Y axis represents the percentage of activity.

Service (Hersbach et al. 2023). The ERA5 data set integrates 12-hourly observations with model data globally, employing the 4D-Var assimilation method to generate hourly estimates of atmospheric, land, and oceanic conditions. The temperature at 2 m above land, measured in degrees Kelvin, was converted to an average nightly temperature in degrees Celsius. Wind speed was recorded as the maximum wind gust at a height of 10 m above the Earth's surface. Rainfall was quantified as the total precipitation accumulated over an hour and converted into millimeters per night. Cloud cover refers to the proportion of a grid box covered by clouds, with cloud fractions ranging from 0 to 1. Moonlight availability denotes the percentage of the moon's brightness at a specific moment during its lunar cycle, relative to the entire cycle, obtained from http://mooncalc.org.

2.4 | Data Analysis

The diel activity time budget was calculated following the method described by Fiore and Rodman (2001). Each scan sample was treated as an independent sample, where the ratio of individuals exhibiting a specific behavior type to the total number of individuals observed in the scan sample was used to represent the proportion of time allocated to that behavior type. Subsequently, the 5 min activity time budget was employed as the primary calculation unit. We calculated the time proportions of resting, movement, foraging, sleeping, and social behaviors throughout the entire diurnal cycle, as well as their respective proportions during the daytime and nighttime. Diel activity patterns were expressed as the average percentages of the main activity types (resting, movement, foraging, sleep, and social) within each 5 min period.

Aggression-submission bouts and mating behavior were recorded ad libitum using a footage camera (SONY China, Beijing, China). Aggressive displays included staring, chases, slaps, grabs, or bites, while submissive displays included bared teeth, avoidance, fleeing, or screaming (Berman et al. 2004). We calculated the total amount of aggressive and submissive interactions and built a matrix of aggression/submission according to the directions of agonistic interactions given and received. Based on this matrix, we determined individual dominance rank using David's Score (Gammell et al. 2003). A larger David's Score value corresponds to a higher rank.

We computed a measure of maternal relatedness for each individual based on a weighted sum, where weights r were determined by the degree of relatedness of that individual with other individuals in the group following methodology in Ueno and Nakamichi 2018: $r = 0.5$ for mother and children; $r = 0.25$ for brothers and sisters; $r = 0.25$ for grandmothers and grandchildren; $r = 0.125$ for aunts and nieces, nephews; $r = 0.0625$ for cousins; $r = 0.0625$ for great-grandmothers and nieces, nephews; $r = 0$ for non-relatives and all others. Thus, higher degrees of relatedness imply closer kin relationships. We calculated the average degree of maternal relationships from kinship relationships recorded as part of the long-term data collection at the project. Sex was defined as male (1) and female (0). Age was divided into five categories: old (≥ 15 years), middle-aged (10–15 years), adult (adult males: 7–10 years; adult females: 5–10 years), subadult (subadult males: 5–7 years; subadult females: 4–5 years), and adolescent (3–4 years).

To analyze daytime and nighttime activity levels, we employed generalized linear mixed models (GLMM) to investigate the ecological, social, and individual factors influencing diurnal and nocturnal activity levels. Ecological factors included temperature, wind speed, rainfall, and day range length; social factors encompassed rank, and relatedness; individual factors comprised age and sex. Due to the unique nature of nighttime environments, we also included moonlight and cloud cover as additional factors influencing nocturnal activity levels.

To address the potential influence of artificial feeding, we excluded foraging scan data during feeding times. Additionally, three individuals L.B., L.H., and W.S. (L.B. and W.S. are middle-aged males, while L.H. is an old male) were challenging to track during the daytime, resulting in the unavailability of their rank data and their exclusion from the GLMM analysis. We developed two different GLMM models to analyze the factors influencing activity levels. In the first model, we defined resting and sleeping as inactive states (0), while movement, foraging, and social interactions were defined as active states (1). In the second model, we defined sleep, rest, movement, and foraging behaviors as 0, and social activities as 1. The models were built assuming a binomial distribution, with individual identity and date considered as a random effect. Additionally, to minimize variability between different days, we added data points sequentially starting from the day with the highest number of scans and used the Fisher exact test to assess whether the newly added data significantly differed from existing data, with a significance level set at $p < 0.05$. We found significant differences when the daytime data reached 11 scans (Fisher test, $p < 0.05$), leading us to remove all data with 11 or fewer scans. For the nighttime data, no significant differences were detected. GLMM were constructed in R using the “glmer” function from the “lme4” package (Bates et al. 2015).

To validate our GLMM models, we used a stepwise forward selection method to optimize the model by successively adding variables, using the corrected Akaike Information Criterion (AICc) as the basis for model selection. After adding each variable, we evaluated its impact on the AICc. A lower AICc value indicates a better-fitting model. If the AICc did not decrease significantly after adding a variable, or if the p-value of the variable was greater than 0.05, we excluded that variable from the model (see Supporting Information S1: Tables S1–S4). Ultimately, we identified the following optimal models: daytime activity and sleep model (Model 18, see Supporting Information S1: Table S1), nighttime activity level model (Model 12, see Supporting Information S1: Table S2), daytime social activity level model (Model 21, see Supporting Information S1: Table S3), and nighttime social activity and sleep model (Model 12, see Supporting Information S1: Table S4). To address multicollinearity among explanatory variables, we calculated the variance inflation factor (VIF) and excluded correlated variables with VIF values exceeding 3. This process was repeated until all remaining variables had a VIF of 3 or less. The VIF analysis showed that no explanatory variables had VIF values exceeding 3 (Supporting Information S1: Table S5). To ensure the robustness of the p-values obtained in the GLMM models, we

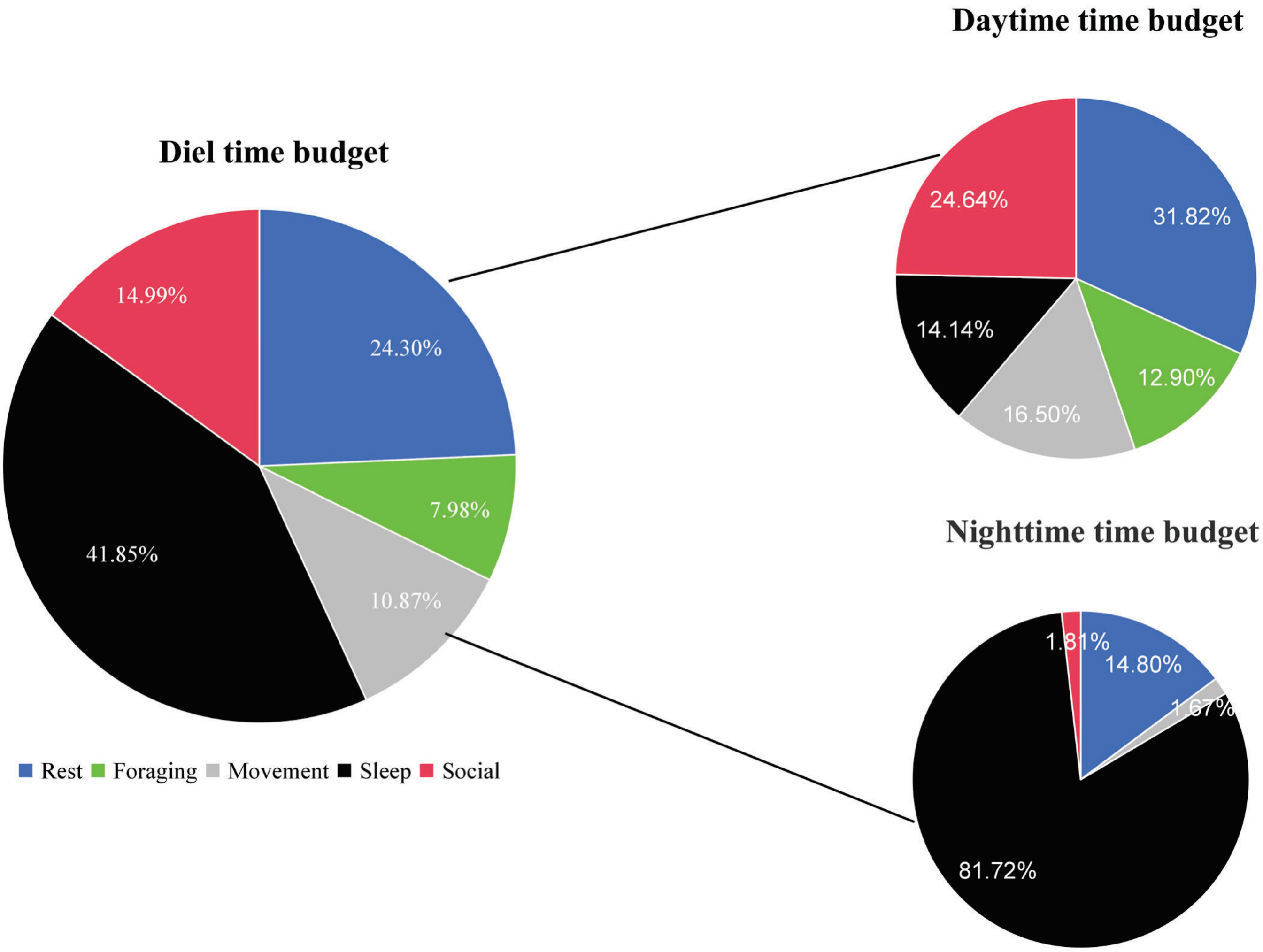

FIGURE 2 | Distribution of diel time budget in a YA1 group.

additionally conducted likelihood ratio tests using the ANOVA function. The χ^2 and *p* values generated by the glmer function confirmed the significance of each fixed effect, and the results were consistent with those from the GLMM models We used the “MuMIn” package to calculate AICc and the “car” package to compute VIF. All analyses were conducted using R software.

3 | Results

We recorded a total of 6614 5-min scans, comprising 2560 during daytime observations, with an average of 7.67 individuals per daytime scan, and 4054 at night, with an average of 11.88 individuals per nighttime scan, spanning approximately 551 h. After data filtering, the analysis included 40 daytime periods (average 57.68 ± 7.39 scans, range 12–133) and 32 nighttime periods (average 125.63 ± 1.97 scans, range 85–132).

We observed distinct patterns in the behavioral activities of the monkeys (Figure 1). Rest has two peak periods: from 6:00:00 to 8:00:00 and from 0:00:00 to 1:00:00. Foraging behaviors showed prominence during two distinct time frames: 8:00:00 to 9:00:00 and 16:00:00 to 17:00:00. Movement activities were specifically noted from 17:00:00 to 18:00:00. Social interactions exhibited peaks during two main periods: 10:00:00 to 12:00:00 and 14:00:00 to 16:00:00. In the nocturnal activity patterns, we found that sleep levels remained high throughout the night, occurring consistently at all periods. We observed a peak in wakefulness between 23:00:00 and 1:00:00, which includes various activities such as resting, movement, and social activity. Based on diel time budget data, we found that individuals spent 18.28% ± 0.45% of the night in a state of wakefulness. Additionally, significant differences were observed in the proportions of various behaviors over the 24 h cycle (Figure 2). Sleep increased significantly from 14.14% ± 0.62% during the day to 81.72% ± 0.57% at night, while no foraging behavior was observed at night. Movement and social activities decreased from 16.50% ± 0.40% and 24.64% ± 0.46% during the day to just 1.67% ± 0.13% and 1.81% ± 0.11% at night, respectively.

In the results of activity levels, temperature significantly influenced both diurnal and nocturnal activity levels. During the daytime, higher temperatures significantly increased activity levels, whereas the converse was true at night: individuals were more active on colder nights (Table 1). We found that wind speed and rainfall were significantly correlated with daytime activity levels; specifically, daytime activity levels were increased with higher wind speeds and

TABLE 1 | Effects of ecological, social, and individual factors on activity levels.

Response variable	Predictor variable	Estimate	Standard error	Z	p
Daytime activity levels	Intercept	0.05	0.23	0.20	0.84
	Temperature	0.12	0.03	4.74	< 0.001***
	Wind speed	0.39	0.03	12.85	< 0.001***
	Rainfall	−0.12	0.02	−5.26	< 0.001***
	Sex	−1.06	0.14	−7.74	< 0.001***
	Age	−0.49	0.23	−2.14	< 0.05*
	Relatedness	0.14	0.07	1.94	0.05
Nighttime activity levels	Intercept	−3.08	0.17	−18.33	< 0.001***
	Temperature	−0.20	0.05	−3.78	< 0.001***
	Day range length	0.24	0.07	3.45	< 0.001***
	Cloud	0.14	0.06	2.21	< 0.05*
	Age	−0.61	0.24	−2.51	< 0.05*
	Rank	0.31	0.05	5.64	< 0.001***

Note: A binary variable indicating sleep and rest was defined as 0, and all other activities were defined as 1.

TABLE 2 | Effects of ecological, social, and individual factors on social activity.

Response variable	Predictor variable	Estimate	Standard error	Z	p
Daytime social activity	Intercept	−1.62	0.23	−7.09	< 0.001***
	Temperature	0.20	0.03	6.96	< 0.001***
	Wind speed	0.52	0.03	14.99	< 0.001***
	Rainfall	−0.16	0.03	−6.19	< 0.001***
	Sex	−1.27	0.25	−5.12	< 0.001***
	Rank	0.28	0.09	3.05	< 0.01**
	Relatedness	0.25	0.12	2.07	< 0.05*
Nighttime social activity	Intercept	−3.94	0.25	–15.86	< 0.001***
	Temperature	−0.16	0.05	−2.85	< 0.01**
	Day range length	0.20	0.06	3.48	< 0.001***
	Sex	0.33	0.14	2.26	< 0.05*
	Age	−0.66	0.33	−1.98	< 0.05*
	Rank	0.46	0.07	6.35	< 0.001***

Note: A binary variable indicating rest, foraging, movement, and sleep was defined as 0, and social activities were defined as 1.

lower rainfall (Table 1). Additionally, in daytime activities, we found that females were more active than males. At night, we found that day range length and cloud had a significant positive impact on activity levels; activity levels were associated with increased longer day range lengths and more cloud (Table 1). Furthermore, at night, dominance rank was significantly positively correlated with activity levels (Table 1). We found that younger individuals tended to be active both during the day and at night (Table 1).

In the results of the model on social activity, we observed that temperature significantly influenced both diurnal and nocturnal social activity levels. Specifically, during the daytime, social activity levels increased with higher temperatures, while at night, social activity levels increased with lower temperatures (Table 2). Wind speed and rainfall were also significantly correlated with daytime social activity, where higher wind speeds and lower rainfall were associated with increased daytime social activity levels (Table 2). Additionally, females, individuals with higher relatedness coefficients, and high-ranking individuals exhibited higher daytime social activity levels compared to other classes of individuals (Table 2). In contrast, male individuals engaged in more social activities at night (Table 2). At night, day range length had a significant positive impact on social activity levels; social activity was higher with longer day lengths (Table 2). Moreover, high-ranking and younger individuals exhibited higher social activity levels at night than other classes of individuals (Table 2).

4 | Discussion

In this study, we utilized advanced starlight camera technology to examine the diurnal and nocturnal activity patterns of Tibetan macaques. This non-invasive technology offers significant advantages, allowing for the collection of data on unhabituated animals in inaccessible areas, especially at night. Our findings support the long-standing view that Tibetan macaques are primarily diurnal (Li 1999), but we also observed that they spent 18.28% ± 0.45% of the night awake, with activity occurring throughout the night. This is consistent with the findings from studies on other primates (Isbell et al. 2017; Loftus et al. 2022). Notably, we discovered a significant peak in activity at midnight, particularly in movement and social interactions. This finding is unusual compared to other primate studies, which typically do not report such nocturnal activity peaks (Kooros et al. 2022; Loftus et al. 2022; Tagg et al. 2018; Pruetz 2018), suggesting a fragmented sleep pattern in Tibetan macaques. Evidence suggests that fragmented sleep mirrors ancestral human sleep patterns, characterized by high activity levels around midnight and terms like “first sleep” and “second sleep” (Bohannan 1953; Ekirch 2006). Modern humans also exhibit fragmented sleep patterns under short photoperiods (Wehr 1992). Additionally, in social animals, the reduced space and increased proximity at night can heighten social pressures and opportunities, prompting individuals to stay awake to engage in social activities, including affiliative, agonistic, and sexual interactions. Therefore, the midnight activity peak might be a strategy for Tibetan macaques to meet both physiological and social needs.

Our study also highlights the impact of environmental factors on diurnal and nocturnal activity patterns. Daytime low temperatures significantly reduced activity levels, while nighttime low temperatures increased activity levels, indicating that extreme temperatures affect activity differently. For instance, Fongoli chimpanzees have developed behavioral strategies such as soaking in pools and seeking refuge in caves to cope with high temperatures (Pruetz 2007; Pruetz and Bertolani 2009). The thermoregulatory costs associated with daytime foraging explain subsequent nocturnal feeding activities (Lindshield et al. 2017; Pruetz and Bertolani 2009). Similarly, Gombe chimpanzees visit feeding areas and water sources at night to avoid daytime heat (van Lawick-Goodall 1968). In humans, temperature can influence sleep duration to maintain a low body-environment temperature differential, thereby reducing energy expenditure (Yetish et al. 2015). Social animals often engage in huddling behavior to conserve body heat, a phenomenon also observed in Tibetan macaques, where huddle sizes increase in low temperatures (Ogawa 2003). Zero-distance huddling can cause the awakening of one individual to trigger the awakening of others, increasing group activity levels. In olive baboons, closer proximity may make individuals more likely to wake up synchronously, influenced by nearby individuals (Loftus et al. 2022).

Despite the link between temperature and rainfall and evidence that extreme weather conditions can alter nocturnal behavior, we did not detect a significant impact of rainfall on nighttime activity, consistent with findings in other primates (Ayers et al. 2020; Tagg et al. 2018; Li et al. 2010). This may be due to Tibetan macaques selecting cliffside sleeping sites during winter, where rock ledges help mitigate the effects of rain and wind. Individuals also alter their huddle shapes to minimize the impact of rain and wind, reducing disruption to group sleep.

As highly social animals, social factors likely influence many aspects of Tibetan macaque behavior, including both diurnal and nocturnal social activities. Our results indicate that females engage in more social activities during the day, while males are more active at night. Females participate more in activities such as social bonding, grooming, and socializing during the day, consistent with previous research showing that females form strong and lasting social bonds within their groups (Berman et al. 2004; Xia et al. 2012). The bright daytime environment enhances antipredator vigilance, allowing females to socialize more safely. At night, high-ranking young individuals, typically males, dominate social activities. Larger body may make males safer during nighttime activities, a theory also applicable to male chimpanzees (Tagg et al. 2018). The reduced distance between individuals at night increases tension, especially among males. During the day, males often move alone or with females and rarely spend extended periods with other males. At night, frequent social activities among male individuals can reduce tension between them.

In summary, we found that Tibetan macaques exhibit variable nighttime activity, demonstrating a predominantly diurnal activity pattern. Our research reveals the influence of ecological, social, and internal factors on diurnal and nocturnal activities, particularly the impact of social factors on nighttime social interactions. We believe that night-vision cameras are a reliable method for studying activity patterns and behavioral flexibility. By collecting extensive data, it becomes easier to quantify the impact of social interactions on species behavior, which is crucial for understanding the social structure and behavioral mechanisms of primates at night. However, night-vision cameras can only monitor fixed areas, and expanding their deployment can enhance data comprehensiveness, although many areas are difficult for humans to reach, and data for some individuals may be inaccessible. Combining accelerometer data can further enhance the comprehensiveness of research. Accelerometer data can provide in-depth insights into daytime activity variations, while night-vision cameras offer valuable tools for social research. Additionally, our study focused only on winter cliffside data, lacking seasonal activity variation data. Seasonal activity data will further enhance our understanding of Tibetan macaque nighttime activities and behavioral flexibility. Overall, our study highlights the feasibility and value of starlight camera-based nocturnal behavior research in studying wild animal activity patterns. Although we focused on Tibetan macaques here, the methods used are not species-specific and can be applied to other research systems, opening new avenues for understanding the drivers of activity patterns across species.

Author Contributions

Pei-pei Yang: conceptualization (lead), data curation (lead), formal analysis (equal), investigation (lead), methodology (lead), software (supporting), validation (lead), visualization (lead), writing – original draft (lead), writing – review and editing (lead). **Wen-bo Li:** conceptualization (supporting), formal analysis (lead), software (lead), validation (equal), writing – original draft (equal), writing – review and editing (equal). **Margaret C. Crofoot** and **Pritish Chakravarty:** conceptualization (equal), formal analysis (equal), writing – review and editing (supporting). **Xi Wang** and **Tong Zhang:** data curation (supporting), investigation (equal), methodology (equal). **Jin-hua Li:** funding acquisition (lead), investigation (supporting), project administration (lead), resources (lead), writing – review and editing (equal).

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

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

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.